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Explaining co-occurrence among helminth species of lesser snow geese (*Chen caerulescens*) during their winter and spring migration

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Abstract The digestive tracts of 771 lesser snow geese (*Chen caerulescens*) collected from January to May 1983 from 12 locations (27 samples) were examined for helminth parasites to determine whether parasite species present in wintering geese or in spring migrants occurred independently of each other. Nine helminth species were identified. Seven had mean prevalences > 5% and were the focus of this study. Six of those species were waterfowl generalists, one was a goose specialist. Our primary objective was to assess the potential contribution of factors, other than species interactions, in determining patterns of co-occurrence between helminth species. There were few negative relationships between helminth species, regardless of whether presence-absence or abundance data were used. However, some species pairs showed recurrent and significant co-occurrences. There were similar and significant effects of timing of sampling, host gender, and host age, on prevalence and mean abundance of particular species. Co-occurrences were found for those species that showed seasonal declines in prevalence, for those expected to have high colonizing ability based on host age profiles (using abundance data), and for abundant species that may have shared vectors or environmental conditions favorable for transmission. Thus, similarities between parasites in their abundance, transmission biology, and phenology seem sufficient to explain species co-occurrences without invoking other processes such as species interactions.

Key words Communities · Helminths · Lesser snow geese · Parasites · Species interactions

Introduction

There has been considerable research into patterns within parasite infracommunities and for evidence of any interactions among species (such as competition or facilitation) that may help explain those patterns (for a recent collection of reviews see Esch et al. 1990). There are certain benefits to using parasites to investigate patterns and processes in animal communities. First, many individual hosts, considered replicates, can be sampled (Bush and Holmes 1986a; Holmes and Price 1986; Simberloff 1990). Second, parasites such as intestinal helminths share a trophic level; thus, the potentially confounding influence of other types of species interactions, such as predation, can be removed (Simberloff 1990; but see Sousa 1994). Third, parasite species that use the same or similar resources may be identified (Holmes and Price 1986; Forbes et al. 1994). These guild members are expected to interact more frequently than non-guild members. Despite these advantages, studies of parasite communities, like studies of free-living communities, have been fraught with problems in ascribing causes to patterns of species co-occurrences or covariation in their abundances.

Much of the research on parasite communities has been directed at determining whether particular species co-occur less often than expected by chance, or whether

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niche shifts appear when species do co-occur (e.g., review by Bush 1990). Such data may be evidence of competition (and that infracommunities are partly interactive, cf. Holmes and Price 1986). Negative interactions have been hypothesized to be relatively more common among guild members, or more likely if species diversity is relatively high (Holmes and Price 1986; but see Bush and Holmes 1986a, 1986b). It is now acknowledged that negative relationships between bird gut parasites are relatively uncommon (Bush 1990) perhaps, in part, because competitive exclusion in the past has produced present-day patterns of host and resource use. Some of the notable exceptions are studies based on relative positions of helminths in the host gut and their relative fecundities under conditions of co-occurrence (e.g., Moore and Simberloff 1990), rather than on the presence or absence of species per se. Thus, present-day competition can explain some patterns in particular infracommunities.

A more common finding has been co-occurrence among parasite species. Some parasite species appear to facilitate colonization and establishment by another species [as suggested by Schall (1990) for two lizard malariae]. But positive relationships between species are also expected if vectors, or environmental conditions favorable for transmission, are shared by parasites (Bush and Holmes 1986b; Forbes et al. 1994). In addition, parasitological measures are often associated with factors such as season (Neraasen and Holmes 1975), habitat (Bush 1990), and host age or gender (Gregory et al. 1990). Differences in these factors among hosts within samples may produce apparent patterns. For example, infective stages of two parasite species may cooccur at a particular breeding site of the host species, but be absent from another site. Samples of wintering birds at single locations might include hosts from different breeding sites. Those two parasite species would cooccur in some hosts and be absent from others, even if no interactions occurred among parasite species. There is continued interest, therefore, in the extent to which these other factors, versus interactions among parasite species, may explain patterns in parasite communities. Importantly, these other factors need not be operating independently of species interactions. For example, Haukisalmi and Henttonen (1993a, b) reasoned that common parasites found in relative abundance in young hosts are early colonizers, but may be poor competitors. Such species will tend to co-occur in young hosts and be less numerous or absent from older hosts; these species could covary within samples including both young and old hosts.

Objectives

We examined the extent to which helminth species in lesser snow geese (*Chen caerulescens*) occurred independently, to test ideas concerning patterns in parasite infracommunities. In particular, we were interested in testing for, and explaining, co-occurrences or covariation between species pairs, as has been found in other studies of avian helminths (Bush 1990; Fedynich and Pence 1994). We also tested for recurrent negative relationships, although previous work with waterfowl (Bush 1990; Fedynich and Pence 1994) suggests that these are relatively uncommon. Throughout this paper, we use the general terms occurrence and covariation to mean relationships between presence and absence of two species, or between abundances of two species, within samples of hosts or infracommunities.

To meet our objectives, we examined the effect of timing of sampling, and host age and sex, on the representation of particular parasite species to determine whether different species show similar relationships through time (e.g., seasonal decreases in prevalence) or similar host age profiles. Such similarities among parasite species might be associated with certain species cooccurring more frequently than expected by chance, despite those same species essentially living independently of one another in hosts. We then controlled for sample (which relates to habitat and timing of sampling) before testing whether co-occurrences or covariation occurred among species that showed similarities in their abundance, transmission biology, and/or phenology.

Study species

Lesser snow geese

Historically, the eastern arctic population of snow geese wintered within a narrow belt of coastal marsh along the Gulf Coast of Texas and Louisiana (Bellrose 1976). Starting in the 1950s, snow geese regularly wintered at higher latitudes of the midcontinent such as the Missouri River valley (Bellrose 1976), and showed marked shifts in the kinds of habitats they used (Bellrose 1976; Alisauskas et al. 1988). Snow geese now winter in areas heavily impacted by agriculture such as rice fields in Texas and Louisiana that were formerly tall-grass prairie, and areas in Iowa with extensive farming of corn. The wintering eastern arctic population of snow geese increased from average counts of 0.7 million in the 1950s to circa 1.6 million in the early 1980s, when our collections were made (Alisauskas 1988).

Parasites

The digenean *Echinostoma trivolvus*, the nematodes *Trichostrongylus tenuis*, *Heterakis dispar*, and *Capillaria anatis*, and the cestodes *Sobolevicanthus gracilis*, *Drepanidotaenia lanceolata*, and *D. barrowensis* all occurred frequently enough to be considered in this study (averaging > 5% of geese infected within samples, Appendix A). *D. barrowensis* is a common helminth of geese (Neraasen and Holmes 1975). The other parasites occur widely in anseriform species (McDonald 1969), but *T. tenuis* is also found in gallinaceous birds (Moore and

Simberloff 1990). Two other cestodes: *Cladogyna longivaginata* and *Platyscolex ciliata* were found occasionally (see Appendix A).

Knowledge of helminth life cycles is important for predicting patterns of coexistence. The life cycles of all three nematodes are direct. Eggs of *C. anatis* and *H. dispar* are passed in feces, and larvae within eggs are ingested by geese (although earthworms may act as intermediate hosts). Eggs of *T. tenuis* hatch and infections result from ingestion of the third-stage juveniles. Cestodes and the digenean require intermediate hosts to complete the life cycle; *E. trivolvus* requires two intermediate gastropod hosts, whereas the cestodes require a single intermediate host, typically an entomostracan (see McDonald 1969). These intermediate hosts typically occur in the same habitats. In its final hosts, *E. trivolvus* has been reported from the large and small intestine, and caeca. The nematodes are principally caecal parasites, whereas the cestodes are found in both the small and large intestine.

Materials and methods

The digestive tracts of 771 geese were obtained as part of a larger study on diet, bill and gut morphology, and body size of snow geese (Alisauskas et al. 1988; Alisauskas and Ankney 1992). Twenty-seven samples were collected from 12 locations in eight states and one province (see Appendix A for descriptions of latitudes and longitudes). Collections were made in January, February, and March, 1983 (Texas and Louisiana), March (Oklahoma), February (Kansas), January and March (Iowa and South Dakota), April (North Dakota and Manitoba) and May (Ontario). Bellrose (1976) describes the chronology of spring migration of lesser snow geese to arctic nesting areas.

Wintering geese were collected in four habitats including coastal marsh in Texas and Louisiana [brackish and saline wetlands dominated by *Spartina patens* (55%), *Distichlis spicata* (13%), *Scirpus olneyi* (5%), and *Spartina alterniflora* (5%)], rice fields in Texas and Louisiana, wheat fields in Oklahoma, and corn fields in Iowa (Alisauskas 1988). Geese in the remaining samples were considered to be migrants. Approximately 95% of all geese collected were shot (usually from previously undisturbed flocks while geese were feeding). A small percentage of geese ($<5\%$) were shot while flying. At two locations (see Alisauskas et al. 1988 for details), rocket nets were used to capture geese.

On the day of collection, each goose was sexed before being frozen in plastic bags. All geese were transported frozen to the laboratory, where birds were thawed and dissections performed. Each goose thawed for 24–48 h, before the esophagus, pyloric stomach, gizzard, intestines and their contents were excised from the body cavity. Birds were aged as subadults if a bursa of Fabricius was present (Hochbaum 1942). Contents of gastrointestinal tracts, complete with helminths and plant and animal digesta, were washed out of digestive organs, frozen and then transported to Concordia University where helminths were identified and counted by J.D.M. Using this procedure, we could not stratify data according to locations of helminths; such data can provide evidence of species interactions that are missed using broader categorizations (cf. Moore and Simberloff 1990).

Measures and analyses

For each parasite species, we obtained sample estimates of prevalence, mean abundance and mean intensity (where applicable), following terminology used by Margolis et al. (1982), and modified by Bush et al. (1997). Prevalence is the proportion of geese infected with that parasite species; mean abundance is the mean number of worms per goose for that sample, including hosts uninfected by that parasite species. Finally, mean intensity is mean number of worms for only those geese infected by that parasite. We note that prevalence, mean abundance, and mean intensity are parasitological measures that are often correlated (e.g., Smith 1988). In this study, we rely largely on prevalence and abundance estimates for reasons discussed below.

We examined characteristics of parasite species such as how common they were, whether they showed seasonal patterns, and whether they were associated with host age or sex. We then used these characteristics, obtained across many samples, to identify species with a similar distribution, abundance, phenology, and life cycle and then determined whether these species were likely to show co-occurrences or covariation across infracommunities within samples of geese.

We first examined parasite prevalence to identify relatively common species. These show co-occurrences in other studies (Bush and Holmes 1986b). We then determined whether prevalence was dependent on timing of sampling. Species showing similar phenology may also be expected to show co-occurrence, unless they have strong negative interactions once they colonize geese. We next examined the effect of host gender and host age on mean abundance of the seven main parasites, after first assessing variation in mean abundance attributable to sample (i.e., ANOVAs blocked by sample). Often, mean abundance data are omitted from studies simply because uninfected hosts (included in samples to calculate mean abundance) may not have been exposed to parasites. We include abundance data here to assess age and gender profiles for parasites. Here, we were specifically interested in whether adults had fewer parasites than younger birds. Such patterns were unlikely to result from adults escaping exposure throughout their lives. A more reasonable explanation is that they once had many parasites and lost many of them. Such early colonization, but limited persistence, is a characteristic of parasites known to co-occur in other studies. We tested for an effect of age by including only those samples for which there were at least two subadult males and two subadult females (see Appendix A). Only 7 of 27 samples fulfilled this criterion, and even those had relatively few subadults. If host age (or gender) is important with respect to parasitism, then variation in age (or sex) distributions across samples could dictate the frequency and strength of co-occurrences or covariation among particular parasites.

Results

Prevalence, abundance and intensity, in relation to sample

On average, there were 28 geese per sample (samples ranged from 13 to 43 geese; Appendix A). Twenty-five of the 27 samples had >20 geese. As indicated, nine helminth species were identified; seven of those species averaged $>5\%$ prevalence across samples and are the focus of this study (ranges in prevalence are shown in Appendix A). The two other species (*C. longivaginata* and *P. ciliata*) were excluded because the statistical tests used to examine patterns among species require that species occur often enough within samples to generate expected frequencies of co-occurrences.

The most abundant parasites were the caecal nematodes *H. dispar* and *T. tenuis* which, on average, were present in 51 and 46%, respectively, of geese sampled (Appendix A). These nematodes averaged 15 and 11 worms per goose, respectively, over all samples, whereas

Table 1 Mean abundance and intensity for seven parasite species in 27 samples. Sample size equals 771 for abundance estimates, but is variable for estimates of mean intensity (based only on geese infected by that species). Ranges for intensity estimates have the same maximum as abundance estimates, but the minimum is 1 rather than 0 (*Hd Heterakis dispar*, *Tt Trichostrongylus tenuis*, *Ca Capillaria anatis*, *Dl Drepanidotaenia lanceolata*, *Db D. barrowensis*, *Sg Sobolevicanthus gracilis*, *Et Echinostoma trivolvus*)

	Abundance			Intensity		
	Mean	SE	Range	n	Mean	SE
Nematodes						
Hd	15.1	1.4	0–370	400	29.0	2.4
Tt	10.8	1.0	0–255	357	23.4	2.0
Ca	0.12	0.02	0–8	55	1.7	0.18
Cestodes						
Dl	0.18	0.029	0–14	75	1.9	0.22
Db	0.14	0.023	0–8	44	2.0	0.27
Sg	0.55	0.10	0–46	92	4.6	0.75
Cl	0.025	0.009	0–5	14	1.5	0.31
Pc	0.034	0.019	0–14	12	2.2	1.1
Trematode						
Et	0.37	0.05	0–25	123	2.3	0.25

their intensity averaged 29 and 23 worms per goose, respectively. The other species were far less numerous (Table 1), averaging <1 worm per goose (including uninfected hosts) and averaging not more than 5 worms per goose (for individuals infected by *S. gracilis*).

Prevalence declined significantly with Julian date of sample for the nematodes *H. dispar* and *T. tenuis* ($r = -0.82$, $P < 0.001$, $r = -0.43$, $P < 0.025$, respectively) and for the cestode, *S. gracilis* ($r = -0.52$, $P < 0.005$) (Fig. 1). Prevalence also declined near significantly with Julian date of sample for the cestode *D. lanceolata* ($r = -0.37$, $0.05 < P < 0.1$) (Fig. 1). There was no significant change in prevalence for either the nematode *C. anatis*, the cestode, *D. barrowensis*, or the trematode, *E. trivolvus* (r values 0.057, −0.087 and 0.29, respectively, all $P > 0.1$).

Abundance in relation to sample, host age, and gender

We transformed [$\log_{10}(x+1)$] data on parasite abundance before statistical analyses. We found that mean abundance of *H. dispar*, *T. tenuis*, *D. lanceolata*, *S. gracilis*, and *E. trivolvus* varied significantly by sample as expected, whereas mean abundance of *T. tenuis* also varied significantly by sex, using ANOVA blocked by sample (Table 2). Male geese had more *T. tenuis* than females for 17 of 27 samples; for two samples, this result was significant ($P < 0.05$, data not shown).

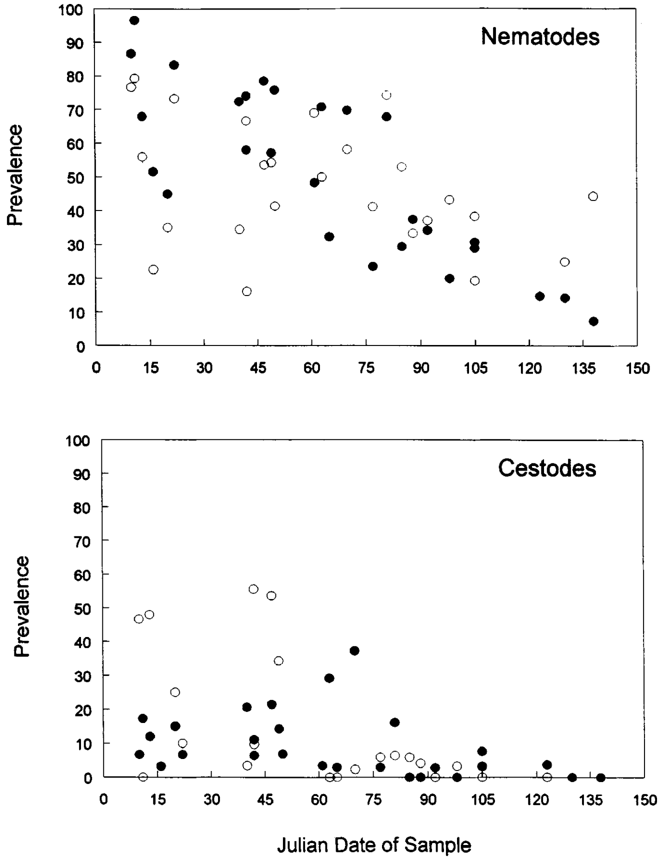

Fig. 1 Prevalence of four species of helminths in relation to Julian date of sample. **a** Nematodes: *Heterakis dispar* (*filled circles*), *Trichostrongylus tenuis* (*open circles*). **b** Cestodes: *Drepanidotaenia lanceolata* (*filled circles*), *Sobolevicanthus gracilis* (*open circles*)

Table 2 Effect of sample, sex of adult geese and sex × sample interactions on mean abundance of seven main parasites. Entries in table are *F*-values for analyses of variance blocked by sample. Parasite designations as in the legend to Table 1

Parasite	Sample	Sex	Interaction
Hd	10.13***	0.72	NS
Tt	5.06***	3.54*	NS
Ca	1.04	0.89	NS
Dl	2.27***	0.36	NS
Db	1.16	3.09	NS
Sg	8.89***	1.04	NS
Et	5.31***	2.51	NS

*$P < 0.05$; ***$P < 0.001$; *NS* non-significant

Of 771 birds, 106 were subadults thereby hindering sex-by-age comparisons. For sex-by-age comparisons, we included only 7 of 27 samples as indicated above. Two parasites (*T. tenuis* and *D. lanceolata*) varied in abundance in relation to host age, whereas *E. trivolvus* varied between host sexes (Table 3). In six of seven samples, subadults had more *T. tenuis* than adults, but differences were significant in only one of seven samples ($P < 0.05$, data not shown). Overall, the mean difference in $\log_{10}$-transformed *T. tenuis* numbers between age groups was 0.26 (or 2.8 worms). *D. lanceolata* was absent from one of seven samples. Similar to *T. tenuis*, subadults had more *D. lanceolata* worms than adults for one sample ($P < 0.05$) and had greater mean abundances than adults for four of the remaining five samples (mean difference was 2.2 worms). In one of seven samples, females had significantly more *E. trivolvus* worms

Table 3 Effect of sample, sex, and age of geese on mean abundance of seven species of parasites. Entries in the table are *F*-values for two-way analyses of variance blocked by sample. Missing entries occur for analyses in which there was a higher-order interaction. Parasite designations as in the legend to Table 1

Parasite	Sample	Sex	Age	Interaction
Hd	9.87***	0.55	0.97	NS
Tt	2.27*	0.26	2.19*	NS
Ca	–	–	–	4.86* (age × sex)
Dl	1.94	0.14	3.88*	NS
Db	2.066	0.29	0.91	NS
Sg	–	–	–	2.28* (sample × sex × age)
Et	2.01	5.98*	0.87	NS

$^*P < 0.05$; $^{***}P < 0.001$; *NS* non-significant

than males ($P < 0.05$); mean *E. trivolvus* numbers were higher in females than males for five of six remaining samples (mean difference was 2.1 worms). In summary, these results show that sex and age composition of samples can influence representation by particular parasites.

Co-occurrences and covariation between species across infracommunities

T. tenuis and *H. dispar* were found in every sample, whereas the trematode *E. trivolvus* was present in all but one sample. *C. anatis*, *D. barrowensis*, *D. lanceolata*, and *S. gracilis*, were present in 24, 22, 19, and 18 samples, respectively. Eleven samples had all seven species represented (21 possible pairwise comparisons per sample), whereas 8 samples had six species (15 comparisons), 6 samples had five species (10 comparisons), and 2 samples had four species allowing six comparisons (Appendix A). Over all samples, there were 423 possible pairwise comparisons.

We found that 14 (or 3.3%) of 423 pairwise associations between species were significant ($P < 0.05$), using Fisher's exact tests based on presence-absence data. Ignoring species groups, such results are expected by chance. However, 5 of these significant co-occurrences were between *H. dispar* and *T. tenuis* (which represented ca 19% of the possible 27 comparisons using these two species). *D. barrowensis* significantly co-occurred with *S. gracilis* in 2 of 13 (or 15%) samples and with *C. anatis* in 2 of 11 (or 18%) samples. In <5% of samples, co-occurrences were found between *H. dispar* and *E. trivolvus*, *T. tenuis* and *D. lanceolata*, *T. tenuis* and *D. barrowensis*, *D. lanceolata* and *D. barrowensis*, and *D. lanceolata* and *S. gracilis*.

Thirty-nine (or ca 9.2%) of 423 Spearman correlations between untransformed species abundances were significantly positive; one correlation (*H. dispar* versus *D. lanceolata*) was significantly negative. Recurrent positive covariation between species included 8 instances between *H. dispar* and *T. tenuis* (29% of all possible samples), 6 between *T. tenuis* and *D. lanceolata* (22% of all samples), 5 between *D. barrowensis* and *S. gracilis* (18.5% of all samples), and 4 between *D. barrowensis* and *C. anatis* (ca 15% of all samples). Other species covaried less often, and these may be explained by chance (3 times: *D. lanceolata* and *S. gracilis*, *D. lanceolata* and *D. barrowensis*; twice: *H. dispar* and *E. trivolvus*, *T. tenuis* and *D. barrowensis*, *E. trivolvus* and *C. anatis*; once: *T. tenuis* and *S. gracilis*, *D. barrowensis* and *E. trivolvus*, *H. dispar* and *D. barrowensis*, and *T. tenuis* and *C. anatis*).

Importantly, the presence of uninfected birds in samples was responsible for finding significance. Using intensity data for species produced only 80 pairwise comparisons and only 22 of those had sample sizes >10. Of these, only one correlation was significant (a positive correlation between *H. dispar* and *T. tenuis*). As such, the significant correlations we observed appeared due to the fact that some geese within a sample escaped parasitism or lost both species being sampled, whereas others harbored one or more individuals of each of these parasites.

Discussion

The lesser snow geese collected in this study had depauperate helminth infracommunities largely due to loss of helminths over time, and perhaps due to limited or no recruitment through new infections during winter or spring migration. Seasonal declines in prevalence resulting in low species diversity and light helminth burdens (as seen here) are consistent with other studies on snow geese (Neraasen and Holmes 1975) and ducks (Buscher 1965; Wallace and Pence 1986; Fedynich and Pence 1994). This situation contrasts with higher overall levels of infection during the breeding season, particularly among young waterfowl (Buscher 1965; Wallace and Pence 1986; Fedynich and Pence 1994). Helminths from birds collected during both the breeding and wintering seasons (when parasite species diversity is relatively high and low, respectively) still show few negative relations (Bush 1990; Fedynich and Pence 1994). Our results were consistent with this general trend.

Determining causes of co-occurrence among parasite species is important for understanding the potential for interactions between parasite species and its impact on host biology. We found that co-occurrences were common between some pairs of helminths, as was the case for other helminth infracommunities of birds (e.g., Bush and Holmes 1986a; Stock and Holmes 1987; Fedynich and Pence 1994; cf. Moore and Simberloff 1990). There are numerous reasons for co-occurrences and covariation among helminth species, including species interactions such as facilitation, but also convergence between species in various aspects of their biology. In this study, co-occurrences were relatively common between *H. dispar* and *T. tenuis*, the two most frequently encountered species. Both have direct life cycles and although transmission details vary, both species would be transmitted well in a variety of habitats given suitable environmental conditions. Other studies have demonstrated co-occurrences between helminths that were common year round and/or were more likely to infect young hosts (e.g., Haukisalmi and Hettonen 1993b). *T. tenuis* and *D. lanceolata* were more abundant in subadult geese after controlling for sample. Such species may have high colonization ability (cf. Haukisalmi and Hettonen 1993b), but potentially low competitive ability. Co-occurrences between such species within samples can be due to their often being numerous in young birds and less numerous in adults.

Three other relatively common co-occurrences were noted (between *D. barrowensis* and *S. gracilis*, *C. anatis* and *D. barrowensis*, and *T. tenuis* and *D. lanceolata*). While the life cycle of *D. barrowensis* is unknown, that of a congener, *D. lanceolata*, is well known, as are the life cycles of many other hymenopelidid cestodes of waterfowl, including *S. gracilis* (see McDonald 1969). A wide variety of copepod and ostracod crustaceans can serve as intermediate hosts. Assuming *D. barrowensis* and *S. gracilis* share a similar range of intermediate hosts, conditions conducive for the transmission of one should be conducive for the other. However, neither of these explanations apply to co-occurrrences between *C. anatis* and *D. barrowensis* and between *T. tenuis* and *D. lanceolata*. *C. anatis* and *T. tenuis* have direct life cycles; *D. barrowensis* and *D. lanceolata* require intermediate hosts. Co-occurrence between these other species may be due to chance.

Alternatively, an overall decline in prevalence or abundance of particular species would reduce the extent of co-occurrences. In fact, Fedynich and Pence (1994) reported that the number of species forming recurrent groups in juvenile mallards declined in winter and that adult mallards had smaller recurrent groups than juveniles. Our results clearly show that prevalence declines with Julian date of sampling (time after the breeding season) for four species showing recurrent co-occurrences (including *T. tenuis* and *D. lanceolata* which otherwise show little reason to co-occur). As indicated, we expect that the age composition of a sample might influence the likelihood of finding significant co-occurrence (e.g., if there are both young birds heavily infected with several parasites and older birds that are less infected or uninfected). Similarly, other factors such as whether some birds are early versus late arrivals at a particular stopover site might influence the likelihood of finding co-occurring parasites (e.g., early arrivals may have lost many of their parasites obtained on the breeding ground, whereas late arrivals may have retained them). Other losses and limited recruitment can occur for birds, such as incubating non-feeding females (Ankney 1977).

While most of the abundant species were waterfowl generalists, all but *S. gracilis* tend to occur predominantly in arctic-nesting geese. In wintering and migrating situations, additional factors need to be considered to explain patterns of co-occurrence because transmission and recruitment of parasites is reduced or unlikely. Such factors include the duration of the recruitment period on the breeding grounds before migration, and the relative longevity of each parasite species in the host after being acquired on the breeding grounds. In the absence of recruitment, helminth communities in wintering birds consist only of the survivors and these form the remnants of communities acquired earlier. With the possible exception of *T. tenuis*, *H. dispar*, and *C. anatis*, recruitment of new infections is less likely on the wintering grounds than on the breeding grounds. Furthermore, transmission would require suitable conditions to support larval development when contaminated areas are actually being used by geese. It is interesting in this regard that geese numbers have increased greatly over the past 45 years; this should increase densities of wintering geese which may increase transmission rates of parasites with direct life cycles, such as the nematodes listed above.

In summary, helminth communities of wintering and migrating lesser snow geese are characterized by few species, and by co-occurrences between particular species. Factors such as how common parasites were, and their expected ability to colonize geese were related to the likelihood of finding such co-occurrences or covariation. Other factors such as the time of acquiring new infections and the duration of those infections in relation to timing of sampling may help explain species abundances and patterns of co-occurrence among helminths in geese, and other host species.

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Appendix A. Sample codes (*Code*), numer of females and males (adults, subadults), Julian date of sampling, and prevalence of each parasite species in the sample [*Hd Heterakis dispar* (Schrank 1790), *Tt Trichostrongylus tenuis* (Mehlis 1846), *Ca Capillaria anatis* (Schrank 1790), *Dl Drepanidotaenia lanceolata* (Bloch 1782), *Db D. barrowensis* (Schiller 1952), *Sg Sobolevicanthus gracilis* (Zedr 1803), *Cl Cladogyna longivaginata* (Fuhrmann 1906), *Pc Platyscolex ciliata* (Fuhrmann 1913), *Et Echinostoma trivolvus* (Cort 1914)]

Code	Location	Females	Males	Julian date	Prevalence								
					Nematodes			Cestodes					Trematode
					Hd	*Tt*	*Ca*	*Dl*	*Db*	*Sg*	*Cl*	*Pc*	*Et*
11	29°50′ N 94°00′ W	12, 2	15, 1	10	86.7	76.7	0	6.7	13.3	46.7	0	0	33.3
12		13, 1	12, 1	42	74.1	66.7	7.4	11.1	7.4	55.5	0	59.3	14.8
21	29°50′ N 93°40′ W	12, 0	10, 3	13	68.0	56.0	4.0	12.0	0	48.0	4.0	16.0	12.0
22		11, 3	13, 1	47	78.6	53.6	10.7	21.4	21.4	53.6	3.6	0	17.9
31	29°40′ N 92°30′ W	14, 1	5, 0	20	45.0	35.0	10.0	15.0	5.0	25.0	10.0	10.0	10.0
32		17, 4	12, 2	49	57.1	54.2	2.9	14.3	5.7	34.3	0	2.9	5.7
41	29°30′ N 96°20′ W	14, 4	8, 3	11	96.6	79.3	14.0	17.2	0	0	0	0	24.1
42		16, 2	10, 1	40	72.4	34.5	13.8	20.7	3.5	3.5	0	0	20.7
43		13, 2	7, 2	63	70.8	50.0	0	29.2	0	0	0	0	8.3
51	30°00′ N 92°40′ W	10, 4	15, 1	22	83.3	73.3	16.7	6.7	6.7	10.0	0	0	20.0
52		11, 1	16, 1	50	75.9	41.4	3.5	6.9	3.5	6.9	0	0	24.1
61	36°20′ N 95°50′ W	17, 3	18, 5	70	69.8	58.1	2.3	37.2	0	2.3	11.6	0	4.7
71	40°40′ N 95°30′ W	9, 1	18, 3	16	51.6	22.6	6.5	3.2	6.5	3.2	0	0	9.7
73		13, 1	14, 1	61	48.3	69.0	10.4	3.5	13.8	3.5	3.5	0	10.4
74		11, 4	9, 7	81	67.7	74.2	12.9	16.1	19.4	6.5	0	0	9.7
72	39°20′ N 95°40′ W	11, 1	16, 3	42	58.1	16.1	3.2	6.5	3.2	9.7	0	0	6.4
91	43°30′ N 97°50 W	18, 0	13, 3	65	32.4	32.4	11.8	2.9	5.9	0	0	05.9	
92		12, 1	14, 7	77	23.5	41.2	2.9	2.9	0	5.9	8.8	0	2.9
93		2, 0	13, 2	85	29.4	52.9	5.9	0	0	5.9	0	0	0
94		13, 3	6, 2	88	37.5	33.3	4.2	0	8.3	4.2	0	0	12.5
101	45°50′ N 98°00′ W	17, 4	13, 1	92	34.3	37.1	5.7	2.9	5.7	0	0	0	8.6
111	48°50′ N 100°50′ W	17, 1	7, 5	98	20.0	43.3	3.3	0	0	3.3	0	3.3	6.7
112		3, 3	5, 2	105	30.8	38.5	15.4	7.7	7.7	0	0	7.7	7.7
121	50°00 N 98°40′ W	13, 1	14, 3	105	29.0	19.4	0	3.2	6.4	0	19.4	0	19.4
122		12, 0	13, 2	123	14.8	14.8	7.4	3.7	7.4	0	3.7	3.7	29.6
131	55°10′ N 82°50′ W	13, 1	12, 2	130	14.3	25.0	10.7	0	0	0	0	0	64.3
132		12, 1	11, 3	138	7.4	44.4	14.8	0	3.7	0	0	0	44.4

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