RESEARCH ARTICLE

Diet and reproductive success of an Arctic generalist predator: Interplay between variations in prey abundance, nest site location, and intraguild predation

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ABSTRACT

Under varying prey abundance, generalist consumers should be less affected than specialists due to their more diverse diet. Nonetheless, when prey availability declines, interspecific competition among consumers should increase and could lead to increased intraguild predation. We examined these potential effects in a generalist predator of the tundra, the Glaucous Gull (*Larus hyperboreus*), over a 7-yr period characterized by large fluctuations in lemming abundance, a potential prey item for gulls. We studied diet by analyzing regurgitated pellets collected at nests and blood nitrogen and carbon stable isotopes, and we monitored annual nesting density and reproductive success on Bylot Island, Nunavut, Canada. Stable isotopes revealed a relatively similar contribution of terrestrial and marine food sources to the gull diet, although the terrestrial contribution increased in the year of high lemming abundance. According to analysis of pellets, diet during incubation was dominated by geese and lemmings, whereas geese were the main prey during chick-rearing. As expected for a generalist predator, annual variation in diet during incubation reflected overall lemming abundance, and the increased consumption of geese during chick-rearing was associated with an influx of goose families into the study area at that time. Gull nest density, laying date, clutch size, and mass gain of chicks did not vary with lemming population fluctuations. Hatching success, on the other hand, was positively related to lemming abundance and was greater for nests located on islets than for those along the shores of ponds and lakes. Intraguild predation on gull eggs by predators such as Arctic foxes, which primarily feed on lemmings during the summer, was probably the main cause of nest failure. Although a generalist predator like the Glaucous Gull has a diversified diet and may feed only opportunistically on lemmings, our results suggest that large cyclical fluctuations in lemming abundance may still affect gull reproductive success through intraguild predation.

Keywords: Arctic, diet, generalist predator, Glaucous Gull, intraguild predation, lemming abundance, nest site location

Régime alimentaire et succès reproducteur d'un prédateur généraliste de l'Arctique: interaction entre des variations dans l'abondance de proies, la localisation du site de nidification et la prédation intra-guilde

RÉSUMÉ

Lorsque soumis à une abondance variable de proies, les consommateurs généralistes devraient être moins affectés que les spécialistes à cause de leur régime alimentaire plus varié. Toutefois, lorsque la disponibilité des proies diminue, la compétition interspécifique entre les consommateurs devrait augmenter et ceci pourrait conduire à une augmentation de la prédation intraguilde. Nous avons examiné ces effets potentiels chez un prédateur généraliste de la toundra, *Larus hyperboreus*, sur une période de sept ans caractérisée par de grandes fluctuations d'abondance des lemmings, une proie potentielle des goélands. Nous avons étudié le régime alimentaire en analysant des boulettes de régurgitation récoltées aux nids et des isotopes stables d'azote et de carbone dans le sang. Nous avons également suivi la densité annuelle de nids ainsi que le succès reproducteur à l'Île Bylot, Nunavut, Canada. Les isotopes stables ont révélé que la contribution des ressources alimentaires terrestres et marines au régime alimentaire des goélands était relativement similaire même si la contribution terrestre a augmenté l'année où l'abondance des lemmings était élevée. Le régime alimentaire basé sur les boulettes de régurgitation était dominé par des oies et des lemmings durant l'incubation alors que les oies représentaient la principale proie lors de la période d'élevage des jeunes. Tel qu'attendu pour un prédateur généraliste, les variations annuelles du régime alimentaire pendant l'incubation ont reflété l'abondance globale de lemmings alors que l'augmentation dans la consommation d'oies pendant l'élevage des jeunes

était associée avec l'arrivée des familles d'oies dans l'aire d'étude à cette période de l'été. La densité de nids de goélands, la date d'initiation, la taille de ponte et le gain de poids des jeunes n'ont pas varié selon les fluctuations d'abondance des lemmings. Par contre, le succès d'éclosion était positivement relié à l'abondance de lemmings et il était plus élevé pour les nids situés sur des îlots que ceux situés sur le bord d'étangs ou de lacs. La prédation intraguilde des œufs de goélands par des prédateurs comme les renards arctiques, lesquels s'alimentent principalement de lemmings durant l'été, serait probablement la principale cause d'échec des nids. Même si un prédateur généraliste comme *L. hyperboreus* possède un régime alimentaire diversifié et peut s'alimenter de lemmings de façon opportuniste, nos résultats suggèrent que les grandes fluctuations cycliques d'abondance de cette proie peuvent tout de même affecter le succès reproducteur des goélands via la prédation intraguilde.

Mots-clés: Arctique, régime alimentaire, prédateur généraliste, *Larus hyperboreus*, prédation intraguilde, abondance de lemmings, localisation du nid

INTRODUCTION

Under varying prey abundance, generalist consumers, i.e. species that feed on a large variety of prey, tend to fluctuate less in abundance than specialists, i.e. species that feed on a small number of prey species (MacArthur 1955, Holling 1959, Andersson and Erlinge 1977, Petchey 2000). Indeed, the large array of potential resources available to generalists makes any single prey less influential on the consumer if it disappears. Weak aggregative and reproductive numerical responses (variations in the number of individuals or offspring produced, respectively), but strong functional responses (variation in diet and consumption rate), are thus expected for generalists facing large temporal variations in the abundance of some of their prey (Solomon 1949, Holling 1959).

When overall prey availability declines, interspecific competition among consumers should increase and could lead to increased intraguild predation (predation on potential competitors; Polis et al. 1989, Lindström et al. 1995, Palomares and Caro 1999, Tannerfeldt et al. 2002), with potentially important consequences for the population dynamics of the species involved. Indeed, intraguild predation has been shown to reduce population growth (Linnell and Strand 2000) or to restrict the distribution of the inferior species (Durant 1998) in a variety of situations. Empirical evidence regarding the occurrence or the effects of intraguild predation nonetheless remains limited, especially in vertebrates.

Strong predator–prey interactions are a common feature of several food webs and this is particularly true in the Arctic tundra (Gilg et al. 2006, Legagneux et al. 2012, Therrien et al. 2014). Herbivorous small mammals, which are well-known for their large, multiannual, cyclical fluctuations in abundance (Ims and Fuglei 2005), are major prey species for a diverse suite of avian and mammalian predators across much of the tundra (Gauthier et al. 2011). This large interannual variability in prey abundance can have a strong, direct influence on predators that feed heavily during reproduction on cyclical prey (Gilg et al. 2006, Schmidt et al. 2012, Therrien et al. 2014). However, previous studies that examined these interactions in the tundra food web primarily focused on the numerical and functional responses of specialist predators and paid little attention to generalist predators or to the possible occurrence of intraguild predation in response to variations in prey abundance.

The Glaucous Gull (*Larus hyperboreus*) is a widespread predator of the tundra ecosystem during the summer and can be defined as a true generalist, considering its broad diet (Barry and Barry 1990, Schmutz and Hobson 1998, Samelius and Alisauskas 1999). In the Arctic, breeding Glaucous Gulls are often associated with seabird or goose colonies and are known to feed on the eggs and especially the chicks of these species (Barry and Barry 1990, Samelius and Alisauskas 1999, Bowman et al. 2004). Nonetheless, small mammals such as lemmings are also a potentially important prey for Glaucous Gulls, especially when abundant. However, conflicting information is available regarding the importance of rodents in the diet of gulls (Strang 1982, Barry and Barry 1990, Samelius and Alisauskas 1999, Weiser and Powell 2011, Weiser and Gilchrist 2012). Interannual variation in the contribution of small mammals to the Glaucous Gull diet has been observed in Alaska, but without concomitant information on variation in small mammal abundance, gull density, and gull reproductive success (Schmutz and Hobson 1998). Therefore, little is known about the functional and numerical responses of gulls to variations in lemming abundance. The reproductive success of gull species breeding outside the Arctic is sometimes affected by food availability (Chudzik et al. 1994, Bukacińska et al. 1996, Oro et al. 1996), although the underlying causes (e.g., chick starvation, competition, and/or predation) remain unclear.

We investigated the effects of large interannual fluctuations in lemming abundance on the diet and reproductive success of Glaucous Gulls over a 7-yr period in the Canadian Arctic. Because our studied population nests near a large Snow Goose (*Chen caerulescens*) colony, geese and lemmings represent 2 important food sources for gulls in this area. We first hypothesized that, as a generalist predator, gulls would exhibit little resource selection; therefore, the importance of lemmings in their diet would vary annually according to fluctuations in lemming

abundance. Because gulls can rely on other prey when lemmings are scarce, we further hypothesized that gulls would exhibit little annual variation in breeding density (i.e. weak aggregative numerical response) and in components of their reproductive success, such as laying date, clutch size, and chick growth. Because Glaucous Gull nests can be depredated by competitors like the Arctic fox (*Vulpes lagopus*), which feeds heavily on lemmings during the summer (Elmhagen et al. 2000, Giroux et al. 2012), we hypothesized that hatching success would be reduced due to intraguild predation in years of low lemming abundance. However, because several gulls in our study area nest on islets in ponds, we expected that predation would be reduced for those individuals compared with gulls that nest on the open tundra, as the former sites should provide a refuge from foxes.

METHODS

Study Site and Species
This study took place from 2005 to 2011 on Bylot Island (Nunavut, Canada; 73°N, 80°W) in a 30 km^2 portion of the Qarlikturvik Valley, a wide and relatively flat valley that opens to the sea. The valley is dominated by a mosaic of mesic tundra and wet polygons interspersed with small lakes and ponds (see Gauthier et al. 2011 for more details). Glaucous Gulls do not form colonies and nest in a dispersed fashion across the study area, but always in association with ponds or small lakes (mostly ≤0.1 km^2). The study site was located ≥20 km north of a large Greater Snow Goose (*Chen caerulescens atlanticus*) nesting colony (~20,000 pairs). Shortly after hatching in early July, goose families disperse outside their colony and a large number use our study site during brood-rearing due to the abundance of wetlands, their feeding habitat (Mainguy et al. 2006). Live (or dead) goslings then become an important potential prey for gulls. Brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings are present and show high-amplitude population cycles with a 3–4 yr periodicity (Gruyer et al. 2008), especially for the brown lemming (>60-fold difference between high and low years). Passerines (primarily Lapland Longspurs [*Calcarius lapponicus*]), shorebirds (*Pluvialis* and *Calidris* spp.), Rock Ptarmigan (*Lagopus muta*), sea ducks (*Somateria* spp. and Long-tailed Ducks [*Clangula hyemalis*]), freshwater fishes (Arctic char [*Salvelinus alpinus*]), and several terrestrial arthropod families (mostly Araneae, Muscideae, Chironomideae, Tipulideae, Carabideae, and Apideae; Bolduc et al. 2013) represent other potential prey species present in the study site. Along the seashore, marine invertebrates in small pools and live or dead fishes could also constitute potential prey. The nearest garbage dump is located near Pond Inlet (Baffin Island, Nunavut), >85 km from the study area. Potential

predators of gull nests and chicks include the Arctic fox, Long-tailed and Parasitic jaegers (*Stercorarius longicaudus* and *S. parasiticus*), the Common Raven (*Corvus corax*), and the polar bear (*Ursus maritimus*).

Main Prey Abundance
We assessed goose abundance and the timing of arrival of families in the study area each year by counting goose feces in 12 transects measuring 1 × 10 m and marked with small pegs in the wet tundra polygons of the study site, preferred goose brood-rearing habitat (Hughes et al. 1994). All old feces were initially removed in mid-June. Feces were subsequently counted at 2-week intervals (early, mid, and late July, and mid-August).

We measured lemming density during the snow-free period each year using live trapping in 2 grids (11 ha each) spaced 2 km apart. One grid was located on a hillside dominated by mesic tundra and the other was in an area dominated by wet habitat in the valley lowlands. Each grid had 144 Longworth traps (Rogers Manufacturing, Kelowna, BC, Canada) set 30 m apart, and traps were opened for 3 or 4 consecutive days during each trapping period; traps were checked at 12-hr intervals. We conducted 3 trapping sessions each summer (mid-June, mid-July, and mid-August), and lemmings were individually marked with PIT tags before release (see Gruyer et al. 2010 for details). We estimated the density of each species in each trapping session using mark–recapture techniques with program DENSITY 4 (Efford 2004). When the number of captured individuals was too low for analysis in DENSITY (i.e. <4 individuals), we used the minimum number known to be alive and divided this number by the effective trapping area (Bilodeau et al. 2013). We averaged the combined densities of both species across the 2 grids for each corresponding trapping session in order to have a global measure of lemming abundance.

Gull Nest Monitoring
The Glaucous Gull breeding season on Bylot Island extends from early June to mid-August. We systematically searched the entire study area for gull nests in June of all years. Glaucous Gulls in our area typically nest on small islands (never more than 1 pair per island) or along the shores of lakes and ponds. Nests are easy to find because they are conspicuous, located on elevated mounds, reused year after year, and gulls often reveal their presence from a relatively long distance away through alarm calls and behavioral displays. We recorded in the field whether a nests was located on an islet or on the shore of a pond and marked its position with a GPS receiver; we later calculated the distance of each nest to the seashore using GIS software (ArcGIS; ESRI, Redlands, California, USA). We estimated nest density by dividing the total number of nests found annually by the size of the study area. We visited nests at

weekly intervals to check their contents and to look for signs of predation (e.g., egg disappearance or broken eggshells). Leaving broken eggshells near the nest is typical of some avian predators (e.g., jaegers). From 2006 to 2008, we also deployed automated cameras at some nests during incubation and chick rearing to identify nest predators.

Laying date was defined as the date that the first egg was laid. For nests found after the completion of laying, we back-calculated the laying date from the hatching date by assuming that eggs were laid every other day, that the incubation period lasted 27 days, and that incubation started with the first egg (Weiser and Gilchrist 2012). We defined total clutch size as the largest number of eggs found in a nest after the start of incubation, and hatching success as the proportion of nests that hatched at least 1 egg. We calculated success on a per-nest basis, rather than per egg, because most eggs disappeared in nests that failed totally (see Results). Sample sizes vary among different components of reproductive success because we did not have all information for all nests. In 2007 and 2008, at each visit after hatching, individually marked chicks were weighed to the nearest 10 g using 1- or 3-kg spring scales.

Diet Determination

During weekly nest visits from 2005 to 2008, we collected all regurgitated pellets surrounding gull nests. We air-dried and dissected pellets individually and identified all prey remains to the lowest taxonomic level possible. We counted the minimum number of prey items consumed based on the number of jaws, skulls, leg bones, or pairs of otoliths, and the frequency of occurrence of prey based on the presence of feathers, hairs, bones, shell fragments, scales, exoskeletons, and claws. We pooled all prey items found in pellets into 4 categories: lemmings, geese, aquatic prey (freshwater and marine fishes, marine invertebrates, and marine mammals), and other prey (passerines, shorebirds, ducks, arthropods, and all remaining unidentified prey). We did not consider garbage (e.g., fishing lines and string), vegetation, and rocks in the analyses, as their overall frequency of occurrence was 5% and these items were probably ingested accidently. We separated the breeding season into 2 time periods, before and after the hatching date of chicks at individual nests. We calculated the frequency of occurrence of food items based on individual pellets. We calculated the mean proportion of each food item (using the minimum number of prey items retrieved per pellet) based on individual nests.

In order to reduce biases associated with diet assessment from pellet analysis, we also used stable isotopes to determine gull diet (Kelly 2000). We captured 3 and 6 adult gulls on their nests during the late incubation period in 2007 and 2008, respectively, with a bownet trap. We also captured by hand 9 and 19 chicks at their nests in 2007 and 2008, respectively, including 5 chicks twice (average age at

capture: 12 days; range: 1–34 days). We collected 1 ml of blood from the ulnar or medial metatarsal vein of captured birds. We also collected samples of potential prey items from 2006 to 2009 to determine their isotopic compositions. These included Snow Goose eggs and goslings, brown and collared lemmings, passerines, freshwater and marine fishes, and terrestrial arthropods (9 different families). All samples were preserved in 70% ethanol until analysis. In the laboratory, samples were frozen at −20°C, freeze-dried or oven-dried at 60°C (>48 hr), and then powdered using a mortar and pestle. Because $\delta^{13}C$ typically differs between lipid and nonlipid tissues (Therrien et al. 2011), we removed lipids from samples from vertebrates to reduce biases in estimating diet (Tarroux et al. 2010). Lipid extractions were done through successive rinsing of powdered samples with 2:1 chloroform:methanol as a solvent following Tarroux et al. (2010). We encapsulated ~0.220 ± 0.001 mg of all samples into tin capsules. Carbon and nitrogen stable isotopes were analyzed by the Stable Isotopes in Nature Laboratory, University of New Brunswick, Fredericton, New Brunswick, Canada (see Therrien et al. 2011 for details). Stable isotope ratios are expressed as δ values and are measured as parts per thousand (‰) difference relative to international standards:

$$\delta X = \left[R_{sample}/R_{standard}) - 1 \right] \times 1000,$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Bond and Hobson 2012). Accuracy was determined with measurements of a commercially available standard (Nicotinamide; Elemental Microanalysis, Okehampton, Devon, UK). Target ratios were $\delta^{13}C = -34.2‰$ and $\delta^{15}N = -1.8‰$, and mean ± SD measured values were $\delta^{13}C = -34.2 \pm 0.1‰$ and $\delta^{15}N = -1.8 \pm 0.1‰$ ($n = 22$).

To reconstruct the diet with isotope mixing models, we used discrimination factors determined for Ring-billed Gulls (*Larus delawarensis*; −0.3‰ for ^{13}C and +3.1‰ for ^{15}N) by Hobson and Clark (1992). We accounted for the fact that these coefficients were determined in growing chicks by increasing the mean value for $\delta^{15}N$ discrimination by 0.55‰ for adults (Sears et al. 2009, Weiser and Powell 2011). However, small errors in discrimination factors due, for instance, to a mixed diet have the potential to bias mixing model output (Bond and Diamond 2011). To assess the robustness of our diet proportion estimates to these potential biases, we ran our mixing models with other parameterizations. First, we ran models with similar discrimination factors for both young and adults, using the values given in Hobson and Clark (1992), and secondly, we used the values (+1.5‰ for ^{13}C and +3.7‰ for ^{15}N) reported in Weiser and Powell (2011).

Climatic Data

As climatic factors are known to influence reproduction in birds, especially in Arctic breeders (Stenseth et al. 2002),

TABLE 1. List of the covariates tested for each dependent variable examined in relation to diet and reproduction of Glaucous Gulls on Bylot Island, Nunavut, Canada, in 2005–2011. Period = before and after hatching of Glaucous Gull chicks; Lemm = lemming abundance; Geese = Greater Snow Goose abundance (based on feces count); Habitat = nesting habitat (on islet or shore of ponds); Nest = nest ID; Age = chick vs. adult; Indivisual/Nest = individual young nested within the nest ID; NAO = North Atlantic Oscillation; Temp = average air temperature.

Dependent variable	Covariates [a]	Random factor	Sample size [b]
Diet proportion using pellets [c]	Period; Year; Lemm; Geese; Habitat	Nest	74 (17)
Blood stable-isotope ratio	Date [d]; Year; Age	Individual/Nest	42 (13)
Gull nest density	NAO; Lemm; Temp	None	7 yr
Laying date (Lay)	NAO; Lemm; Temp; Habitat	Nest	47 (25)
Total clutch laid (TCL)	NAO; Lemm; Temp; Habitat; Lay	Nest	47 (25)
Hatching success	NAO; Lemm; Temp; Geese; Lay; Habitat	Nest	87 (33)
Chick growth	NAO; Lemm; Temp; Geese; Habitat; Lay; TCL	Individual/Nest	42 (13)

[a] The appropriate periods (June, July, or August) for lemming abundance, goose abundance, NOA, and temperature were selected for each dependent variable. For instance, for gull nest density, laying date, and total clutch laid, June values were used; for hatching success, June and July values were used, etc.
[b] The numbers in parentheses refer to the number of different nest sites.
[c] Analyses were performed on the following prey categories separately: lemmings, geese, aquatic, and other (see Figure 1 for details).
[d] Day of the year, standardized as follows: $x_{stand} = (x_i - \bar{x})/\sigma$.

we controlled for climatic conditions when analyzing annual variation in breeding parameters. Local climatic factors thought to be important during the gull nesting period are air temperature and timing of snowmelt in spring, which is highly correlated with June temperature (Dickey et al. 2008). We used climatic data from an automated weather station installed at our study site (20 m above sea level; CEN 2014). From these data, we extracted monthly average temperatures for June, July, and August. We also used the North Atlantic Oscillation (NOA) index as a global climatic index because the NAO has been found to affect the reproduction of other species at our study site (Morrissette et al. 2010). The NAO is a major source of atmospheric mass balance measured as the mean deviation in average sea-level pressure between the sub-Arctic and subtropical Atlantic (Hurrell 1995, Stenseth et al. 2002). High NAO values on Bylot Island are associated with cold temperatures in spring (Morrissette et al. 2010). We obtained monthly NAO indices for June, July, and August from the Climate Prediction Center of the National Weather Service (http://www.cpc.ncep.noaa.gov).

Statistical Analyses

We analyzed the effects of various covariates (Table 1) on dietary proportions in regurgitated pellets with generalized linear mixed models (GLMM) in the 'nlme' package in R (Pinheiro et al. 2006) using arcsine-transformed data. Nest ID was treated as a random factor to account for repeated measures of diet at the same nest before and after hatching of gull chicks ('time period' in our analysis) and among years (Pinheiro and Bates 2000). Sample size was used as an offset term to adjust for variable numbers of pellets analyzed per nest in each time period (Pinheiro and Bates 2000). We also used GLMM to analyze the sources of variation in the blood

stable-isotope ratios ($\delta^{13}C$ and $\delta^{15}N$). Given that multiple blood samples were sometimes available for the same individual, we considered individual (nested within the nest ID) as a random effect in the analyses, which resulted in giving the same weight to each individual from different nests and avoided pseudoreplication (Pinheiro et al. 2006). We estimated the contribution of various food sources to the diet with the Bayesian stable isotope mixing model provided in the 'siar' package in R (Parnell et al. 2010). We applied the 'siarsolomcmcv4' function, which runs a Markov chain Monte Carlo (MCMC) on the stable isotope ratios of each individual to determine its dietary habits. We incorporated no prior information. The isotopic signatures of the sources (prey) were compared using MANOVA pairwise comparisons ('lm' function in R; R Development Core Team 2014), with $\delta^{13}C$ and $\delta^{15}N$ considered as dependent variables.

We analyzed factors affecting most reproductive parameters (laying date, clutch size, hatching success, and chick growth) using GLMM; for gull nest density we used simple regression. Fixed and random effects differed according to the dependent variable tested (see Table 1 for the list of covariates used). Because the same nests were often reused year after year, possibly by the same individuals, we used nest ID as a random factor in the analyses. To minimize the risk of having overparameterized models, we never included at the same time more than one variable for which we had a single annual value (i.e. temperature, NAO, and lemming and goose abundance). These variables were tested in alternative models. We also avoided including variables that were highly correlated in the same model ($r > 0.70$; see Appendix Table 2 for the correlation matrix). Models were ranked according to Akaike's Information Criterion corrected for small sample size (AIC$_c$) using the 'AICcmodavg' package in R (Mazerolle 2015). We estimated variability in mass gain of individual
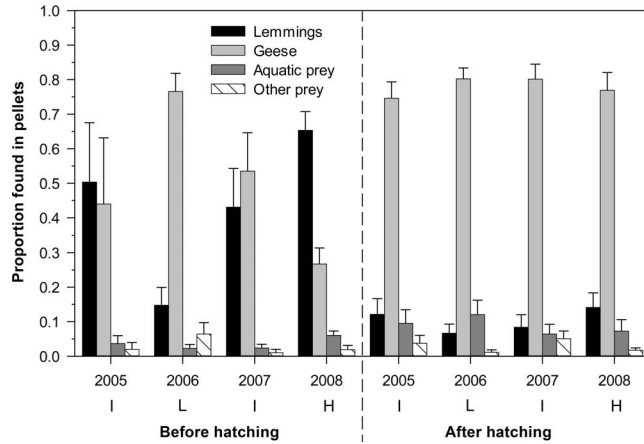
FIGURE 1. Mean proportion (+ SE) of food items, grouped into 4 categories, found in regurgitated pellets collected at Glaucous Gull nests before and after hatching of chicks on Bylot Island, Nunavut, Canada, from 2005 to 2008. Proportions are calculated on a per-nest basis and sample size can be found in Appendix Table 3. Aquatic prey included fishes, marine invertebrates, and marine mammals. Other prey included birds other than geese, terrestrial mammals other than lemmings, and arthropods (full details in Appendix Table 3). An index of lemming abundance based on live trapping data is indicated below each year: L = low, I = intermediate, and H = high lemming abundance.

chicks from the residuals of a Gompertz growth curve relating the mass and age of all measured chicks using the 'Nonlinear Least Squares' package in R (R Development Core Team 2014). The adjusted equation was:

$$\text{Mass} = 1542 \times e^{(-3.18 \times 0.91^{\text{age}})}.$$

All 3 parameters of the equation were highly significant (all $t > 13.0$, all $P < 0.001$). Residuals from this relationship were used as the dependent variable to test for the effect of the different covariates (Table 1). All means are presented with SE, unless otherwise specified. Significance for all statistical analyses was set at $P < 0.05$. Statistical analyses were performed in R version 3.1.1 (R Development Core Team 2014).

RESULTS

Annual Variability in Main Prey Abundance
Annual lemming abundance (both species combined) varied widely from 2005 to 2011 (range of annual density in July: 0.1–6.2 lemmings ha^{-1}; CV = 106%). Our index of goose numbers also varied annually, but to a lesser extent (range of annual cumulative feces density from mid-July to mid-August: 27–111 feces per 10 m^2; CV = 62%).

Diet Determination
   Pellets. Among the 1,405 regurgitated pellets examined, goose and lemming remains were the most frequent items

found. Geese appeared in most pellets collected before hatching of gull chicks and in almost all pellets after hatching, whereas lemming occurrence followed the opposite pattern (Appendix Table 3). Among goose parts found in pellets before hatching, 82% were from goslings or embryos and 18% were from adults; 5% of pellets also included eggshell fragments. After hatching of gull chicks, goslings accounted for 99% of goose parts found in pellets. Of the 2 lemming species, the collared lemming was the more abundant overall (65%).

   The proportions of lemmings and geese found in pellets differed according to the time period ($F_{1,53} = 40.5$, $P < 0.001$ and $F_{1,53} = 26.8$, $P < 0.001$, respectively). Before hatching of gull chicks, both items were found in comparable proportions (except in 2006, when lemming density was very low), but after hatching gull diet was always largely dominated by geese (≥ 0.75; Figure 1). The increased contribution of geese to the diet after hatching of gull chicks occurred as the abundance of geese in the study area swelled rapidly as goose families moved to their brood-rearing areas (median annual hatching date of geese at the colony ranged from July 6 to 11). After mid-July, the rate of goose feces deposition in transects was 2.11 feces per day per 10 m^2, compared with 0.20 before this date (Appendix Figure 2). The overall proportion of geese and lemmings in the diet varied in relation to lemming abundance ($F_{1,53} = 10.0$, $P = 0.003$ and $F_{1,53} = 8.9$, $P = 0.04$, respectively), but the pattern for geese differed between the 2 time periods (interaction of lemming $\times$ period: $F_{1,53} = 4.0$, $P = 0.05$). Before hatching of gull chicks, lemming contribution was highest and goose contribution lowest during the year of high lemming abundance, whereas the opposite pattern was found during the year of low lemming abundance; these effects were absent after hatching (Figure 1). Aquatic food and other prey items were a small proportion of the diet based on pellet analysis (≤ 0.1), and were not influenced by any of the tested covariates (all $F_{1,53} < 2.3$, all $P > 0.15$).

   Stable isotopes. Blood δ^{13}C values were not influenced by year (2007 vs. 2008), date of capture, or age (adult vs. chick; all $F_{1,23} < 2.6$, all $P > 0.12$; total $n = 42$). Blood δ^{15}N values also did not vary according to the date of capture or age ($F_{1,23} < 0.3$, $P > 0.60$), but were slightly lower in 2008 (9.4 ± 0.3) than in 2007 (10.6 ± 0.2; $F_{1,23} = 6.6$, $P = 0.02$; Figure 3). The δ^{15}N and δ^{13}C isotopic signatures of marine fishes, freshwater fishes, and terrestrial prey differed considerably (Figure 3). Even though the isotopic signatures of terrestrial arthropods, lemmings, geese, and passerines also differed significantly from each other (MANOVA: Wilks $\lambda = 0.55$, $F_{3,41} = 4.7$, $P < 0.004$), the relative similarity of their positions on the δ^{15}N vs. δ^{13}C biplot suggested that an isotopic analysis would have low power to discriminate among these sources. We thus pooled all terrestrial prey and ran the multisource isotope
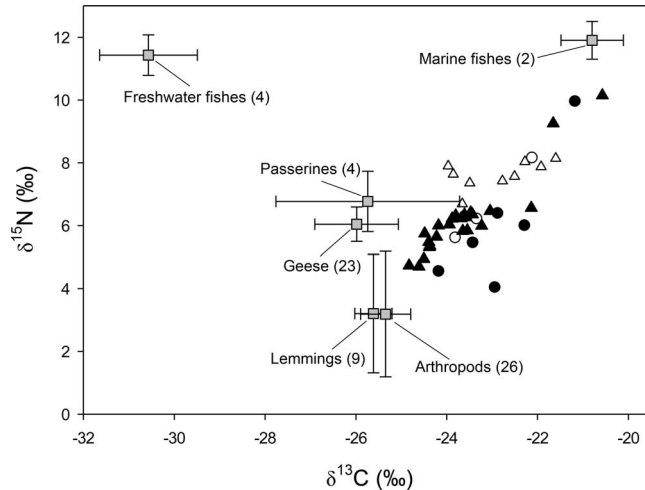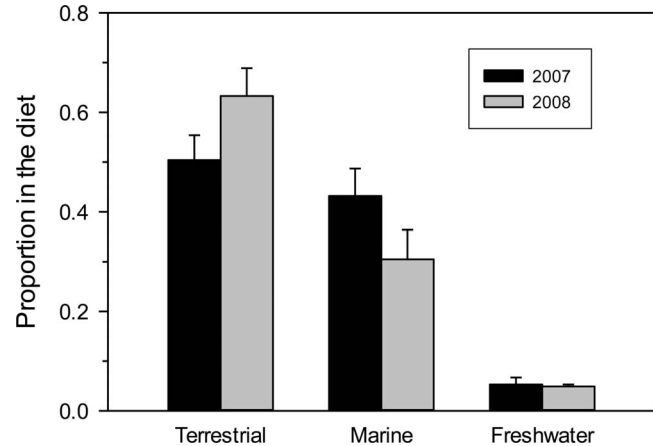
FIGURE 3. Stable carbon and nitrogen isotope values corrected for discrimination factors of whole blood drawn from Glaucous Gull adults (circles) and chicks (triangles) captured on Bylot Island, Nunavut, Canada, in 2007 (white symbols) and 2008 (black symbols). Isotope values of various prey categories (sources) are also shown with means (grey squares) and SD (horizontal and vertical lines) based on sample sizes given in parentheses. For geese, the isotope signatures of eggs and goslings were combined.


FIGURE 4. Contribution (mean + SE) of various sources to the diet of Glaucous Gulls on Bylot Island, Nunavut, Canada, in 2007 and 2008, calculated based on blood isotopic signatures ($n = 42$) using isotope mixing models in package 'siar' in R (Parnell et al. 2010).

mixing models with only 3 sources. The terrestrial contribution to the diet was 50% and 63% in 2007 and 2008, respectively, and the marine contribution was 43% and 31%, respectively (Figure 4). These percentages were relatively similar regardless of the discrimination factors used (terrestrial contribution: 42% to 50% in 2007 and 57% to 63% in 2008; marine contribution: 38% to 49% in 2007 and 26% to 36% in 2008; Appendix Table 4). Stable isotopes thus revealed a much higher contribution of the aquatic environment to the diet of gulls than the pellet analysis. The proportion of freshwater prey in the diet increased for nests located farther away from the seashore ($\beta = 0.007 \pm 0.001$, $F_{1,40} = 23.1$, $P < 0.001$, $r^2 = 0.35$), but the proportion of marine prey did not show any trend with distance to the seashore (mean: 2.9 km, range: 0.1–8.8 km; $\beta = -0.010 \pm 0.012$, $F_{1,40} = 1.5$, $P = 0.23$, $r^2 = 0.01$).

Gull Reproduction

The number of gull nests present in the study area was relatively constant throughout the 7-yr study period (mean = 12 nests per 30 km^2, range = 10–14, CV = 14%). Lemming abundance in June did not affect annual variation in gull nest density ($F_{1,5} = 3.0$, $P = 0.15$), and, among the other covariates tested (Table 1), only the relationship between nest density and June NAO approached significance ($\beta = -1.42 \pm 0.65$ SE, $F_{1,5} = 4.8$, $P = 0.08$).

The median annual laying date of gulls ranged from June 7 to 20, and the median hatching date varied from

July 9 to 18. NAO and average air temperature in June showed similar trends with laying date (e.g., temperature: $\beta = -5.84 \pm 2.97$ SE, $F_{1,21} = 3.9$, $P = 0.06$), and indicated that nest initiation tended to be delayed in cold springs with late snow melt. Neither lemming abundance in June nor nesting habitat (islet vs. shore) were good predictors of laying date ($F_{1,21} = 1.3$, $P = 0.26$ and $F_{1,23} = 1.4$, $P = 0.19$, respectively). Clutch size averaged 2.5 eggs overall (annual range: 2.1–2.9 eggs). Nests that were initiated early in the season had higher clutch sizes than those that were initiated later ($\beta = -0.04 \pm 0.01$ SE, $F_{1,21} = 27.7$, $P < 0.001$). All other covariates tested, including lemming abundance, had no effect on clutch size (all $F_{1,21} < 2.1$, all $P > 0.17$).

All eggs disappeared in 21 of 87 nests with known fate, and eggs were abandoned in 2 others (1 nest in 2008 and 1 in 2010, both years with high lemming abundance). In addition, 1 egg (or 2 in one case) disappeared in 13 nests that successfully hatched ≥ 1 chick. Broken eggshell was found at only 1 nest. We identified predators with automated cameras at 3 nests that suffered total predation: 1 nest was depredated by a fox, 1 by a raven (both nests on the shore of a pond), and 1 by a polar bear (nest on an islet).

The hatching success of gulls was positively related to lemming abundance in July ($\beta = 0.56 \pm 0.17$ SE, $z_{83} = 3.3$, $P < 0.001$; the same result was achieved with June lemming abundance), and was greater for nests located on islets than for those along the shores of ponds ($z_{83} = -2.3$, $P < 0.001$). On islets, hatching success started to decline only when lemming abundance was ≤ 3 lemmings ha^{-1}, but on the shore it declined more or less linearly with lemming abundance (Figure 5). However, the interaction between habitat and lemming abundance on hatching
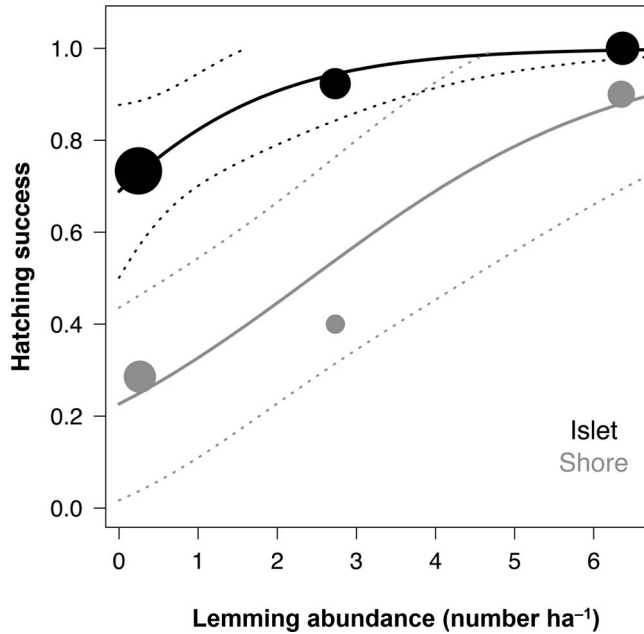
FIGURE 5. Mean hatching success of Glaucous Gulls nesting on Bylot Island (Nunavut, Canada) in relation to lemming abundance in July and nesting habitat (shore vs. islet) from 2005 to 2011. Observed values were pooled in years of low, intermediate, and high lemming abundance for presentation purposes only. The fitted logistic models (solid line) with 95% confidence intervals (stippled lines) are shown. Circle sizes are proportional to $\sqrt{n}$.

success was not significant ($\beta = -0.23 \pm 0.45$ SE, $z_{83} = -0.5$, $P = 0.60$). No other variable affected hatching success. Finally, the mass of growing chicks was not influenced by any climatic variables or factors such as prey abundance (lemmings and geese), timing of adult reproduction, and nesting habitat (all $F_{1,50} < 0.8$, all $P > 0.36$).

DISCUSSION

Even though lemmings were consumed by Glaucous Gulls in variable proportions among years, the gull diet was dominated by other food sources, especially Greater Snow Geese and marine sources, in all years. As expected for a generalist predator, the numerical response (in terms of breeding density and reproductive performance) of gulls to varying lemming abundance was very weak, except for hatching success (but see below). As a result, the gull breeding population remained remarkably stable over time regardless of lemming abundance.

Accurately assessing the diet of a generalist consumer is always difficult due to the diversity of prey consumed, made even more so when individuals can feed in different food webs (e.g., aquatic and terrestrial), as is the case for gulls. Highly digestible prey or those that leave few remains, such as small fishes and insects, will be underrepresented in pellet

analyses (Mariano-Jelicich and Favero 2006, Lindsay and Meathrel 2008). The use of stable isotopes, which is not affected by such biases, in conjunction with pellet analysis can alleviate some of these problems and provide a better overall assessment of diet (Schmutz and Hobson 1998, Weiser and Powell 2011). This is shown by our data, in which pellet analysis revealed a small percentage of aquatic prey in the diet (<10%) but stable isotopes indicated that aquatic prey could contribute 35–48% of the diet. However, stable isotopes have a low taxonomic resolution when isotopic signatures of prey are similar, as was the case in our study, and are most useful for distinguishing prey sources from contrasting habitats (e.g., terrestrial vs. freshwater vs. marine). At this level stable isotopes perform well, and in our study revealed that the contribution of terrestrial food items to the diet was higher in the year of high lemming abundance than in the years of intermediate abundance.

Terrestrial prey contributed slightly more than marine prey to the diet of breeding Glaucous Gulls in our study area. This contrasts with some other studies, which have shown a predominance of marine items in the diet (Weiser and Gilchrist 2012). Several studies have reported substantial variation in the diet of Glaucous Gulls among sites due to factors such as distance to the sea or local availability of specific food sources such as bird colonies or garbage dumps (Barry and Barry 1990, Schmutz and Hobson 1998, Weiser and Powell 2011). On Bylot Island, the Greater Snow Goose colony remained relatively stable over the study period (Legagneux et al. 2012, Bêty et al. 2014) and represented a predictable resource for Glaucous Gulls, despite some annual variation in density due to climatic conditions (Dickey et al. 2008). During incubation, gulls must travel a relatively long distance to prey on geese and their eggs as the main colony is ≥20 km from our study area, although, in some years, a few geese also nest in a dispersed fashion in the vicinity of the gull nesting area (Bêty et al. 2001). Therefore, it is not surprising that it is during the incubation period that lemmings are consumed the most, as they are available close to nest sites. Nonetheless, the contribution of lemmings to the gull diet was variable among years and mirrored their availability, which fluctuated greatly over time due to the cyclical nature of their populations on Bylot Island (Gruyer et al. 2008, Gauthier et al. 2013). It is possible that the dietary switch from lemmings to geese after hatching is due to a change in food requirements with the emergence of chicks. However, hatching also coincides with the movement of goose families into the study area; thus, the increase in goose consumption may simply be due to the fact that goslings are relatively easy to catch and become abundant close to gull nests at that time. A high reliance on geese, and especially goslings, by Glaucous Gulls nesting near goose colonies seems to be a general feature in the Arctic (Schmutz and Hobson 1998, Bowman et al. 2004, this study).

Hatching success was the only component of gull breeding performance that was reduced in years of low lemming abundance. The disappearance of eggs from most nests that failed suggests that predation was the main cause of nest failure. The much lower hatching success of nests on shorelines compared with those on islets further suggests that mammalian predation was important. Even though one nest was destroyed by a polar bear, bears were rarely observed in the study area. In contrast, Arctic foxes are common (Giroux et al. 2012) and were observed almost daily. The disappearance of all eggs from a nest is typical of fox predation because, when they are successful in getting an egg, they often cache it and come back quickly for more (Careau et al. 2007). Previous studies have shown that water is an impediment to egg predation by foxes in the tundra (Lecomte et al. 2008), which could explain the higher success of nests on islets. Islets still offered only a partial refuge from predation, as nest success was also reduced in this habitat when lemming abundance was very low. The motivation of foxes to attack gull nests despite attacks by parents may increase when their main prey, lemmings, is scarce (Bêty et al. 2002). Foxes can also gain access to islands by walking on ice in years of late spring breakup, or by jumping or swimming when distance to the shoreline is short.

Because we found very few abandoned nests in general and none in years of low lemming abundance, it appears unlikely that poor reproductive success of gulls in those years was a consequence of increased nest abandonment due to low resource availability. Moreover, most nests from which eggs disappeared were still attended by parents who attacked observers during nest visits, another indication that these nests had not been abandoned. Laying was not delayed and clutch size was not reduced in low lemming abundance years, both of which also indicate that resource availability was not a problem for gulls. Nonetheless, it is possible that nest attentiveness by gulls was reduced in years of low lemming abundance, for instance because gulls had to travel a longer distance to prey on geese or marine prey during incubation, which may have increased predation risk.

The diverse diet of gulls, which may include birds, small mammals, and marine prey, likely contributes to the relative stability of their local breeding population on Bylot Island despite large annual fluctuations in lemming abundance (Therrien et al. 2014). The ability of generalist predators to switch to alternative prey explains why they are usually considered to be unaffected by large fluctuations in some resources, unlike more specialized predators (Hanski et al. 1991, Schmidt et al. 2012). Nonetheless, our results show that generalists may be affected indirectly through intraguild predation if the foraging of other predators, such as foxes in our case, is also altered by fluctuations in prey numbers, e.g., lemming abundance (Elmhagen et al. 2000). Indirect effects due to prey that share the same predators and mediated through variations in small mammal populations appear

widespread in the Arctic food web as they have now been reported for geese (Bêty et al. 2002, Morrissette et al. 2010, Nolet et al. 2013), shorebirds (McKinnon et al. 2013), and passerines (P. Royer-Boutin personal communication). Our study shows that such indirect effects may also affect the reproduction of a generalist avian top predator.

This study adds to a growing body of literature showing that predation may be a dominant force shaping the Arctic food web (Gilg et al. 2006, Legagneux et al. 2014, Therrien et al. 2014). Studies documenting strong direct and indirect predator–prey interactions in the tundra food web, including intraguild predation as reported here, have been increasing, and suggest that these interactions may have been underestimated in the past due to a lack of basic knowledge about several Arctic wildlife species. Intraguild predation also provides an additional pathway through which this food web may be affected by global change, such as that linked to the collapse of lemming cycles as reported in some parts of the Arctic (Ims et al. 2008, Schmidt et al. 2012, Nolet et al. 2013). Although large increases in goose populations reported in several parts of the Arctic, including at our study site (Gauthier et al. 2005), may provide a stable prey source for many Glaucous Gull populations, this may not be enough to mitigate indirect effects of predators such as foxes that depend heavily upon lemmings (Elmhagen et al. 2000, Giroux et al. 2012).

ACKNOWLEDGMENTS

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APPENDIX TABLE 2. Correlation matrix among covariates examined in relation to diet and reproduction of Glaucous Gulls on Bylot Island, Nunavut, Canada, in 2005–2011. Correlations >0.70 are in bold. Lemm = lemming abundance; Geese = Greater Snow Goose abundance (based on feces count); NAO = North Atlantic Oscillation; Temp = average air temperature.

	Lemm, Jun	Lemm, Jul	Lemm, Aug	Geese, Jul	Geese, Aug	NAO, Jun	NAO, Jul	NAO, Aug	Temp, Jun	Temp, Jul	Temp, Aug
Lemm, Jun	1.00	**0.94**	**0.73**	−0.06	−0.24	−0.40	−0.34	−0.47	**0.83**	0.05	−0.03
Lemm, Jul		1.00	**0.86**	−0.07	−0.19	−0.36	−0.27	−0.50	**0.79**	0.18	0.07
Lemm, Aug			1.00	−0.23	−0.32	−0.35	−0.14	−0.49	**0.79**	0.06	−0.20
Geese, Jul				1.00	**0.76**	−0.37	−0.03	0.35	−0.28	−0.23	0.16
Geese, Aug					1.00	−0.29	−0.23	**0.80**	−0.46	0.12	0.06
NAO, Jun						1.00	**0.82**	−0.19	−0.61	−0.26	0.12
NAO, Jul							1.00	−0.33	−0.53	−0.60	−0.01
NAO, Aug								1.00	−0.49	0.11	−0.29
Temp, Jun									1.00	0.15	−0.17
Temp, Jul										1.00	0.60
Temp, Aug											1.00

APPENDIX TABLE 3. Frequency of occurrence of food items, grouped into 4 categories, found in individual regurgitated pellets collected at Glaucous Gull nests on Bylot Island, Nunavut, Canada, from 2005 to 2008.

Year	Period [a]	Dates	n nests	n pellets	Lemmings [b]	Geese [c]	Aquatic prey [d]	Other prey [e]
2005	Before	June 11–July 12	5	26	62%	54%	8%	4%
	After	July 13–August 3	5	97	13%	95%	17%	3%
2006	Before	June 18–July 17	6	118	20%	87%	4%	3%
	After	July 18–August 15	6	114	6%	96%	15%	2%
2007	Before	June 16–July 12	10	68	43%	77%	6%	3%
	After	July 13–August 16	10	228	18%	86%	8%	7%
2008	Before	June 8–July 9	15	313	59%	52%	10%	2%
	After	July 10–August 16	15	426	19%	88%	8%	4%

[a] Before and after hatching of gull chicks (median annual hatching dates are indicated as a reference).
[b] Brown and collared lemmings.
[c] Eggshells, gosling and adult goose bones (fragments and whole), down, and feathers.
[d] Fishes (bone fragments, vertebra, scales, and otoliths), marine invertebrates (exoskeletons and shell fragments), and marine mammals (seals).
[e] Birds other than geese (e.g., ducks, jaegers, Lapland Longspurs, shorebirds, and unidentified birds), terrestrial mammals other than lemmings (Arctic fox hair, bones, and claws, and unidentified mammals), and arthropods.

APPENDIX TABLE 4. Contribution of various sources (mean, with SE in parentheses) to the diet of Glaucous Gulls on Bylot Island, Nunavut, Canada, in 2007 and 2008, calculated based on blood isotopic signatures using isotope mixing models in package 'siar' in R (Parnell et al. 2010), using (**A**) discrimination factors from Hobson and Clark (1992), but values for adults corrected according to Sears et al. (2009); (**B**) discrimination factors form Hobson and Clark (1992), uncorrected for adults; and (**C**) discrimination factors from Weiser and Powell (2011).

	Year	Terrestrial	Marine	Freshwater
A	2007	0.504 (0.050)	0.432 (0.055)	0.053 (0.014)
	2008	0.633 (0.056)	0.305 (0.059)	0.049 (0.004)
B	2007	0.419 (0.078)	0.491 (0.066)	0.080 (0.023)
	2008	0.573 (0.069)	0.356 (0.069)	0.059 (0.009)
C	2007	0.456 (0.087)	0.380 (0.096)	0.154 (0.028)
	2008	0.603 (0.068)	0.259 (0.076)	0.121 (0.011)
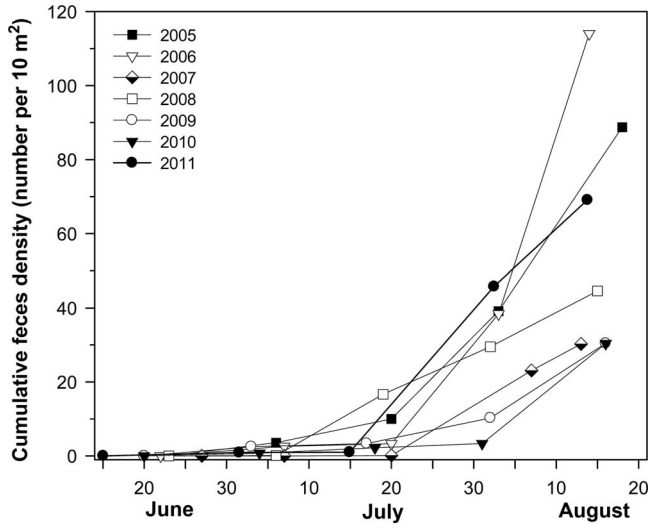
APPENDIX FIGURE 2. Mean cumulative density (number per 10 m^2) of goose feces recorded on transects throughout the summer in the study area (Bylot Island, Nunavut, Canada) from 2005 to 2011.