ÉCOSCIENCE
13 (4): 497-502 (2006)

Habitat shifts and parasite loads of lesser snow geese (*Chen caerulescens caerulescens*)[1]

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Abstract: Responding to degradation in their original coastal habitat, increasing numbers of lesser snow geese are rearing their broods farther inland. Goslings collected in this inland, fresh water habitat have substantially lower loads of two species of caecal nematodes than do goslings collected in coastal, salt marsh habitat. This likely reflects differences between the habitats in the levels of infective stages of the parasites that are ingested by goslings during their summer foraging. In the spring, several million northward migrating adult lesser snow geese use the coast of Hudson Bay for staging and feeding rather than using more inland habitat because the latter is usually still snow- and icebound. The spring migrants leave behind copious amounts of feces in the coastal marshes that contain the eggs and larvae of the nematodes. By contrast, the inland habitat receives little fecal deposition until mid-summer and then only by the much smaller resident population of nesting lesser snow geese. There is some evidence that the infectious stages of these parasites survive the winter, but multi-year accumulations would only tend to amplify habitat differences in infective loads related to the spring deposition by migrants. The role of migrants in transmitting these nematodes highlights the important point that local host–parasite dynamics must be considered from a broader spatial scale.
Keywords: habitat selection, heterokid, lesser snow geese, parasite load, trichostrongylid.

Résumé : En réponse à la dégradation de leur habitat côtier original, de plus en plus de petites oies des neiges élèvent leurs jeunes à l'intérieur des terres. Les jeunes récoltés dans cet habitat d'eau douce à l'intérieur des terres sont considérablement moins infectés par deux espèces de nématodes gastro-intestinaux que leurs congénères des habitats côtiers de marais salants. Ceci reflète probablement des différences entre les habitats dans les niveaux de parasites à des stades infectieux qui sont ingérés par les jeunes oies durant leur quête alimentaire estivale. Au printemps, des millions de petites oies des neiges adultes en migration vers le nord utilisent la côte de la Baie d'Hudson pour se nourrir durant leurs haltes migratoires au lieu d'utiliser les habitats à l'intérieur des terres qui sont encore recouverts de neige et de glace. Les migrants printaniers laissent derrière eux dans les marais côtiers de grandes quantités de fèces qui contiennent des œufs et des larves de nématodes. À l'opposé, les habitats à l'intérieur des terres reçoivent peu de fèces jusqu'au milieu de l'été et encore, à partir de ce moment là, seulement celles d'une population résidente beaucoup plus petite d'oies nicheuses. Il y a des évidences qui démontrent que les stades infectieux des parasites survivent à l'hiver mais l'accumulation d'année en année ne ferait qu'accentuer les différences entre les habitats dans la quantité de parasites infectieux déposés au printemps par les oies en migration. Le rôle des oies en migration dans la transmission de ces nématodes met en lumière l'importance de considérer une échelle spatiale plus grande lors de l'analyse de la dynamique locale hôte-parasite.
Mots-clés : charge parasitaire, *Heterakis*, petite oie des neiges, sélection d'habitat, *Trichostrongylus*.

Nomenclature: Porsild & Cody, 1980; American Ornithologists' Union, 1998; Anderson, 2000.

Introduction

As a population's size increases, various factors become important in slowing further growth. These include limitations of space and food, as well as increases in disease agents (Newton, 1998). One way members of a population (or their offspring) can escape such limitations is to disperse to less heavily used habitat. By doing so, individuals may fare better, and the population increases geographically, if not also in number. Lesser snow geese (*Chen caerulescens caerulescens*) in the La Pérouse Bay and Cape Churchill region (near Churchill, Manitoba) are a prime example of this pattern (Cooch, Rockwell & Brault, 2001). Population growth and over-consumption of forage species have led to severe habitat degradation in what were once lush coastal salt marshes (Jefferies & Rockwell, 2002; Jefferies, Rockwell & Abraham, 2003; Abraham, Jefferies & Rockwell, 2005). Much of the local population has responded by dispersing to adjacent but less degraded salt or fresh water marshes for nesting, brood-rearing, or both, and the reproductive success of those birds is substantially higher (Cooch, Rockwell & Brault, 2001; Jefferies, Rockwell & Abraham, 2003).

The West Hudson Bay snow goose colony (near Arviat, Nunavut) underwent a similar pattern of growth, local degradation, and dispersal from the core area (MacInnes & Kerbes, 1987; Abraham & Jefferies, 1997). Gomis *et al.* (1996) examined the potential involvement of disease agents in the dynamics at the West Hudson Bay colony by comparing the parasite load of pre-fledgling snow geese collected in a degraded coastal portion of the region to that of pre-

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[1] Rec. 2006-01-25; acc. 2006-05-09.
Associate Editor: Keith Hobson.
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fledglings collected 15 miles inland in less degraded, freshwater habitat. They found that birds from the less degraded, inland region were larger, in better condition, and had lower loads of trichostrongylids, a caecal nematode. In this paper, we expand those studies by comparing the parasite load of two different caecal nematodes in pre-fledging lesser snow geese sampled over a wide expanse of coastal and inland habitat in the La Pérouse Bay and Cape Churchill region.

Methods

STUDY SITE

In 1994 and 1995, up to five male and five female juvenile lesser snow geese were collected at each of 37 sites in the La Pérouse Bay and Cape Churchill region of northern Manitoba, Canada. Twenty-three sites were within 1 km of coastal salt marsh habitat and were classified as coastal habitat (*e.g.,* Figure 1a). Fourteen sites, whose habitat was predominantly fresh water based (*e.g.,* sedge fen meadows, mires) and which were at least 3 km from salt marshes, were classified as inland habitat (*e.g.,* Figure 1b). Birds were approximately 35 d old when they were collected and euthanized using cervical dislocation (Gaunt *et al.,* 1999). During necropsy, both caecae were removed and preserved in 10% neutral formalin and shipped to the City College of New York for further processing.

Each caeca was removed from the formalin solution, rinsed, and placed on a 300-micron sieve. The caeca was sliced open length-wise and the contents were washed onto the sieve with de-ionized water and then washed into a 20-mL vial using 70% ethanol. Vials were filled to a constant 20-mL volume using 70% ethanol and labelled with the individual's tag number. Caeca from the same individual were placed in separate vials.

The contents of each vial were emptied into a 9.5-mm Petri dish. The dish was placed on a marked grid (4 squares per inch) under a dissecting scope. The grid was marked with 10 randomly chosen squares. Each outlined square was examined under 6, 12, and 25 power in the same order for each vial. The contents of each square were counted two times. Any worm with 50% (or more) of its length inside the outline of the marked square was counted as being present in that square. Nematodes were categorized as being either *Trichostrongylus tenuis* (tiny and thread-like, henceforth trichostrongylid) or *Heterakis dispar* (or possibly *H. gallinarum*) (much fatter and much larger, henceforth heterokid).

Data were tallied as counts of heterokids and trichostrongylids found in both enumerations of each of the 10 random squares for both caeca of each gosling. Preliminary analyses provided no support for heterogeneity among the 10 squares or between caeca for any goslings so the counts were averaged across squares and caeca for each gosling to yield relative indices of load for each of the two identified parasites.

Following Bush *et al.* (1997), we evaluated parasite load using three measures: *prevalence,* the proportion of geese sampled from a given habitat that were infected with a particular parasite; *intensity,* the mean number of a particular parasite among infected geese sampled from that habitat; and *abundance,* the mean number of a particular parasite among all geese sampled from that habitat.

Prevalence data were treated as a dichotomous state variable (the numbers of geese either infected or uninfected for a given parasite) that was cross-classified by year, habitat, and sex. Data were modeled with respect to the classification variables using multidimensional contingency analysis (Bishop, Feinberg & Holland, 1975) implemented in PROC CATMOD from SAS® 9.1. Intensity and abundance were treated as continuous variables and modeled with respect to habitat, year, and their potential interaction using analyses of variance implemented in PROC GLM from SAS® 9.1. In all cases, model fit was assessed with the Akaike Information Criterion corrected for small sample size (AIC_c) following Burnham and Anderson (2002).

Preliminary analyses indicated that there was no support for a sex effect on prevalence, intensity, or abundance of either parasite species, and the data were pooled over sexes for all subsequent analyses of parasite load. Consistent with general trends reported by Bush *et al.* (1997), those analyses (and all subsequent ones) indicated that the three measures of parasite load displayed concordant patterns of habitat and year effects. As such, only the analytical results for abundance (which combines prevalence and intensity) are presented and discussed hereafter.

Results

Our primary interest was to estimate any difference in parasite load between inland and coastal habitat. Following

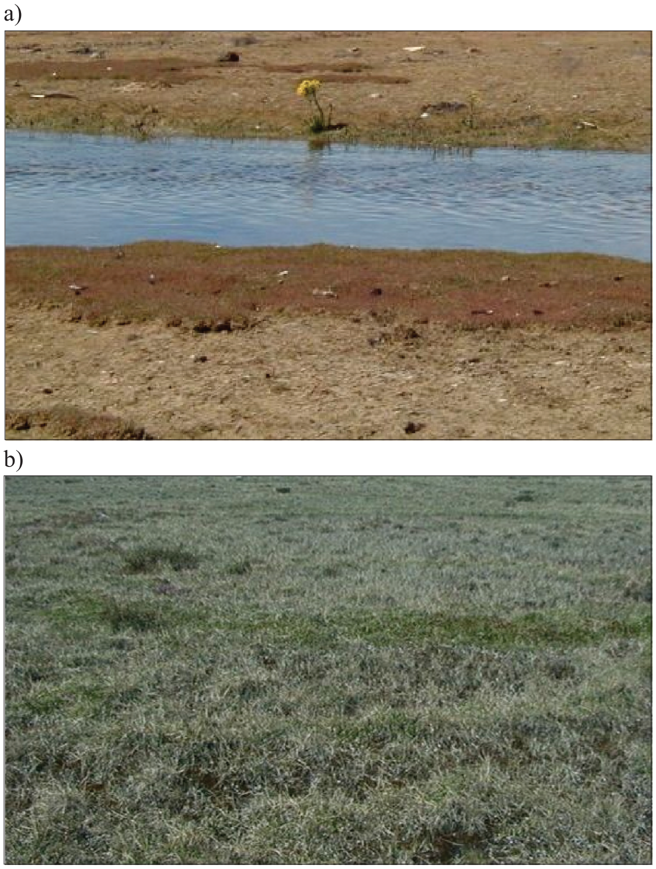

FIGURE 1. Typical habitat for coastal (a) and inland (b) sites.

Williams, Nichols, and Conroy (2002), we formed three *a priori* competing models that involved Habitat and Year (H + Y + H × Y, H + Y, and H) and evaluated model fit with an information-theoretic approach. As there was support for all three models for each parasite (Table I), we estimated the habitat effect (coastal *versus* inland) using multi-model averaging based on Akaike weights (derived from AIC_c values) and included a measure of model uncertainty in the confidence limits (Anderson, Burnham & Thompson, 2000; Burnham & Anderson, 2002). The load of both parasites was clearly higher in coastal habitat (Figure 2). It should be noted that although there is some support for a non-additive effect of habitat and year (model including H × Y), the effect is small and ordinal in that the parasite load was higher in coastal habitat in both years (*cf.* Pezzanite *et al.,* 2005).

We also were interested in evaluating the possibility that parasite load is related to the accumulation of infective stages of these caecal parasites over time. To do this, we estimated the parasite loads of goslings collected at the La Pérouse Bay colony (which has been used by staging and breeding lesser snow geese since at least the late 1950s) and of goslings collected at other coastal sites that are either not used for staging and breeding or for which staging and breeding has only recently begun (R. F. Rockwell, unpubl. data). Again, we formed three *a priori* competing models that involved Habitat and Year. There is support for all three models for trichostrongylids, while the saturated model, including the H × Y term, received highest support for heterokids (Table II). Year-specific habitat effects on heterokids were small and ordinal, with parasite load being higher in goslings collected at La Pérouse Bay in both years, so we estimated the overall habitat effect (La Pérouse Bay *versus* other sites) for both parasites using multi-model averaging as above. The overall habitat effect for both parasites indicates that the load was higher in goslings collected at La Pérouse Bay (Figure 3).

Discussion

Two nematodes, most likely *Trichostrongylus tenuis* and *Heterakis dispar* (or possibly *H. gallinarum*), were found in the caecae of near-fledging lesser snow geese in the La Pérouse Bay and Cape Churchill region. Both species have direct life cycles, involving no intermediate hosts. Infective eggs (heterokids) or infective third instar larvae (trichostrongylids) are ingested during the brood-rearing period by goslings foraging on vegetation associated with moist soil (Anderson, 2000). These infective stages hatch (heterokids only), molt (both species) and travel through much of the intestine to the caecae (Clapham, 1933; Friend & Franson, 2001). There, they mature into adults and reproduce (Delahay, Speakman & Moss, 1994). The resulting fertile eggs are shed into the environment where the cycle of parasitism continues with further ingestion of infective stages. It is important to stress that there is no development of newly produced eggs within the caecae (Lee & Atkinson, 1977). Thus, the load of parasites in individual birds is strictly a function of the number of infective stages consumed and the survival of those infective stages once ingested.

TABLE I. Comparison of parasite abundance models involving Habitat (coastal, inland), Year (1994, 1995), and their interaction.

Parasite	Model	AIC_c	ΔAIC_c	w
Heterokid	H + Y + H × Y	-80.39	2.45	0.14
	H + Y	-82.27	0.56	0.37
	H	-82.84	0.00	0.49
Trichostrongylid	H + Y + H × Y	-38.65	0.53	0.41
	H + Y	-39.18	0.00	0.53
	H	-34.67	4.50	0.06

Computations of AIC_c, ΔAIC_c, and w follow Burnham and Anderson (2002).

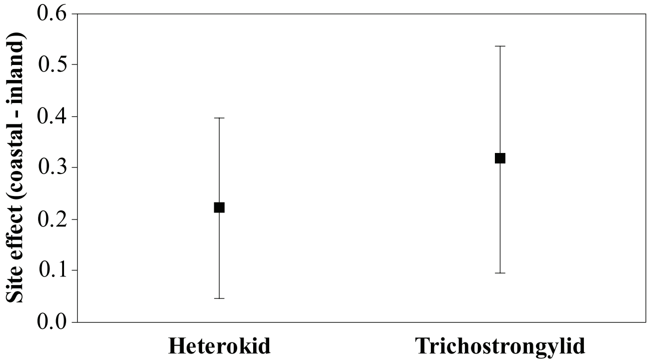

FIGURE 2. Model-averaged effects of habitat (coastal–inland) on parasite load in Lesser Snow Geese near La Pérouse Bay, 1994–1995. Ninety-five percent confidence limits account for uncertainty of models used from Table I.

TABLE II. Comparison of parasite abundance models involving Habitat (La Pérouse Bay *versus* more recently used coastal sites), Year (1994, 1995), and their interaction.

Parasite	Model	AIC_c	ΔAIC_c	w
Heterokid	H + Y + H × Y	-42.69	0.00	0.98
	H + Y	-33.49	9.20	0.01
	H	-33.19	9.50	0.01
Trichostrongylid	H + Y + H × Y	-4.61	0.97	0.28
	H + Y	-4.55	1.02	0.27
	H	-5.58	0.00	0.45

Computations of AIC_c, ΔAIC_c, and w follow Burnham and Anderson (2002).

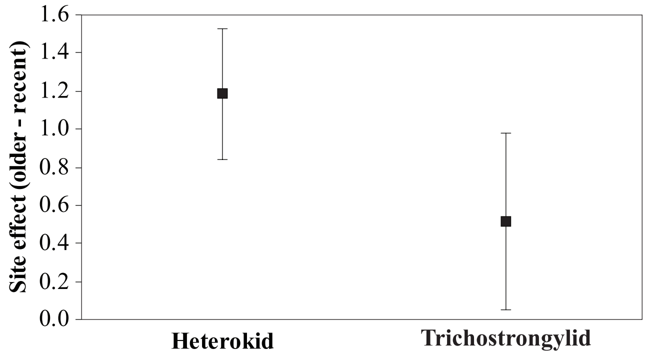

FIGURE 3. Model-averaged effects of duration of habitat use (older–recent) on parasite load in Lesser Snow Geese near La Pérouse Bay, 1994–1995. Ninety-five percent confidence limits account for uncertainty of models used from Table II.

The load of both parasites was substantially greater in birds collected in coastal habitat of the La Pérouse Bay and Cape Churchill region than in birds collected in inland habitat. This is consistent with the pattern found by Gomis *et al.* (1996), who evaluated only trichostrongylids in lesser snow geese from the Tha-Anne River colony located along the west coast of Hudson Bay, approximately 300 km north of our location. There are at least two explanations for this general pattern, and they are not necessarily mutually exclusive. 1) The infective stages of the two nematode species may be more tolerant of or more infective in coastal, salt-marsh habitat than in inland, freshwater marsh habitat. 2) Coastal habitat may harbour higher numbers of the infective eggs or larvae of these nematode species than inland habitat, possibly reflecting the annual or cumulative pattern of use of the landscape by staging and locally nesting lesser snow geese.

Few studies actually have examined environmental effects on survival or infectivity of these nematode parasites. The available data for these (or closely related) species show that trichostrongylids are able to survive and remain infective after 16 weeks at temperatures ranging from -20 °C to + 4 °C (Cram & Cuvillier, 1934; Herlich, 1966), while heterokids can survive up to 230 weeks in the soil and 24 weeks at freezing temperatures (Olsen, 1974). However, the eggs and/or larvae must be kept moist (Shaw, Moss & Pike, 1989). For both parasites, humidity appears to have a greater effect on survival than does temperature (Crofton, 1948), likely reflecting water losses from evaporation across the soft, semi-permeable outer covering of both eggs and larvae (Anderson, 2000). Trichostrongylids appear to be more sensitive to moisture levels than heterokids, and this may be related to the manner in which their larvae infect foraging birds. For example, studies of parasitism of red grouse (*Lagopus lagopus scoticus*) in Scotland found that the infective stage-three larvae migrate to the tips of heather and accumulate in drops of moisture, where foraging grouse encounter and ingest them (Saunders, Tompkins & Hudson, 1999). Infective eggs of heterokids also are acquired during feeding, but through their passive association with forage plants in moist soil.

Coastal portions of this region are dominated by a series of relict beach ridges running parallel to the coast (Dredge & Dixon, 1992). Vegetation in "lows" between successively inland and older beach ridges quickly changes from salt-water plant communities to freshwater communities away from the immediate coastline. The brackish and freshwater communities are dominated by the sedge *Carex aquatilis*. Farther inland, beyond the beach ridges, there is a gentle rise in elevation, and wet sedge meadows, dominated by a string and flark topography, are interspersed with patches of shrubs (primarily *Salix* spp.) often associated with thermokarst lakes (Washburn, 1973). In most years, coastal habitat becomes free of deep-standing melt water and snow before inland habitat, sometimes by as much as two weeks (R. F. Rockwell, unpubl. data). This stems in part from higher amounts of over-winter snow trapped and held by shrubs, which are more prevalent in inland habitat. Habitat with less snow melts earlier in the spring, exposing vegetation and soil, which in turn decreases albedo and leads to more rapid substrate warming and an ever-increasing rate of melt. Surface water drains more slowly from inland habitat because the beach ridges act as barriers, ponding the run-off water in the interior regions.

In spring, the more available coastal habitat, especially the *Carex aquatilis*–dominated low areas between the first few seaward beach ridges, serves as a staging and feeding area for several million lesser snow geese destined to nest at more northern locations as well as the snow geese that nest in the La Pérouse Bay and Cape Churchill region (Abraham & Jefferies, 1997). The birds forage extensively in the coastal habitat, leaving copious amounts of feces (Jefferies, Rockwell & Abraham, 2003). Because these adults carry both of the nematode parasites we found in juveniles (Forbes *et al.,* 1999), they heavily inoculate the coastal habitat with eggs that reach infective stages after approximately 20 (heterokids) to 40 d (trichostrongylids) (Clapham, 1933; Crofton, 1948; Olsen, 1974). These are acquired by goslings foraging during the brood rearing period that starts 4 to 5 weeks after the more northern migrants have left.

By contrast, the more inland habitat is usually unavailable for spring foraging since it is seldom thawed and drained of deep water by the time the millions of migrants have moved further north (R. F. Rockwell, unpubl. data). Some of the 50,000 to 100,000 snow geese nesting in the La Pérouse Bay and Cape Churchill region do forage in the inland habitat once it becomes available in later spring. This likely provides a lower-level inoculation of eggs, which become infective after 20 to 40 d but 1 to 2 weeks later than is the case for more coastal habitat. The reduced parasite load of goslings collected in inland habitat could thus simply reflect delayed and lower levels of infective stages ingested there during brood rearing.

Parasites may have also accumulated over time. As indicated above, both trichostrongylids and heterokids can survive freezing temperatures, although not for extended time periods. Thus, parasite loads could be higher in areas that have been used for longer periods of time. The observed differential pattern of parasite load in coastal *versus* inland habitat is certainly consistent with this possibility, because the use of inland habitat for brood rearing is a recent event in this region (Jefferies, Rockwell & Abraham, 2003). The finding that there are higher parasite loads in coastal habitat that has been used longer (Figure 3) provides additional support for this general explanation. The combination of annual and historic inoculation leads simply to there being more infective stages in coastal habitat when goslings hatch and begin feeding.

The large numbers of transient snow geese moving from the south to more northern nesting colonies are the primary vector for the spring inoculum of eggs of both trichostrongylids and heterokids. The earlier spring availability of coastal habitat leads to its higher early use by these geese, and this in turn leads to higher levels of infective stages in coastal rather than inland habitat. The geese nesting in the La Pérouse Bay region also contribute to the initial coastal load of parasites and continue to do so in both habitats during the brood-rearing period.

Although the transient lesser snow geese are the same species as those geese rearing their broods at La Pérouse Bay, their effect as a vector is identical to the multi-species host models discussed by Morgan *et al.* (2004), highlighting the important point that local host–parasite dynamics must be considered from a broader spatial scale. Our data also support their argument that local patterns and dynamics of parasite loads can be substantially influenced by landscape heterogeneity and environmental variation. In our case, the fact that the landscape itself varies in its reaction to spring melt adds an interesting level of complexity to the pattern and dynamics.

Further insights on those patterns and dynamics and their relation to the population growth of lesser snow geese require delineation of the time course of acquisition of the parasites by juveniles and the spatial distribution of habitat use across the landscape. For example, is the pattern of higher parasite loads in birds using coastal habitat the same for immediately post-hatching or mid-season birds as it is for the older pre-fledging birds? And do all goslings use both coastal and inland habitat over the brood-rearing period, or is the population structured into coastal and inland segments? Finally, what is the actual consequence of a higher load of these parasites on gosling survival? Studies in progress will, we hope, provide this information.

Acknowledgements

We appreciate the help of the many individuals who were involved with the collection of snow geese and tissues used in this work. J. Boles, M. Collins, J. Gleason, D. Kennedy, M. Owen, and C. Witte were especially important in that vein. S. Brault and M. Siddall provided insights on parasites in general and nematodes in particular. K. Abraham, E. Cooch, B. Grand, and B. Jefferies provided useful comments on an earlier draft of this manuscript. This work was supported in part by the Arctic Goose Joint Venture, the Central and Mississippi Flyway Councils, the City University of New York (PSC/CUNY Program), and Wapusk National Park.

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