

Associations between body composition and helminths of lesser snow geese during winter and spring migration

Dave Shutler^{a,*}, Ray T. Alisauskas^{b,c}, J. Daniel McLaughlin^d

^a Department of Biology, Acadia University, Wolfville, Nova Scotia, Canada B4P 2R6

^b Environment Canada, Prairie & Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada S7N 0X4

^c Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, Canada S7N 5E2

^d Department of Biology, Concordia University, 7141 Sherbrooke St. W., Montreal, Que., Canada H4B 1R6

ARTICLE INFO

Article history:

Received 9 May 2012

Accepted 15 May 2012

Available online 17 June 2012

Keywords:

Chen caerulescens caerulescens

Body condition

Fat

Helminths

Lesser snow geese

Minerals

Nematodes

Protein

ABSTRACT

Costs of parasitism are predicted to be higher with greater parasite intensities and higher inter-parasite competition (diversity). We tested whether greater helminth intensities and diversity were associated with poorer body composition (whole-body fat, protein, mineral and true body mass) in lesser snow geese, *Chen caerulescens caerulescens*. As part of a larger study on nutritional ecology, 828 wintering or migrating geese were shot between January and May 1983 in 27 different date–locations (samples) during their northward migration through mid-continental North America. A large proportion of overall variation in body composition and parasite communities was among samples, so we analyzed data within each of the 27 samples, controlling for structural body size (the first principal component of 10 body size measurements), sex and the age of geese. There was no compelling evidence that cestodes, trematodes or helminth diversity were associated with variation in body composition but nematodes had several negative associations with fat reserves. However, negative associations between fat reserves and nematodes occurred most often in geese collected between March and May when nematode prevalences and intensities were relatively low. This suggests several possibilities: that the most common nematodes (*Heterakis dispar* and *Trichostrongylus tenuis*) were more virulent at this time, that infected individuals had been chronically infected and suffered cumulative nutrient deficits that lasted until late in the spring migration, or that geese became more vulnerable to the effects of parasites at this time of year, possibly because they redirected resources away from immunity toward fat storage in preparation for reproduction.

© 2012 Australian Society for Parasitology Inc. Published by Elsevier Ltd. All rights reserved.

1. Introduction

Many species of birds rely on fat, protein, minerals and other nutrient reserves for migration and reproduction. For example, greater fecundity in lesser snow geese (*Chen caerulescens caerulescens*) is associated with greater pre-breeding fat reserves on arrival at arctic nesting areas (Ankney and MacInnes, 1978). A variety of intrinsic factors can affect nutrient accumulation, including parasite infection. Parasites may affect hosts directly by converting the latter's nutrients to propagules (defined here as life stages that can be transmitted; Crompton, 1991; Eckert, 1991), or indirectly if hosts invest nutrients in immune function or in repair of tissues damaged by parasite feeding (Connors and Nickol, 1991; Hanssen et al., 2004). A straightforward prediction is that higher intensity infections will be associated with reduced nutrient reserves. Parasite competition (inter- or intraspecific) could also accelerate

depletion of nutrient reserves because parasites that detect other parasites may more rapidly attempt to exploit host resources to produce propagules, racing against their competitors (van Balen and Sabelis, 1995; Lipsitch and Moxon, 1997; MacKinnon and Read, 1999; Lello et al., 2004). In competitive interactions, a benign parasite may be left behind in a race against a more virulent one (virulence is defined here as the extent of reduction in host fitness caused by parasites; Read et al., 1999), and may not be transmitted at all if a virulent parasite debilitates the host. The prediction here is that greater nutrient depletion should be observed in hosts with higher parasite species richness. Here, we test for associations between parasites and body composition in lesser snow geese.

Although many studies describe helminth communities of wild avian hosts (e.g., Storer, 2000; Righi and Gauthier, 2002; Fedynich et al., 2005), few have directly assessed relationships between host body composition and helminths. Sepúlveda et al. (1994) found a higher prevalence of a nematode (*Cosmocephalus obvelatus*) in nestling roseate spoonbills (*Ajaia ajaja*) with no fat reserves compared with birds with extensive reserves. Holmstad and Skorping

* Corresponding author. Tel.: +1 902 585 1354; fax: +1 902 585 1059.

E-mail address: dave.shutler@acadiau.ca (D. Shutler).

(1998) reported a negative association between body mass and helminth intensity in willow ptarmigan (*Lagopus lagopus*), but they did not control for structural body size, so their data do not permit evaluation of a relationship between parasites and nutrient reserves. Bosch et al. (2000) found a negative relationship between condition (ratio of body mass to tarsus length) and helminth load in yellow-legged gulls (*Larus cachinnans*), but it is not clear whether poorer condition was a consequence of lower lipid levels or lower mass in some other tissue. With so few studies, it is difficult to assess generality of relationships between parasites and body composition; clearly more work is needed, particularly on wild birds.

We quantified the body compositions of 828 lesser snow geese collected between January and May 1983, controlling for goose body size, sex and age. For 771 of these geese, we also quantified helminths. Lesser snow geese overwinter primarily along and north of the Gulf of Mexico, and beginning in March make several migratory stops, increasing their foraging intensity on their way to arctic breeding areas (Alisauskas and Ankney, 1992; Cooke et al., 1995). Each habitat exposes them to potentially new helminth communities. Elsewhere (Forbes et al., 1999; Shutler et al., 1999), we describe spatiotemporal variation in their helminth (cestode, trematode and nematode) communities. In the present study, we test whether reduced body composition is associated with higher helminth intensities and with more helminth species, which is likely to result in costs to host fecundity and other aspects of host fitness.

2. Materials and methods

We shot geese from undisturbed feeding flocks between 9 January and 19 May 1983 on their winter quarters and during their spring migration (Alisauskas, 2002). Details about timing and location of these 27 samples of between 17 and 47 geese are described elsewhere (Alisauskas et al., 1988; Alisauskas and Ankney, 1992; Alisauskas and Hobson, 1993; Forbes et al., 1999; Supplementary Tables S1–S4). Collections were made during winter (January–February) from three landscapes described by Alisauskas (1998): coastal marsh in Texas and Louisiana, rice prairie in Texas and Louisiana, and corn in Iowa. Geese were also collected in February from Oklahoma (winter wheat habitat). Migrant geese were collected during spring (March–May) from South Dakota, North Dakota, southern Manitoba (all from agricultural landscapes) and northern Ontario (coastal lowlands of Hudson Bay).

Following methods detailed elsewhere (Forbes et al., 1999; Shutler et al., 1999; Alisauskas, 2002), geese were frozen until dissection. All organs were removed and gastrointestinal tracts were washed and scraped empty of contents; the latter were frozen in plastic bags for parasite enumeration by one of the authors (J.D. McLaughlin). Age (based on absence of the bursa of Fabricius in adults) and sex (using external criteria and gonads) were also determined. Body composition was measured following the methods in Alisauskas (2002). Briefly, one half of a leg, one half of the breast, the liver and the rest of the defeathered bird minus gonads and gut contents, were each passed through a commercial meat grinder to homogenize them. Then, four 10 g tissue samples from each of these parts of the carcass were dried to a constant mass in an oven at 80–90 °C and reweighed to determine moisture loss. Each was then ground in an electric coffee mill to reduce them to powder consistency. Lipids were extracted in a modified Soxhlet apparatus using petroleum ether as a solvent. Following lipid extraction, samples were weighed to determine the amount of lipid removed. Body fat was dry mass multiplied by the proportion of lipid in the sample. The resulting lean dry tissue was burned at 550 °C in a muffle furnace to obtain ash, with the difference in

weight represented by protein loss. Body mineral was the lean dry mass multiplied by the proportion of ash. Body protein was the lean dry mass multiplied by the proportion of sample that was burned off (Alisauskas, 2002). We thus obtained fat, protein, minerals and true body mass (i.e., dry body mass with ingesta removed) in grams for each carcass.

Not all measurements were taken on all geese, so sample sizes varied among tests. Data were analyzed in SAS (SAS Institute, Cary, North Carolina). We computed a univariate measure SIZE using scores of the first Principal Component (PC) from analysis of 10 structural measures made to the nearest 0.1 mm (culmen, wing chord, tarsus length, keel length, body length, skull length, skull height, skull width, bill height and bill width) on all geese without regard to age or sex. Treating each parasite species independently would have significantly weakened statistical inference even with our sample sizes. Therefore, following John (1995), helminths were grouped into cestodes, trematodes and nematodes. Total numbers were used in analyses (see Section 4). General linear models (GLMs) were used where a body composition variable was the response variable, and sample, SIZE, sex, age, log (cestodes + 1), log (trematodes + 1) and log (nematodes + 1) were modeled as simultaneous explanatory variables with additive effects. Analyses were repeated with helminth diversity (number of helminth species) as the explanatory variable of interest. Non-significant explanatory variables were sequentially removed from models until only significant associations remained (Crawley, 2005).

3. Results

Of the geese examined, 85% were adults and 50% were female. Sixteen species of helminths were identified; nine had prevalences less than 3% (Forbes et al., 1999) and are not included in the following summary. Twenty-six percent of geese carried cestodes (*Sobolevicanthus gracilis* 11% prevalence, *Drepanidotaenia lanceolata* 9%, *Drepanidotaenia barrowensis* 5%), 19% carried trematodes (*Echinostoma trivolvis* 15%), 70% carried nematodes (*Trichostrongylus tenuis* 42%, *Heterakis dispar* 47%, *Capillaria anatis* 6%), and 78% carried at least one helminth species.

There was substantial variation in body composition among the 27 samples (for fat, sample $F_{26,699} = 55.1$, partial $R^2 = 0.49$; for protein $F_{26,699} = 10.6$, partial $R^2 = 0.16$; for minerals $F_{26,705} = 5.1$, partial $R^2 = 0.12$; for true body mass $F_{26,716} = 34.0$, partial $R^2 = 0.27$; all P s < 0.0001; Fig. 1). Moreover, parasite communities differed substantially among samples (Fig. 2; also see Forbes et al., 1999). Thus, relationships within each sample were analyzed separately (Supplementary Tables S1–S5). This resulted in a total of 108 GLMs with the three helminth groups as concomitant explanatory variables, as well as another 108 with helminth diversity as an explanatory variable. Assuming the null hypothesis is true, this significantly raises the chance of finding spurious statistical significance (Rice, 1989; Rothman, 1990); we return to this below. By combining individual species into taxonomic groups, even greater extremes were avoided in the number of analyses that would arise had we treated each of the 16 helminth species as separate explanatory variables. These extremes were clearly not warranted even with our extensive data set, particularly because the majority of parasites were absent from most samples. Moreover, analyses of interactions were not warranted by sample sizes within samples.

Relationships between nutrients and SIZE, sex and age that are controlled for in analyses are not reviewed here and are part of the results in Supplementary Tables S1–S5; only summaries of relationships among body condition metrics and parasite burdens are detailed. Little evidence was found for a relationship between cestodes or trematodes and body condition (Table 1). However, for nematodes, there were more negative relationships with fat

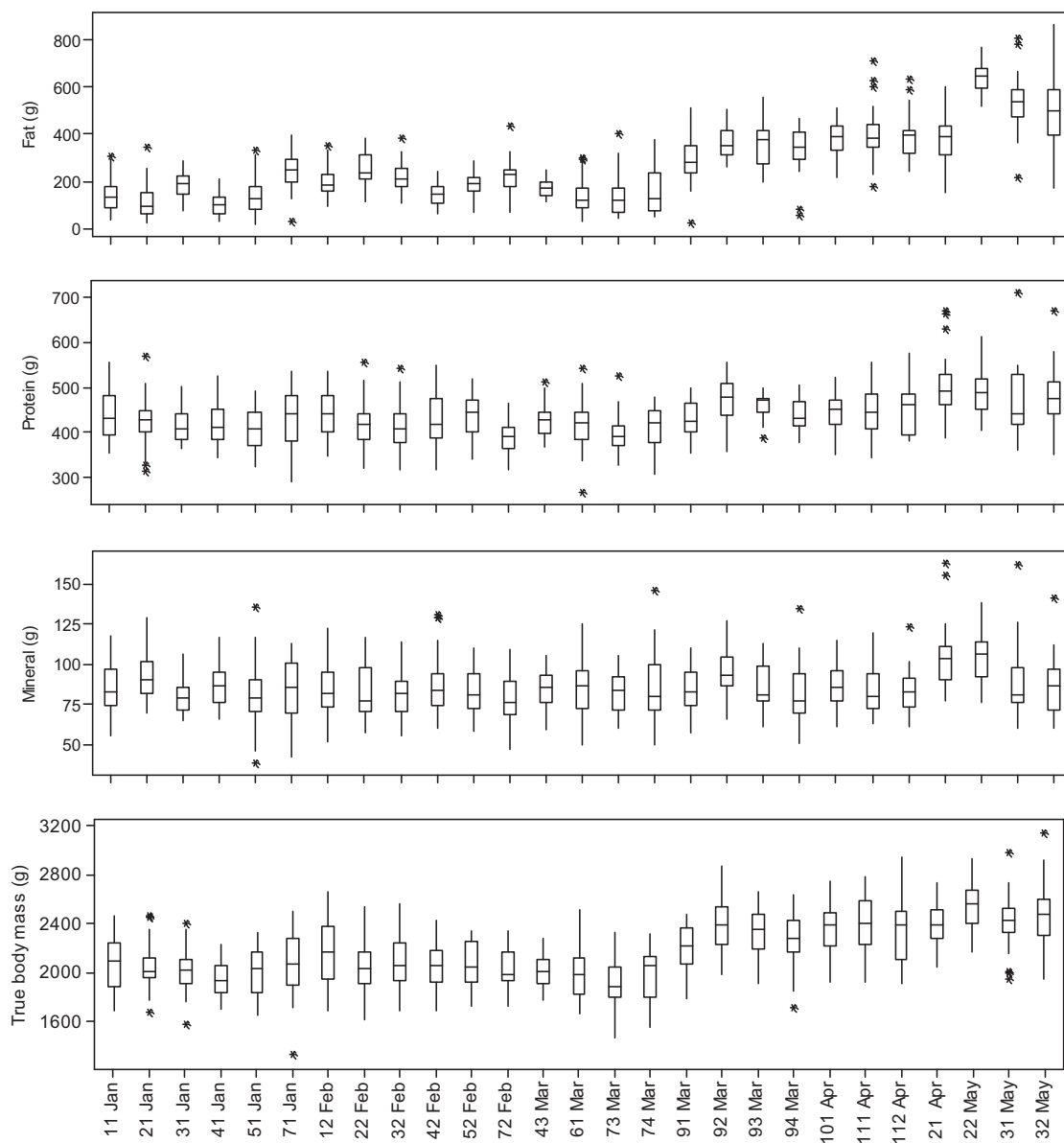


Fig. 1. Variability (\pm S.E.) in body composition in lesser snow geese in successive samples collected in a south–north gradient during migration in 1983. Boxplots show interquartile range (box), median (horizontal line within box), data range (vertical line), and outliers (asterisks). Additional information is provided in [Supplementary Tables S1–S4](#).

and true body mass, and for these two metrics, the number of significant results exceeded the chance expectation of 1.4 (5% of 27; [Table 1](#)). Most of the significant results for fat occurred later in the spring migration, including each of the last three samples collected in May ([Fig. 3](#)).

Only two helminths, *Trichostrongylus tenuis* and *Heterakis dispar*, both nematodes, occurred in all samples. Based on the number of significant negative associations between nematodes and fat, we tested (with GLMs) whether these taxa individually influenced fat (as before, sex, SIZE, age and with each nematode species as simultaneous explanatory variables). After sequential removal of non-significant associations, *T. tenuis* was negatively associated with fat in five samples (22, 31, 43, 94, 131) and *H. dispar* was negatively associated with fat in three (31, 74, 94). In two samples, both nematodes were significantly and negatively associated with fat, and samples 22, 31 and 43 had no significant associations with nematodes combined ([Supplementary Table S1](#)). Spearman rank correlations between fat and *T. tenuis* were negative in 20/27

samples (Binomial test, $P = 0.01$) and between fat and *H. dispar* in 18/27 samples (Binomial test, $P = 0.08$).

Higher helminth diversity was associated with lower fat reserves significantly more often than expected by chance and all significant associations were negative ([Table 1](#)). In contrast, higher helminth diversity was associated with higher total minerals more often than expected by chance, but the single positive significant association was balanced by a single negative association. There was no significant evidence for an association between helminth diversity and either variation in total protein or true body mass ([Table 1](#)).

Seasonal patterns in the explanatory values of the different helminths were investigated by computing the Pearson correlation (r) between partial R^2 values and sampling date. For the relationship between cestodes and true body mass, there was a significant positive increase in partial R^2 with sampling date ($r = 0.46$, $P = 0.01$); remaining correlations were not significant (all $|r| \leq 0.29$, $P_s > 0.14$). There were no significant relationships for trematodes

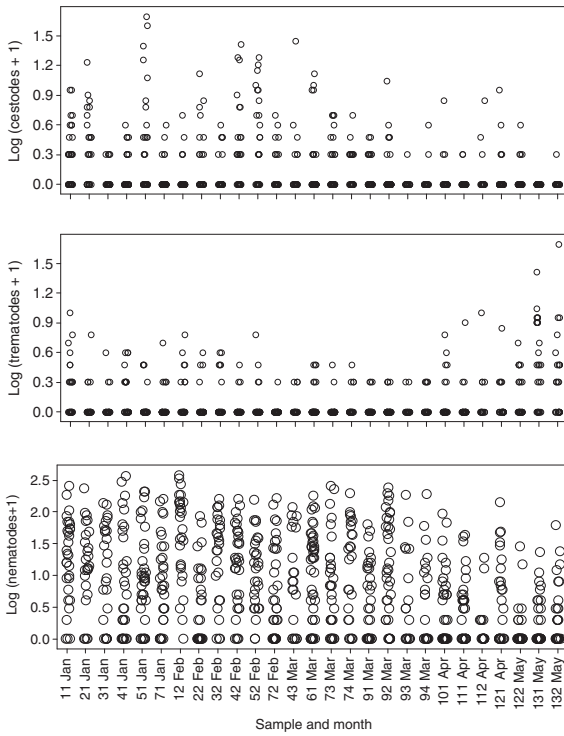


Fig. 2. Variability (\pm S.E.) in lesser snow geese helminth intensities in successive samples collected in a south–north gradient during migration in 1983. Overlapping points are shifted horizontally so that all data are visible. Additional information is provided in [Supplementary Tables S1–S4](#).

(all $|r| \leq 0.36$, $P_s > 0.07$). For nematodes, there were significant associations between partial R^2 and sampling date for fat ($r = -0.42$, $P = 0.03$), minerals ($r = 0.50$, $P = 0.01$) and protein ($r = 0.43$, $P = 0.02$) but not for true body mass ($r = 0.02$, $P = 0.92$).

4. Discussion

We found several statistically significant associations between helminths and body condition but we also conducted a large number of tests. Following various authorities (Rothman, 1990; Nakagawa, 2004), we do not assume that these significant results are automatically spurious, but instead evaluate the total weight of evidence. Trematodes and cestodes had fewer significant associations with fat than expected by chance, suggesting that these taxa have no effect on the fat reserves of lesser snow geese. However, for nematodes, more than the expected number of possible associations with fat reserves were negative, as predicted, and several associations were significantly negative. Our null expectation of 1.4 ($= 0.05 * 27$) significant tests is two-tailed (i.e., both negative and positive associations could occur by chance), so it is more compelling that all seven significant nematode-fat associations were

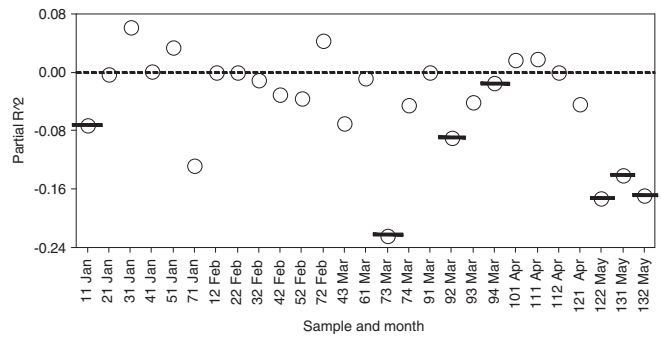


Fig. 3. Partial R^2 of variation in fat load explained by nematode intensities in lesser snow geese in successive samples collected in a south–north gradient during migration in 1983. Signs of R^2 values indicate directions of relationships. Significant associations are indicated by negative signs over data points.

negative. Moreover, Shutler et al. (1999) predicted, on the basis of slightly greater evidence of immune response indexed by spleen size, that nematodes would be the most likely of the three helminth taxa enumerated here to exert effects on their goose hosts. Our evidence does not suggest that any of the helminth groups negatively affected minerals or protein. However, due to the negative effects of nematodes on fat, and the high variance in body mass attributable to fat mass, it is not surprising that we also obtained several significant negative associations between parasites and true body mass (although we also obtained two significant positive associations). Finally, although several associations between body condition and helminth diversity were significant, many of these were opposite to the direction predicted. In sum, our evidence is only persuasive that fat and to a lesser extent true body mass were negatively affected by higher nematode intensities. That we obtained such evidence without experiment amidst a multitude of other ecological influences (e.g., non-helminth parasites; Weatherhead et al., 1993) is illuminating.

Similar to what we observed, dramatic seasonal fluctuations in helminth intensities are common in wild birds (Drobney et al., 1983; Moore and Simberloff, 1990). A closer inspection of the seasonal patterns in nematode intensities makes interpretation of our results more interesting, because we detected negative impacts on fat reserves most often between March and May, during the highest daily rates of fat storage but when nematode burdens and prevalence had declined (Forbes et al., 1999). Possibly, infected individuals at these later dates were a minority that failed to eliminate infections they had carried over the winter. If so, their lower fat reserves could represent cumulative effects of chronic infections. Nevertheless, if these individuals are typically unable to eliminate infections later, or are unable to acquire sufficient nutrients before breeding (B ety et al., 2003), this could have implications for their reproductive success (Ankney and MacInnes, 1978).

Why should the nematodes we found (primarily *Heterakis dispar* and *Trichostrongylus tenuis*) be more likely than trematodes and cestodes to have negative impacts on their hosts? Although

Table 1
Number of samples where relationships between response variables and parasites were in the predicted direction in General Linear Models (GLMs; see Section 3). $n = 27$ except for cestodes because there were only 26 samples in which those occurred. Values in parentheses are number of times in GLMs where relationships were statistically significant in the predicted negative direction, followed by the number of times they were statistically significant in the opposite direction. Cells in bold reflect significant ($P < 0.05$) deviation from random expectation of 50% of the number of tests in one direction (binomial tests).

Response variable	Explanatory variable							
	Trematodes		Cestodes	Nematodes	Helminth diversity			
Fat	17	(0,1)	15	(0,0)	19	(7,0)	20	(4,1)
Minerals	11	(1,2)	12	(0,0)	15	(1,1)	7	(0,3)
Protein	13	(2,0)	12	(2,1)	17	(2,0)	11	(3,0)
True body mass	15	(4,0)	11	(0,1)	20	(4,1)	14	(2,0)

approximately twice the size of *T. tenuis*, *H. dispar* is considered avirulent in most host species (Fedynich, 2008; Roberts and Janovy, 2008) whereas *T. tenuis* is more often considered virulent (Tompkins, 2008). However, with few exceptions (e.g., Hudson and Dobson, 1990; Hudson et al., 1992), virulence of *T. tenuis* in most wild hosts is unknown (Tompkins, 2008) and information on virulence of *H. dispar* is limited to captive birds, particularly poultry (Fedynich, 2008). We found limited evidence that *T. tenuis* was more virulent than *H. dispar*. Among the proximate explanations for greater virulence of nematodes compared with cestodes and trematodes may be greater conversion of host nutrients to parasite biomass. Another explanation is that, in contrast to most gut trematodes and cestodes, many nematodes (including to some extent *Heterakis* and *Trichostrongylus*) undergo a stage of migration through other host tissues before they reach the gut, and they may also be more likely than trematodes or cestodes to cause tissue damage while they occupy the gut (Read and Skorping, 1995; Roberts and Janovy, 2008). In addition, nematodes may be more likely to provoke immune responses that entail energetic costs to hosts that may be reflected in reduced fat storage. Accordingly, John (1995) reported that nematodes were more likely than cestodes or trematodes to provoke immune responses (indexed by spleen size), consistent with subsequent studies (Shutler et al., 1999; Morand and Poulin, 2000; but see Mallory et al., 2007). Alternatively, nematodes may directly affect host ability to absorb nutrients for fat synthesis and storage, particularly because both of these parasites occur in the caeca. *Trichostrongylus tenuis* penetrates the caecal mucosa and probably affects the digestion of fibrous vegetation; intense infections may cause haemorrhage and caecal inflammation (Tompkins, 2008). Finally, nematodes may benefit more than do trematodes and cestodes from greater virulence via enhanced transmission, although the reasons for this are not immediately apparent. For example, *T. tenuis* is not transmitted if its weakened host is preyed upon (Hudson et al., 1992), nor are the nematodes we observed more likely to be transmitted horizontally to conspecifics than trematodes and cestodes (horizontal transmission can also select for greater virulence; Clayton and Tompkins, 1994).

Relating conventional parasite data to virulence is difficult (Shutler et al., 1999). Counts of total numbers of parasites ignore differences in parasite biomass that may better reflect the extent to which parasites have extracted host nutrients. However, high parasite biomass may be independent of host investment in an immune response. In fact, if savings in immune investment are sufficient, this could lead to positive associations between parasitism and body composition (Shutler, 2011). On the other hand, hosts in poor condition often have higher rather than lower parasite intensities (Roberts and Janovy, 2008). Another problem with using parasite intensity as a measure of virulence is that instantaneous measures do not capture propagules that have already been shed; in comparison to larger parasites, smaller parasites may convert more host energy into propagules. Neither numbers nor biomass need be related to host investment in tissue repair or immunity. Ideally, the virulence of parasitism would have to be based on energetic investment by hosts relative to infection intensity, for each parasite species, and for each combination of potentially competing parasites. This ideal is not likely to be achieved, especially in wild animals; nonetheless we need to consider improving the ways of assessing the costs of parasitism.

On the whole, we found that helminths had few and only small effects on their adult goose hosts, consistent with Rausch's (1983) assessment that helminths have low virulence. Helminths are likely to be more virulent in young hosts; for example, Slattery and Alisauskas (2002) found that experimental administration of cestocides increased survival of fledgling Ross's Geese (*Chen rossii*) relative to saline-treated birds. For adult hosts, apparently low

virulence may arise from effective immune responses, but parasites have faster generation times and in comparison to their hosts, far more of their propagules do not survive, so that they are under greater selection to influence virulence (which can relate to propagule production; MacKinnon and Read, 1999). However, although geese regularly seed foraging areas with helminth propagules via defecation, transmission opportunities may be brief and spatially limited, and parasites may be selected to reduce effects on hosts long enough to ensure transmission at one of several stopover sites. Accordingly, recent, dramatic increases in snow goose populations across the arctic (Alisauskas et al., 2011) may be having unforeseen consequences for parasite virulence. High host density can favor parasite virulence (Read et al., 1999) so that fairly weak relationships between parasites and goose nutrients in our 1983 data may be stronger now, with implications for the population-level production of offspring. Alisauskas (2002) described a decades-long declining trend in production of young by mid-continental snow geese, suggesting a density-dependent response in the ability to store fat related to over-grazing on subarctic and arctic staging areas. However, increasing virulence of nematode infections may affect the ability of geese to fatten in spring and breed, a hypothesis not mutually exclusive from that of density dependence. This may also have contributed to the observed long-term decline in the production of young. On the other hand, the habitat damage resulting from goose population expansion (Jano et al., 1998) may also negatively affect the ability of parasites to complete their life cycles (e.g., if intermediate hosts are less available) or if the habitat is hostile to propagules of species with direct life cycles (e.g., *H. dispar*, *T. tenuis*). Thus, currently expanding goose populations may be selecting for host-parasite relationships that differ from those reported here.

Acknowledgments

Various forms of assistance were provided by Dave Ankney, Dorothy Riley, Gloria Dobush, Janet Rokas, Blair Cribb and Spiros Fengos. Financial assistance was provided by the Natural Sciences and Engineering Research Council of Canada. All geese were collected under scientific collection permits from state, provincial and federal jurisdictions in which our research was done. We appreciate several constructive reviewers for improving this paper.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ijpara.2012.05.008>.

References

- Alisauskas, R.T., 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent Lesser Snow Geese. *Auk* 115, 851–862.
- Alisauskas, R.T., 2002. Arctic climate, spring nutrition, and recruitment in midcontinent Lesser Snow Geese. *J. Wildl. Manage.* 66, 181–193.
- Alisauskas, R.T., Ankney, C.D., Klaas, E.E., 1988. Winter diets and nutrition of midcontinental Lesser Snow Geese. *J. Wildl. Manage.* 52, 403–414.
- Alisauskas, R.T., Ankney, C.D., 1992. Spring habitat use and diets of midcontinent adult Lesser Snow Geese. *J. Wildl. Manage.* 56, 43–54.
- Alisauskas, R.T., Hobson, K.A., 1993. Determination of Lesser Snow Goose diets and winter distribution using stable isotope analysis. *J. Wildl. Manage.* 57, 49–54.
- Alisauskas, R.T., Rockwell, R.F., Dufour, K.W., Cooch, E.G., Zimmerman, G., Drake, K.L., Leafloor, J.O., Moser, T.J., Reed, E.T., 2011. Harvest, survival, and abundance of midcontinent Lesser Snow Geese relative to population reduction efforts. *Wildl. Monogr.* 179, 1–42.
- Ankney, C.D., MacInnes, C.D., 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95, 459–471.
- Bêty, J., Gauthier, G., Giroux, J.-F., 2003. Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. *Am. Nat.* 162, 110–121.

- Bosch, M., Torres, J., Figuerola, J., 2000. A helminth community in breeding Yellow-legged Gulls (*Larus cachinnans*): pattern of association and its effect on host fitness. *Can. J. Zool.* 78, 777–786.
- Clayton, D.H., Tompkins, D.M., 1994. Ectoparasite virulence is linked to mode of transmission. *Proc. R. Soc. Lond. B* 256, 211–217.
- Connors, V.A., Nickol, B.B., 1991. Effects of *Plagiorhynchus cylindraceus* (Acanthocephala) on the energy metabolism of adult starlings, *Sturnus vulgaris*. *Parasitology* 103, 395–402.
- Cooke, F., Rockwell, R.F., Lank, D.B., 1995. The snow geese of La Pérouse Bay: natural selection in the wild. Oxford University Press, Oxford.
- Crawley, M.J., 2005. *Statistics: An introduction using R*. Wiley, West Sussex, England.
- Crompton, D.W.T., 1991. Nutritional interactions between hosts and parasites. In: Toft, C.A., Aeschlimann, A., Bolis, L. (Eds.), *Parasite-host Associations: Coexistence or Conflict?* Oxford University Press, Oxford, pp. 228–257.
- Drobney, R.D., Train, C.T., Fredrickson, L.H., 1983. Dynamics of the plathyhelminth fauna of Wood Ducks in relation to food habits and reproductive state. *J. Parasitol.* 69, 375–380.
- Eckert, J., 1991. Interactions between cestodes and their vertebrate hosts. In: Toft, C.A., Aeschlimann, A., Bolis, L. (Eds.), *Parasite-host Associations: Coexistence or Conflict?* Oxford University Press, Oxford, UK, pp. 201–227.
- Fedynich, A.M., Finger, R.S., Ballard, B.M., Garvon, J.M., Mayfield, M.J., 2005. Helminths of Ross' and greater white-fronted geese wintering in South Texas, USA. *Compar. Parasitol.* 72, 33–38.
- Fedynich, A.M., 2008. Heterakis and Ascaridia. In: Atkinson, C.T., Thomas, N.J., Hunter, D.B. (Eds.), *Parasitic Diseases of Wild Birds*. Wiley-Blackwell, Iowa, USA, pp. 388–412.
- Forbes, M.R., Alisauskas, R.T., McLaughlin, J.D., Cuddington, K.M., 1999. Explaining co-occurrence among helminth species of Lesser Snow Geese (*Chen caerulescens*) during their winter and spring migration. *Oecologia* 120, 613–620.
- Hanssen, S.A., Hasselquist, D., Folstad, I., Erikstad, K.E., 2004. Costs of immunity: immune responsiveness reduces survival in a vertebrate. *Proc. R. Soc. Lond. B* 271, 925–930.
- Holmstad, P.R., Skorpung, A., 1998. Covariation of parasite intensities in Willow Ptarmigan, *Lagopus lagopus* L. *Can. J. Zool.* 76, 1581–1588.
- Hudson, P.J., Dobson, A.P., 1990. The direct and indirect effects of the caecal nematode, *Trichostrongylus tenuis*, on red grouse. In: Loye, J.E., Zuk, M. (Eds.), *Bird-parasite Interactions: Ecology, Evolution and Behaviour*. Oxford University Press, Oxford, pp. 49–68.
- Hudson, P.J., Dobson, A.P., Newborn, D., 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. *J. Anim. Ecol.* 61, 681–692.
- Jano, A.P., Jeffries, R.L., Rockwell, R.F., 1998. The detection of vegetational change by multitemporal analyses of LANDSAT data: effects of goose foraging. *J. Ecol.* 86, 93–99.
- John, J.L., 1995. Parasites and the avian spleen: helminths. *Biol. J. Linn. Soc.* 54, 86–106.
- Lello, J., Boag, B., Fenton, A., Stevenson, I.R., Hudson, P.J., 2004. Competition and mutualism among the gut helminths of a mammalian host. *Nature* 428, 840–844.
- Lipsitch, M., Moxon, E.R., 1997. Virulence and transmissibility of pathogens: what is the relationship? *Trends Microbiol.* 5, 31–37.
- MacKinnon, M.J., Read, A.F., 1999. Genetic relationships between malaria parasite virulence and transmission in the rodent malaria *Plasmodium chabaudi*. *Evolution* 53, 689–703.
- Mallory, M.L., McLaughlin, J.D., Forbes, M.R., 2007. Breeding status, contaminant burden and helminth parasites of Northern Fulmars *Fulmarus glacialis* from the Canadian high Arctic. *Ibis* 149, 338–344.
- Moore, J., Simberloff, D., 1990. Gastrointestinal helminth communities of Bobwhite Quail. *Ecology* 71, 344–359.
- Morand, S., Poulin, R., 2000. Nematode parasite species richness and the evolution of spleen size in birds. *Can. J. Zool.* 78, 1356–1360.
- Nakagawa, S., 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav. Ecol.* 15, 1044–1045.
- Rausch, R.L., 1983. The biology of avian parasites: helminths. In: Farner, D.S., King, J.R., Parkes, K.C. (Eds.), *Avian Biology*, vol. VII. Academic, New York, pp. 367–442.
- Read, A.F., Aaby, P., Antia, R., Ebert, D., Ewald, P.W., Gupta, S., Holmes, E.C., Sasaki, A., Shields, D.C., Taddei, F., Moxon, E.R., 1999. What can evolutionary biology contribute to understanding virulence? In: Stearns, S.C. (Ed.), *Evolution in Health and Disease*. Oxford University Press, Oxford, UK.
- Read, A.F., Skorpung, A., 1995. The evolution of tissue migration by parasitic nematode larvae. *Parasitology* 111, 359–371.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Righi, M., Gauthier, G., 2002. Natural infection by intestinal cestodes: variability and effect on growth in Greater Snow Goose goslings (*Chen caerulescens atlantica*). *Can. J. Zool.* 80, 1077–1083.
- Roberts, L.S., Janovy Jr., J.J., 2008. *Foundations of parasitology*, 8th ed. McGraw-Hill, New York.
- Rothman, K.J., 1990. No adjustments are needed for multiple comparisons. *Epidemiology* 1, 43–46.
- SAS Institute Inc., 1990. *SAS/STAT user's guide*, version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- Sepúlveda, M.S., Spalding, M.G., Kinsella, J.M., Bjork, R.D., McLaughlin, G.S., 1994. Helminths of the Roseate Spoonbill, *Ajaia-ajaja*, in southern Florida. *J. Helminthol. Soc. Wash.* 61, 179–189.
- Shutler, D., 2011. Sexual selection: when to expect trade-offs. *Biol. Lett.* 7, 101–104.
- Shutler, D., Alisauskas, R.T., McLaughlin, J.D., 1999. Mass dynamics of the spleen and other organs in geese: measures of immune relationships to helminths? *Can. J. Zool.* 77, 351–359.
- Slattery, S.M., Alisauskas, R.T., 2002. Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (*Chen rossii*): a case study. *J. Appl. Stat.* 29, 497–508.
- Storer, R.W., 2000. The metazoan parasite fauna of grebes (Aves: Podicipediformes) and its relationship to the birds' biology. *Misc. Publ. Mus. Zool., Univ. Michigan* 188.
- Tompkins, D.M., 2008. *Trichostrongylus*. In: Atkinson, C.T., Thomas, N.J., Hunter, D.B. (Eds.), *Parasitic Diseases of Wild Birds*. Wiley-Blackwell, Iowa, USA, pp. 316–325.
- van Balen, M., Sabelis, M.W., 1995. The dynamics of multiple infections and the evolution of virulence. *Am. Nat.* 146, 881–910.
- Weatherhead, P.J., Metz, K.J., Bennett, G.F., Irwin, R.E., 1993. Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds. *Behav. Ecol. Sociobiol.* 33, 13–23.