

Effects of parasitic infections on clutch size of lesser snow geese from a northern breeding colony

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A density-dependent decline in the average clutch size of lesser snow geese (*Anser caerulescens caerulescens*) occurred from 1973 to 1989 at the breeding colony on the shores of La Pérouse Bay, Manitoba. An increase in average parasite load was hypothesized to be one of the two most likely causes of this decline. We shot 28 incubating adult female lesser snow geese at the La Pérouse Bay colony and examined the carcasses for parasites to determine if there was any proximate association between parasitic infections and the size of the clutch a female laid. We found no convincing evidence that parasitic infections were the proximate cause of any reduction in clutch size. In the absence of evidence of any direct effect of parasites, we conclude that an increase in the average parasite load is probably not the cause of the long-term decline in clutch size at La Pérouse Bay. By default, we suggest that increased intraspecific competition for food at the staging areas on the migratory flyway is the most likely cause of the decline in clutch size.

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Nous avons constaté une diminution (sous l'influence de la densité) du nombre moyen d'oisillons par couvée chez les Petites Oies blanches de la colonie reproductrice des côtes de La Pérouse Bay, Manitoba, de 1973 à 1989. L'augmentation du fardeau moyen de parasites semble être l'une des deux causes les plus probables de cette diminution. Nous avons tué au fusil 28 femelles adultes couveuses dans la colonie et en avons examiné les carcasses dans le but d'y dénombrer les parasites et déterminer ainsi s'il y a une association directe entre les infections de parasites et le nombre d'oeufs par couvée. Les résultats ne nous permettent pas de conclure que les infections de parasites sont la cause immédiate de la réduction du nombre d'oeufs. En l'absence de preuve, nous devons conclure qu'une augmentation du fardeau moyen de parasites n'est probablement pas la cause de la diminution à long terme du nombre d'oeufs par couvée à La Pérouse Bay. Peut-être est-ce alors la compétition intraspécifique pour la nourriture dans les zones d'étape le long des voies de migration qui entraîne cette diminution.

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Introduction

A density-dependent decline in the average clutch size of lesser snow geese (*Anser caerulescens caerulescens*) occurred from 1973 to 1989 at the breeding colony on the shores of La Pérouse Bay, Manitoba (58°4'N, 94°4'W; Cooch et al. 1989, 1991). Cooch et al. (1989) reviewed the possible causes and were able to rule out all but two: increased parasite loads, and (or) increased intra-specific competition for food.

Parasites affect reproduction in various avian hosts. Probably the most well-documented association involves the cecal nematode *Trichostrongylus tenuis* and red grouse (*Lagopus lagopus scoticus*) in Britain. Potts et al. (1984) demonstrated a negative correlation between the logarithm of the number of *T. tenuis* per bird and the breeding success of adult red grouse. Moreover, Hudson (1986) determined that red grouse treated with an anthelmintic to reduce infections of *T. tenuis* produced significantly more young per female than did an untreated control group.

Rainnie (1983) observed significant lesions associated with *T. tenuis* in lesser snow goose goslings collected from La Pérouse Bay in late summer. Unfortunately, Rainnie (1983) did not examine adult females in the spring for evidence of *T. tenuis* infections and so could not evaluate the effect of *T. tenuis* infections on clutch size. Nonetheless, the

well-established negative relationship between *T. tenuis* infection and reproduction in red grouse led us to expect a similar relationship among lesser snow geese.

We investigated the effects of parasitic infections on the size of clutches laid by individual lesser snow geese at La Pérouse Bay. This is the first step in determining whether an increase in the average parasite load could be the cause of the long-term decline in clutch size at La Pérouse Bay.

Methods

Geese

General field methods regarding the collection of data on snow goose ecology at La Pérouse Bay are described in Finney and Cooke (1978).

Twenty-eight incubating adult female lesser snow geese were shot while they were on or near their nests, from 2 to 14 June 1989. Data on failed nesters and nonbreeders would have been useful for our purposes; however, such individuals move away from the main part of the colony (Ankney and MacInnes 1978) or depart altogether (Abraham 1980) and could not be collected. We chose to collect females during incubation rather than prior to or during egg laying because we wanted data on egg size for other purposes and because we wanted data on the history of each nest (see below). The 28 females we selected were from a larger group for which complete nest histories were available. Two criteria were used in determining which females to collect. Firstly, we collected a sample of females demonstrating the full range of possible clutch sizes, 2–6 eggs, in

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TABLE 1. Intensity and prevalence of parasitic infections, and site in host, in 28 incubating adult female lesser snow geese collected from La Pérouse Bay, Manitoba, between 2 and 14 June 1989

Parasite species	Intensity ^a		Prevalence (% infected)	Site in host
	Median	Range		
Nematodes				
<i>Amidostomum anseris</i>	2	1-7	75	Gizzard
<i>Amidostomum spatulatum</i>	15	3-35	100	Gizzard
<i>Epomidiostomum crami</i>	15	2-39	100	Gizzard
<i>Heterakis dispar</i>	5	1-518	82	Ceca
<i>Trichostrongylus tenuis</i>	74	1-242	100	Ceca
Trematodes				
<i>Notocotylus attenuatus</i>	15	1-220	86	Ceca
Protozoans				
<i>Sarcocystis</i> sp.	—	—	29	Pectoral muscle

^aNumber of individual parasites per infected host.

lesser snow geese (Rockwell et al. 1987). Secondly, to control for the effects of laying date on clutch size (Hamann and Cooke 1989), we chose only females that had initiated laying within 48 h of each other, on either 31 May or 1 June.

Approximately 20% of the nests at La Pérouse Bay contain eggs that have been "dumped" into the nest by other geese (Lank et al. 1989). Consequently, it is preferable to judge clutch size by the number of postovulatory follicles in each bird's ovaries, rather than from the number of eggs in the nest (Ankney and MacInnes 1978). However, identification of postovulatory follicles becomes more difficult the longer a female has been incubating, and 5 of the 28 females were more than a week into incubation at the time they were killed. The number of postovulatory follicles could be identified with complete certainty in 14 of the 28 females. In the remaining cases we determined clutch size using two sources of information: (i) the number of follicles, both obvious and questionable ones, and (ii) the nest history. The minimum clutch size for an individual was set by the number of obvious follicles, while the maximum clutch size was set by the number of obvious follicles plus the number of questionable ones. Within these limits the actual clutch size was equated with the number of eggs in the nest at the completion of laying (Ankney and MacInnes 1978), unless the nest history revealed obvious evidence of egg dumping. Obvious evidence of egg dumping included: (i) multiple eggs found in a nest in 1 day; (ii) eggs found outside the nest cup; (iii) eggs laid in the nest after none had been laid for 2 days, and (iv) eggs laid in the nest 2 or more days after the onset of incubation (Lank et al. 1989).

Parasites

Blood smears were prepared from each of the birds within 30 s of death (see Bennett 1970). Smears were air-dried, then fixed in 100% methanol. Smears were later stained with Wright's solution and scanned for hematozoa. Scanning involved 30 fields at 40× power, using light microscopy.

Necropsies followed the procedures of Wobeser and Spraker (1980). The gizzard, both ceca, and both kidneys were removed intact for detailed examination. Tissues selected for histopathological examination were fixed in 10% neutral buffered formalin (NBF), processed by standard histological techniques, sectioned at 5 μm thickness, and stained with hematoxylin and eosin (H&E). Tissues included pectoral muscle, heart, liver, lung, esophagus, proventriculus, pancreas, duodenum, jejunum (at Meckel's diverticulum), ileum, and adrenal glands.

Examination of the gizzard followed the procedures of Tuggle and Crites (1984). A single 1 cm thick transverse section was removed from both ceca at approximately the midpoint and fixed in 10% NBF for histopathological examination. Each cecum was opened and the contents were scraped out using the edge of a microscope slide. Contents were mixed with tap water and strained through a 250-μm mesh. Material retained in the mesh was rinsed into a dissecting dish and five drops of Lugol's iodine solution were added. After 20 min,

TABLE 2. Correlations of clutch size and intensity of six of the parasite species observed in female lesser snow geese, using Spearman's rank correlation coefficient

Parasite species	Clutch size	
	r_s	P
Nematodes		
<i>Amidostomum anseris</i>	0.446	0.046
<i>Amidostomum spatulatum</i>	0.027	0.890
<i>Epomidiostomum crami</i>	0.095	0.622
<i>Heterakis dispar</i>	-0.145	0.496
<i>Trichostrongylus tenuis</i>	-0.109	0.570
Trematodes		
<i>Notocotylus attenuatus</i>	0.016	0.940

NOTE: The intensity of protozoan infections cannot be determined, so no similar analysis involving *Sarcocystis* sp. was possible. Statistical significance was set at $P \leq 0.005$.

three drops of 10% aqueous sodium thiosulphate solution were added, and the contents of the dish were immediately examined for helminths with the aid of a dissection microscope. The left kidney from each bird was fixed in 10% NBF, while the right kidney was preserved in 2.5% aqueous potassium dichromate solution. Four 5 μm thick, H&E-stained transverse sections of the left kidney were examined microscopically for the presence of coccidia and (or) associated pathology. The right kidney was examined for oocysts of renal coccidia by means of simple flotation (Gajadhar et al. 1983).

Terminology for parasite ecology used in this paper follows the recommendations of Margolis et al. (1982). Intensity is the number of individual parasites per infected host, and prevalence refers to the proportion of infected hosts in the host population.

Statistical analyses

Using the standardized Morisita index of dispersion (Krebs 1989) we found that for several of the species of parasites we observed, the distribution among hosts deviated significantly from randomness. Because of the nonrandom distribution of parasites, we used Spearman's rank correlation coefficient (Siegel and Castellan 1988) to examine the correlations between parasite intensities and clutch size. We compared clutch sizes between infected (parasite present) and uninfected (parasite absent) hosts for each species of parasite using the Student's t test, since clutch size was randomly distributed. Overall, there were 10 correlations and comparisons. We used the Bonferroni procedure (Keppel and Zedeck 1989) of dividing α (traditionally $\alpha = 0.05$) by the total number of tests to determine the critical level of significance. Consequently, statistical significance was set at $P \leq 0.005$.

TABLE 3. Comparisons of clutch size in infected (parasite present) and uninfected (parasite absent) female lesser snow geese for four of the parasite species observed, using Student's *t* test

Parasite species	Prevalence	Clutch size		Comparison	
		Mean	SE	<i>t</i>	<i>P</i>
Nematodes					
<i>Amidostomum anseris</i>	Present	4.14	0.21	0.982	0.335
	Absent	3.71	1.11		
<i>Heterakis dispar</i>	Present	3.83	0.20	-2.628	0.014
	Absent	5.00	0.32		
Trematodes					
<i>Notocotylus attenuatus</i>	Present	4.08	0.20	0.610	0.547
	Absent	3.75	0.63		
Protozoans					
<i>Sarcocystis</i> sp.	Present	3.88	0.35	-0.531	0.599
	Absent	4.10	0.23		

NOTE: Prevalence of the other three parasite species observed was 100% (Table 1), so no similar analysis was possible for these species. Statistical significance was set at $P \leq 0.005$.

Results

Seven species of parasites were present in the incubating female lesser snow geese we examined (Table 1). The median intensity, rather than the mean, is presented in Table 1, since the median is a better indicator of central tendency in nonrandom distributions (SoKal and Rohlf 1981). The intensity of *Sarcocystis* sp. infections is not reported in Table 1 because it is not possible to determine the intensity of protozoan infections. No hematozoa were found. Significant lesions were only found associated with the three species of gizzard nematodes: *Amidostomum anseris*, *Amidostomum spatulatum* and *Epomidiostomum crami*. The lesions have been described (Clinchy 1990) and resemble published descriptions (Tuggle and Crites 1984). There were no gross lesions associated with *T. tenuis* or any of the other parasites.

We found no significant associations between either the intensity (Table 2) or prevalence (Table 3) of parasitic infections and clutch size.

Discussion

We found no convincing evidence that parasitic infections were the proximate cause of a reduction in the size of clutches laid by female lesser snow geese at the La Pérouse Bay breeding colony.

In the absence of the Bonferroni correction, the correlation between the intensity of *A. anseris* and clutch size (Table 2) would have been judged to be significant, using a critical value of $P = 0.05$. Even if this correlation had been deemed to be statistically significant, however, the correlation is a positive one (Table 2) and could not, therefore, be the cause of a reduction in clutch size. The absence of an effect of infection with gizzard nematodes (*A. anseris*, *A. spatulatum*, and *E. crami*) is surprising because (i) all lesser snow geese appear to be infected all the time (McDonald 1969; Rainnie 1983; Tuggle and Crites 1984; this study), and (ii) infections are always associated with significant lesions (Rainnie 1983; Tuggle and Crites 1984; this study).

As with *A. anseris*, the relationship between the prevalence (presence or absence) of *Heterakis dispar* and clutch size would have been deemed significant in the absence of the Bonferroni correction. Yet, as with *A. anseris*, even if this relationship had been found to be statistically significant, there would still be doubt as to whether this was a causal

relationship, for at least two reasons. Firstly, no gross lesions were associated with *H. dispar* in the birds examined in the present study, nor has *H. dispar* ever been cited as the cause of significant pathology among waterfowl (McDonald 1969; Wobeser 1981). Secondly, although the prevalence of *H. dispar* may have borne a relationship to clutch size (Table 3), the intensity of *H. dispar* definitely did not (Table 2). It is unlikely that the simple presence of an infection could affect clutch size while the size of infection has no effect.

Our expectation that *T. tenuis* infections might demonstrate some association with reproduction in lesser snow geese was not confirmed. More surprising was the complete absence of infections of renal coccidia, *Eimeria* sp. Rainnie (1983) reported a 55% prevalence of *Eimeria* sp. infections among incubating adult female lesser snow geese collected at La Pérouse Bay in 1981. Such interannual variability does not appear to be unusual, since Gajadhar et al. (1983) reported a 5% prevalence of *Eimeria* sp. infections in spring (April–June) among adult lesser snow geese collected in southern Saskatchewan in 1980, compared with a prevalence of 46% among adults collected in the same vicinity in the spring of 1982. As regards the potential proximate effects of *Eimeria* sp. infections on clutch size, Rainnie (1983) observed only very mild lesions associated with *Eimeria* sp. in adult geese and concluded that such effects would be of little significance to the host. Rainnie did not know the size of the clutches laid by the females he examined and so could not evaluate whether *Eimeria* sp. infections had any effect on clutch size. We think it unlikely that we would have found a significant association between *Eimeria* sp. infections and clutch size, even if *Eimeria* sp. infections had been found in our sample, given Rainnie's observations on the absence of adverse effects.

Failing to find a proximate effect of parasitic infections on host reproduction or survival is analogous to failing to find any evidence that a particular predator eats a particular prey. In the absence of such evidence, it is difficult to see how the predator could have any effect on the prey population, or analogously, how parasites could have any effect on the host population. Consequently, we conclude that an increase in the average parasite load is probably not the cause of the long-term decline in clutch size at La Pérouse Bay. We suggest that increased intraspecific competition for food at the

staging areas on the migratory flyway is the most probable cause of the decline in clutch size at La Pérouse Bay because, with the addition of our results, which argue against any direct role for parasites, all other alternatives have been ruled out (see review by Cooch et al. 1989).

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