

Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic

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Abstract. Predation has been suggested to be especially important in simple food webs and less productive ecosystems such as the arctic tundra, but very few data are available to evaluate this hypothesis. We examined the hypothesis that avian predators could drive the population dynamics of two cyclic lemming species in the Canadian Arctic. A dense and diverse suite of predatory birds, including the Snowy Owl (*Bubo scandiacus*), the Rough-legged Hawk (*Buteo lagopus*), and the Long-tailed Jaeger (*Stercorarius longicaudus*), inhabits the arctic tundra and prey on collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings during the snow-free period. We evaluated the predation pressure exerted by these predators by combining their numerical (variation in breeding and fledgling numbers) and functional (variation in diet and daily consumption rates) responses to variations in lemming densities over the 2004–2010 period. Breeding density and number of fledglings produced by the three main avian predators increased sharply without delay in response to increasing lemming densities. The proportion of collared lemmings in the diet of those predators was high at low lemming density (both species) but decreased as lemming density increased. However, we found little evidence that their daily consumption rates vary in relation to changes in lemming density. Total consumption rate by avian predators initially increased more rapidly for collared lemming but eventually leveled off at a much higher value for brown lemmings, the most abundant species at our site. The combined daily predation rate of avian predators exceeded the maximum daily potential growth rates of both lemming species except at the highest recorded densities for brown lemmings. We thus show, for the first time, that predation pressure exerted without delay by avian predators can limit populations of coexisting lemming species during the snow-free period, and thus, that predation could play a role in the cyclic dynamic of these species in the tundra.

Key words: functional response; lemmings; Long-tailed Jaeger; numerical response; population limitation; predation; Rough-legged Hawk; Snowy Owl; tundra.

INTRODUCTION

Predation pressure by second-order consumers has the potential to regulate vertebrate communities in several ecosystems (Krebs et al. 1995, Korpimäki and Norrdahl 1998, Ripple et al. 2001, Korpimäki et al. 2002, Schmitz 2006). This force has been hypothesized to be especially important in simple food webs characterized by a low primary productivity such as the boreal forest or the arctic tundra (Strong 1992, Korpimäki and Krebs 1996). However, according to an alternative view, the tundra food web could be primarily controlled from the bottom-up (i.e., by food resources; Oksanen and Oksanen 2000). Assessing the relative strength of top-down vs. bottom-up forces in an ecosystem is essential

to understand the food web functioning and to predict impacts of anticipated environmental changes.

In the tundra, small mammals such as lemmings (*Dicrostonyx* and *Lemmus* spp.) are often the dominant herbivores (Krebs et al. 2003). Those herbivores show tremendous variations in numbers from year to year and exhibit population cycles in most circumpolar regions (Elton 1924, Stenseth 1999, Predavec et al. 2001, Gilg 2002). The potential causes of those fluctuations have been studied for a long time but still remain unclear (e.g., Gauthier et al. 2009, Oksanen et al. 2009, Krebs 2011), although in several systems high predation rates have been reported, especially during the summer (Korpimäki and Norrdahl 1991a, Reid et al. 1995, Korpimäki and Krebs 1996, Wilson et al. 1999, Hanski et al. 2001, Gilg et al. 2003, Korpimäki et al. 2004, Ims et al. 2011). Very few studies, however, have quantified the numerical and functional responses of arctic predators to fluctuations in small-mammal abundance and their combined impact on prey populations (but see

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Pitelka et al. 1955, Gilg et al. 2006), an essential prerequisite to evaluate the role of predation in the control of food webs (Korpimäki and Krebs 1996). Moreover, among-year variation in daily consumption rates of small mammals by avian predators has rarely been investigated, but is essential to determine their functional response.

Birds present high diversity of predators compared to mammals in the tundra. Snowy Owls (*Bubo scandiacus*), Rough-legged Hawks (*Buteo lagopus*), Long-tailed and Parasitic Jaegers (*Stercorarius longicaudus*, *S. parasiticus*), Peregrine Falcons (*Falco peregrinus*), and Glaucous Gulls (*Larus hyperboreus*) all dwell in the tundra during the snow-free period. Diet has been previously described individually for those predators in different regions of the Arctic (reviewed in Birds of North America accounts: Glaucous Gull, Gilchrist 2001; Long-tailed Jaeger, Wiley and Lee 1998; Parasitic Jaeger, Wiley and Lee 1999; Peregrine Falcon, White et al. 2002; Rough-legged Hawk, Bechard and Swem 2002; Snowy Owl, Parmelee 1992) and showed that the primary prey for most of them are small mammals. However, there have been very few studies that simultaneously investigated their breeding numbers, diet, and consumption rates when these predators occur in sympatry during contrasting years of lemming abundance.

The response of Snowy Owls and Long-tailed Jaegers to varying abundance of lemmings has been studied in northern Greenland by Gilg et al. (2003, 2006). They found that density-dependent predation by these two species could induce summer decline in lemming populations. However, the food web at this site is simpler than at most other tundra sites. Indeed, whereas only one species of lemming and two species of avian predators breed in Greenland, much of the circumpolar tundra is inhabited by at least two species of small mammals and four or more competing species of avian predators. Therefore, competition for scarce resources among these multiple predators could be high in the relatively unproductive tundra ecosystem. As suggested by Reid et al. (1995) and Wilson et al. (1999), we anticipated that avian predators could have a significant impact on small-mammal numbers, and thus, on the food web functioning.

Our aim was to assess the predation pressure of sympatric avian predators by simultaneously determining variations in numbers (numerical response) and in diet and consumption rates (functional response) to varying lemming density. Arctic avian predators are predominantly migrants and predation on lemmings mostly occurs when snow cover is absent (typically from early June to early October). These predators are highly mobile and have the potential to track small-mammal outbreaks over large geographic areas (Korpimäki and Norrdahl 1991b, Norrdahl and Korpimäki 1996). We thus hypothesized that (1) lemming-eating avian predators of the tundra would exhibit strong numerical

responses without any time lag to local variations in lemming abundance, (2) consumption rate of lemmings by avian predators would increase in response to an increase in lemming abundance, and (3) the combined predation pressure by avian predators would be sufficient to limit the summer growth of lemming populations during the snow-free period and cause population declines. Here we present a unique and detailed evaluation of the numerical, functional, and total responses of avian predators in order to provide further insights into the trophic control of arctic terrestrial food webs.

MATERIALS AND METHODS

Study area

The 100-km² study area was located on Bylot Island (Nunavut, Canada; 73° N, 80° W) and field work occurred during summers 2004 to 2010. The study area is dominated by rolling hills and low-elevation plateaus interspersed by streams and rivers that created numerous valleys ranging in size from narrow gullies to wide and relatively flat valley bottoms. Mesic tundra (dominated by prostrate shrubs and a sparse forb and graminoid cover) was most common in the hilly landscape, whereas flat areas had a mosaic of mesic and wet tundra (the latter habitat being dominated by graminoid plants growing through a ground moss cover; see Gauthier et al. 2011).

Brown (*L. trimucronatus*) and collared (*D. groenlandicus*) lemmings have a widespread distribution across most of the Canadian tundra and are the sole small mammals present on Bylot Island. Both species exhibit three-to-four year cyclic fluctuations in abundance, but the amplitude of fluctuations is much larger in the brown lemming (Gruyer et al. 2008). Breeding predatory birds are dominated by the Snowy Owl, the Rough-legged Hawk, the Long-tailed Jaeger, the Glaucous Gull, the Peregrine Falcon, and the Parasitic Jaeger. No nesting Raven (*Corvus corax*) or Gyrfalcon (*F. rusticolus*) was found during the study, although the former species is also present in small numbers. Other major predators present include the arctic fox (*Vulpes lagopus*) and the stoat (*Mustela erminea*). Bylot Island has a large Snow Goose (*Chen caerulescens*) breeding colony situated roughly 30 km to the south of the study area, which can be an alternative prey for some predators. Other alternative prey include passerines (*Calcarius* and *Plectrophenax* spp.), shorebirds (*Charadrii* spp.), the Rock Ptarmigan (*Lagopus mutus*), ducks (*Somateria* and *Clangula* spp.), as well as many arthropods taxa (such as *Arachnidae*, *Tipulidae*, *Muscidae*).

Small-mammal density

We measured small-mammal density throughout the snow-free period each year by live-trapping them on two trapping grids (11 ha each) spaced by 2 km. We set up trapping grids in areas representative of the typical habitat; one grid was located in hill side dominated by

mesic tundra and one grid in a valley bottom dominated by wet habitat. Each trapping grid had 144 Longworth live traps that were opened over three or four consecutive days at each trapping period, and checked at 12-h intervals. We conducted three (sometimes four) trapping sessions each summer (mid-June, mid-July, and mid-August). We individually marked all animals with passive integrated transponder (PIT) tags before release (see Gruyer et al. 2010 for details). We estimated densities of each species at each trapping session using capture-mark-recapture (CMR) techniques with the Program DENSITY 4 (Efford et al. 2004, Efford 2009). 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 (MNA) divided by the effective trapping area (see Bilodeau et al. 2013b). Given that both wet and mesic habitats are present in similar proportions in the study area, we averaged densities of each species between the two grids for each corresponding trapping session.

Avian predators

Numerical responses.—We conducted systematic searches for nests of predatory birds during June and early July. Over hilly terrain, we followed ridges and scanned the surrounding landscape from vantage points. Nests of most avian predators are conspicuous and typically located on elevated mounds. Moreover, nesting predators often reveal their presence from a relatively long distance through alarm calls and behavioral displays. For jaegers that prefer lowland habitats and exhibit less conspicuous nests, we conducted systematic searches by walking parallel transects 250 m apart over a 30-km² area suitable for nesting. Because a portion of the whole study area (~30%) was unsuitable for jaegers (mostly steep hills), we multiplied the density measured over the 30-km² search area by 0.7 to determine jaeger nesting density over the whole study area. Although we did not assess the nest detection probability, we are confident that it was very high for all avian predator species in this open landscape. However, any possible bias related to detection probability would result in an underestimation of nest density, and hence, predation pressure on lemmings. Nonbreeding, resident adults were seldom encountered in any species. We divided the number of nests of each species by the area searched annually to obtain nesting density. We assessed the numerical responses of avian predators by plotting their annual nesting densities separately against the density of lemming (both species combined) measured during the first two trapping season (June and July, thereafter called: early summer period). We determined fledgling numbers by revisiting nests on a weekly basis. We considered chicks able to sustain flight as fledglings. This number should be considered a minimum estimate as young avian predators sometimes disperse

over large areas and are difficult to find away from the nest.

Functional responses.—We used methods similar to Gilg et al. (2006) to assess functional responses. We measured the relative proportions of collared and brown lemming in the diet of Snowy Owls, Rough-legged Hawks, and Long-tailed Jaegers with pellet analyses (Errington 1930, Lewis et al. 2004) collected throughout the breeding season annually. Nests were visited weekly and all pellets found in its surrounding (<20 m) were collected. We later analyzed pellets in the laboratory to identify ingested prey using hair, bones, and feather remains. We determined the minimal number of prey ingested by counting the number of jaws and skulls found in pellets. Overall, we collected and analyzed 1668, 28, and 147 pellets for Snowy Owls (25 nests), Rough-legged Hawks (9 nests) and Long-tailed Jaegers (30 nests), respectively. We plotted the annual proportion of collared lemmings in the diet of the three main predators in relation to the density of both lemming species on the study area and compared it to the proportion of collared lemmings in the overall lemming population.

We used direct observations to assess the number of prey consumed daily by the three major avian predators from 2007 to 2010. We set up blinds ~150 m from focal nests and conducted behavioral observations during 3-h to 8-h bouts using a spotting scope. Observations covered the 24-h period to account for any possible circadian variation in predator activity despite the 24-h daylight during the summer. We conducted observations from the mid-incubation (20 June) through the chick-rearing period (until 15 August). We conducted a total of 50, 50, and 80 h of direct visual observations on Snowy Owls (7 nests), Rough-legged Hawks (4 nests), and Long-tailed Jaegers (8 nests) respectively. We also set automatic-triggered cameras at ~5 m from 11 Snowy Owl and 5 Rough-legged Hawk nests to monitor food delivery over periods of two to seven days. We programmed the motion-sensitive cameras to take pictures every time a movement was detected and under fixed intervals (ranging from 1 to 20 s). Cameras worked well for Snowy Owls and Rough-legged Hawks, but not for jaegers because the chicks leave the nest one or two days after hatching and cannot be followed by a fixed camera. We recorded a total of 3876 and 314 h of observations with cameras on Snowy Owl and Rough-legged Hawk nests, respectively. Since identification of lemmings to the species level by both observational techniques was difficult, we used the proportion of each lemming species found in the pellets to split overall lemming consumption rates of predators among the two species.

We assessed the functional response of the three main avian predators by plotting their mean daily consumption rates (DCR; individual lemmings consumed per day) in relation to mean daily lemming density on the study area. We calculated the lemming density associ-

ated with each DCR estimate by assuming a linear change in density between the two closest trapping sessions. We assessed consumption rates on a nest rather than an individual basis and we averaged repeated measures for each nest. Since the two techniques (direct observations and cameras) were directed toward the nest, they could not assess prey consumed away from the nest by adults. This was especially true for Snowy Owls and Rough-legged Hawks, which nest in territories with topographical features that prevent observers from monitoring provisioning adults away from the nest. In those cases, the measured consumption at the nest applies only to the incubating/brooding adult and the growing chicks. We thus assigned the consumption level recorded during incubation to the other adult. Any possible bias resulting from this estimation would likely tend to underestimate consumption rates because the energetic needs of an incubating adult is expected to be lower than that of a foraging one. Long-tailed Jaegers, on the other hand, nest in flatter landscape and were seldom foraging out of view during observations. We are therefore confident that almost all feeding events were recorded, whether close to the nest or further away in the territory.

Total responses.—We obtained the total response or predation rate (the number of lemmings eaten/day \times km²) by multiplying the numerical (number of nests/km²) and functional (number of lemming consumed daily per nest) responses of individual predators. We plotted the total response in relation to the density (individuals/km²) and summer growth rate of each lemming species. We compared the estimated daily predation rates to the maximum daily potential growth rates of lemming populations as estimated in other studies. Maximum growth rate was estimated at 1.97% for brown lemmings (Batzli et al. 1980) and 2.27% for collared lemmings (Gilg 2002). According to Stenseth and Ims' (1993) review of lemming demography, if we assume that they suffer no mortality, that each adult female produces seven offspring per month with a sex ratio of 1:1, and that young females become mature at about one month old (the most extreme values), maximum potential growth rate of lemmings could be as high as 2.44% per day (finite rate of increase for one year: $r = 8.88$, assuming constant reproductive rate year round). Although such extreme values probably never occur in the wild, we used these three estimates to assess if our conclusions were robust to the estimate chosen.

We examined if the summer lemming population change was related to the annual percentage of lemmings consumed daily by predators. For each year, we calculated the percentage of population change for both species using the density measured in early summer and late summer (mid-August).

Statistical analyses

We used sigmoid functions (Eq. 1) to fit the numerical responses (breeding densities expressed as BD and

number of fledglings produced per square kilometer expressed as NFP) as provided by Gilg et al. (2006):

$$\text{BD(or NFP)} = aN^2/(b^2 + N^2) \quad (1)$$

where a is the asymptotic value of the curve, b is lemming density at the inflexion point of the curve, and N is lemming density per square kilometer in early summer. We then fitted the same equations with the lemming density measured at year $t - 1$ to test if the model would better fit the data with a time lag of one year.

We used simple regressions to assess the relationship between the proportion of collared lemmings in the diet of the three main predators and the combined density of both lemming species. We could not simultaneously examine the effect of the abundance of each lemming species separately because their early summer densities were strongly correlated (Pearson correlation, $r = 0.77$, $P = 0.04$, $df = 6$; Fig. 1).

For the functional response, given that the main avian predators were absent from the site at low prey density, Type III curves did not improve the fit than the simpler Type II curves (in terms of R^2). We thus present functional response curves (daily consumption rates, expressed as DCR) with the Type II equation (i.e., the simplest model; Eq. 2) provided by Gilg et al. (2006):

$$\text{DCR} = cN'/(d + N') \quad (2)$$

where c is the asymptotic value of the curve, N' is lemming density per square kilometer, and d is the half-saturation constant (i.e., the N' value when $\text{DCR} = c/2$).

We estimated all parameters (a , b , c , and d) by fitting curves where the least-square residuals were minimized iteratively. We performed analyses with the "nlin" procedure using the Gauss-Newton algorithm in SAS release 9.2 (SAS Institute 2008). The "nlin" procedure in SAS allows using a grid of starting values to avoid local minima; therefore, the starting values for the estimated parameters were $a = 0.1$ to 1 by 0.1 increments, $b = 1$ to 10 by 1.0 increments, $c = 1$ to 10 by 1.0 increments, and $d = 1$ to 10 by 1.0 increments. We calculated a pseudo- R^2 for nonlinear models as: $1 - \text{sum of square (residual)}/\text{sum of square (corrected total)}$. Results are presented as mean \pm SE unless otherwise stated. The log scale has only been used for graphical purposes.

The relationship between the summer population change and consumption rate by predators was examined with a Pearson correlation coefficient. A problem arose, however, in years where lemming density was estimated by the minimum number alive (years of very low abundance; two years for the collared and three years for the brown lemmings) because summer population change is likely to be poorly estimated in those situations. We thus present the analysis with all years and with only those where population density was estimated with robust CMR methods.

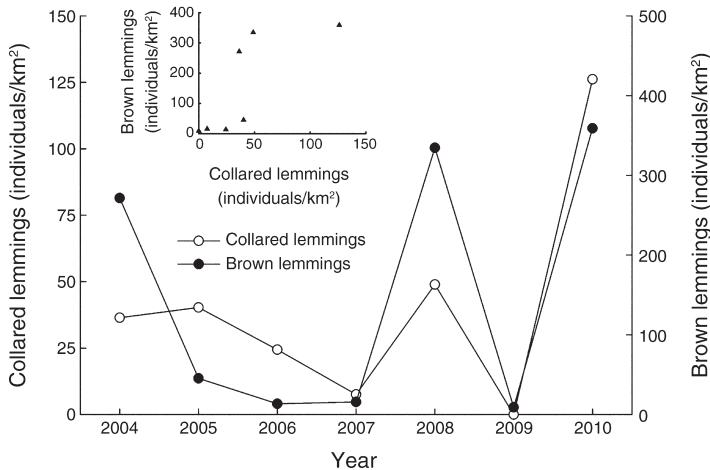


FIG. 1. Annual collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemming density measured in early summer (June/July) on Bylot Island, Canada (2004–2010). The insert shows the linear relationship between the two species.

RESULTS

Small-mammal density

Both lemming species exhibited strong, rather synchronized variations in density from one year to the next, although the amplitude of fluctuations was much greater in the brown lemming (Fig. 1). That species reached peak densities in 2004, 2008, and 2010.

Numerical responses

We recorded a total of 30 Snowy Owl, 21 Rough-legged Hawk, 98 Long-tailed Jaeger, 64 Glaucous Gull, 3 Peregrine Falcon, and 3 Parasitic Jaeger nests over the seven years of the study. The breeding density of some predators changed considerably in response to variation in lemming density at time t , but not all of them (Fig. 2). We observed strong numerical responses in the Snowy Owl ($a = 0.13$, $b = 224.2$, $F_{2,5} = 41.2$, $P < 0.01$) and Rough-legged Hawk ($a = 0.11$, $b = 29.9$, $F_{2,2} = 18.4$, $P = 0.05$). The Long-tailed Jaeger also showed a strong numerical response to variations in lemming density ($a = 0.92$, $b = 46.1$, $F_{2,5} = 34.5$, $P < 0.01$) and reached the highest densities among all avian predator species (0.92 nests/km²). Adding a time lag of one year to the response to lemming density provided a much poorer fit for all the relations described in this paragraph (all $F < 0.6$, all $P > 0.63$). The other avian predators exhibited no detectable response to an increase in lemming density at time t or $t - 1$ (Fig. 2).

With an increase in lemming density, the number of fledglings produced per square kilometer increased sharply in Snowy Owls ($a = 0.43$, $b = 278.5$, $F_{2,5} = 38.4$, $P < 0.01$), Rough-legged Hawks ($a = 0.38$, $b = 27.8$, $F_{2,2} = 13.7$, $P = 0.07$), Long-tailed Jaegers ($a = 1.42$, $b = 254.9$, $F_{2,5} = 186.6$, $P < 0.01$), and Glaucous Gulls ($a = 0.22$, $b = 13.7$, $F_{2,2} = 62.0$, $P = 0.02$), but remained constant in Peregrine Falcons and Parasitic Jaegers (Fig. 3). Overall, for species exhibiting the strongest responses in breeding numbers (Snowy Owl, Rough-legged Hawk, and Long-tailed Jaeger), there was an average of 3.0 ± 0.3 ($n = 18$), 3.0 ± 0.7 ($n = 5$), and 1.0 ± 0.1 ($n = 71$)

young fledged per nest at the highest recorded lemming density, respectively.

Functional responses

The proportion of collared lemming in the diet of all three predators tended to vary with the overall lemming density (for Snowy Owls, $F_{1,42} = 3.7$, $P = 0.06$; Rough-legged Hawks, $F_{1,9} = 5.6$, $P = 0.05$; and Long-tailed Jaegers, $F_{1,29} = 3.8$, $P = 0.06$; Fig. 4). Given the large difference in lemming density (and most probably availability) between the two species in years of peak abundance (brown lemmings averaged three times the density of collared lemmings), the proportion of collared lemmings in the diet decreased sharply in those years. Nonetheless, the proportion of collared lemmings in the diet of all three predators remained higher than its proportion in the overall lemming population at all densities (Fig. 4). At low lemming density, collared lemmings represented 82%, 61%, and 83% of the diet of Snowy Owls, Rough-legged Hawks, and Long-tailed Jaegers, respectively, whereas at high lemming density, those proportions fell to 24%, 13%, and 8%.

We did not detect any increase in the daily consumption rate of collared lemmings by Snowy Owls, Rough-legged Hawks, and Long-tailed Jaegers with increasing collared lemming density (all $F < 6.2$, $P > 0.1$; no equation could be fitted to owls due to a decreasing trend; Fig. 5). Average daily consumption of collared lemmings by a breeding pair was 6.7 ± 0.7 individuals ($n = 13$) for Snowy Owl, 2.8 ± 0.3 ($n = 6$) for Rough-legged Hawk, and 2.1 ± 0.8 ($n = 8$) for Long-tailed Jaeger (Fig. 5). Similarly, daily consumption rate of brown lemmings did not vary according to its density in both Snowy Owls and Long-tailed Jaegers (all $F < 2.1$, $P > 0.21$). Snowy Owls consumed an average of 11.0 ± 2.1 ($n = 13$) individual brown lemmings per pair per day, whereas Long-tailed Jaegers consumed 6.5 ± 2.1 ($n = 8$) lemmings. Daily consumption rate of brown lemmings by Rough-legged Hawk breeding pairs increased gradually with prey density and reached 9.5 individuals per

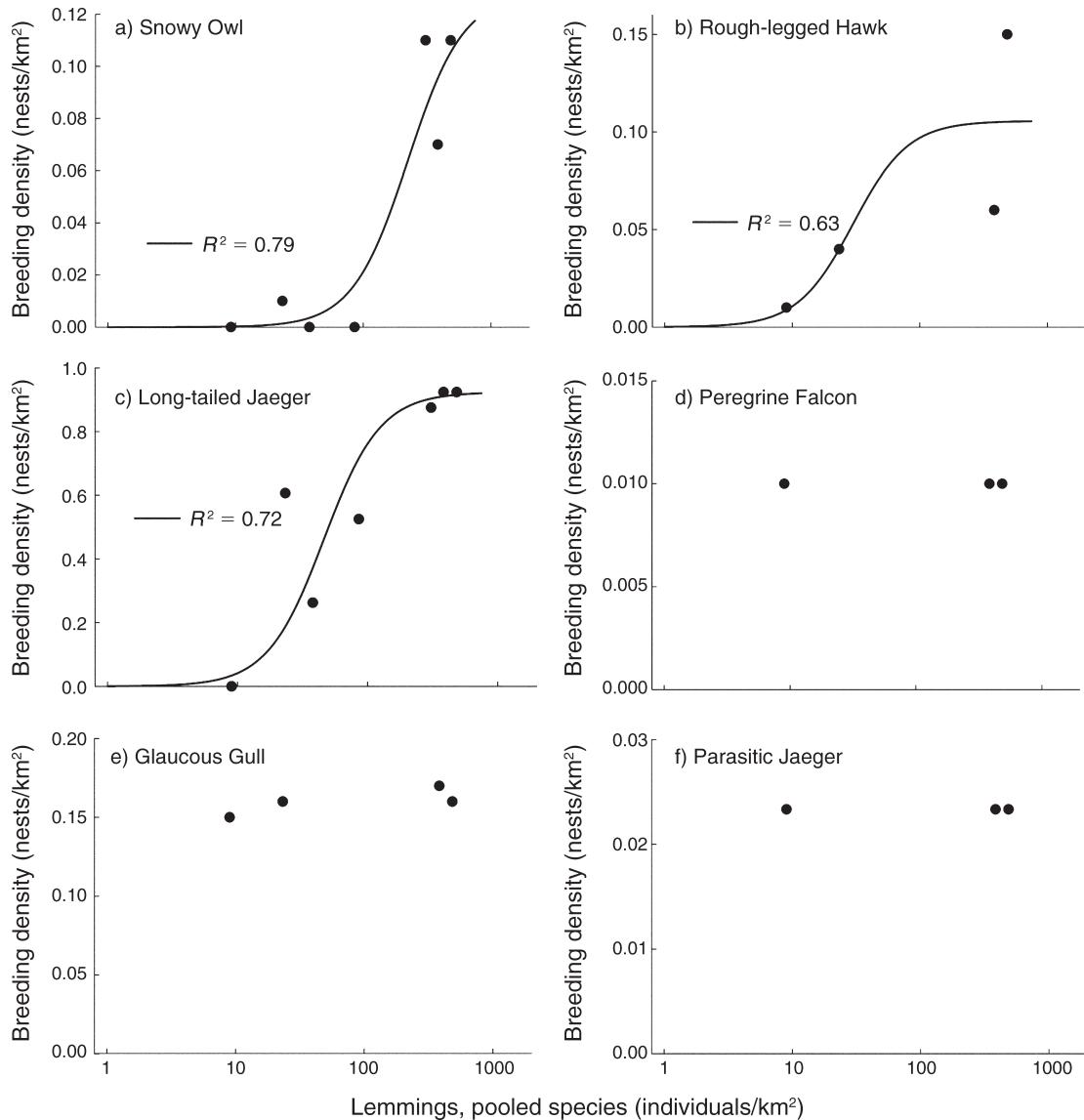


FIG. 2. Breeding density of avian predators (Snowy Owl [*Bubo scandiacus*], Rough-legged Hawk [*Buteo lagopus*], Long-tailed and Parasitic Jaegers [*Stercorarius longicaudus*, *S. parasiticus*], Peregrine Falcon [*Falco peregrinus*], and Glaucous Gull [*Larus hyperboreus*]) in relation to pooled lemming density (both species combined) in early summer on Bylot Island, Canada (2004–2010). Significant relationships are shown.

pair/d when brown lemming density reached 500 individuals/km² ($c = 10.2$, $d = 39.6$, $F_{2,6} = 41.6$, $P < 0.01$; Fig. 5).

Total responses

Total consumption of collared lemmings by the three main avian predators gradually increased as their density increased and tended to stabilize around 3.0 individuals consumed daily/km² above 100 individuals/km² (Fig. 6). Total consumption of brown lemming also increased gradually with their density to level off around 8.2 individuals consumed daily/km² above 500 individuals/km² (Fig. 6). It is noteworthy that the Long-tailed

Jaeger showed the highest consumption rate per square kilometer of all avian predators for both lemming species (consumption by the Snowy Owl, Rough-legged Hawk, and Long-tailed Jaeger was 0.6, 0.3, and 1.9 collared lemmings/km² at 100 collared lemmings/km² and 1.2, 1.0, and 6.0 brown lemmings/km², respectively). This was mainly due to the higher breeding densities of jaegers compared to the two other species.

All three avian predators consumed a high proportion of the summer lemming populations on Bylot Island. Their combined daily predation rate exceeded the maximum daily potential growth rates of both lemming

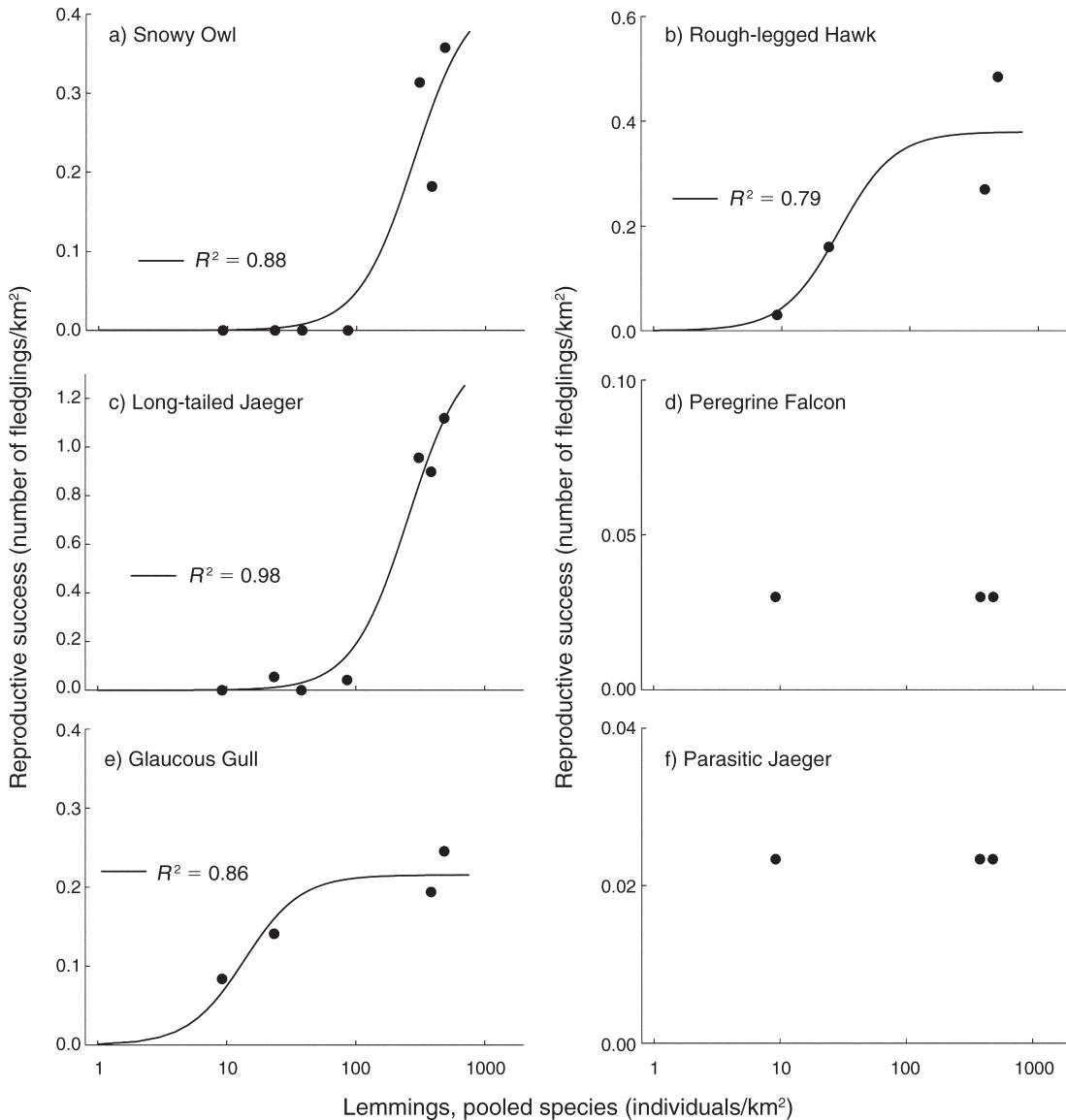


FIG. 3. Reproductive success (number of fledglings produced) of avian predators in relation to pooled lemming density (both species combined) in early summer on Bylot Island, Canada (2004–2010). Significant relationships are shown.

species over a wide range of recorded densities, suggesting a control of those species by predation (Fig. 7). The shapes of the curves were similar between the two lemming species, as predation rate increased to reach a peak value at intermediate prey densities and fell at higher densities. However, predation rate peaked at lower density and reached a higher maximum value for collared than brown lemming. Total daily predation rate fell below the maximum potential growth rate of lemmings only at around 125–135 and 325–410 individuals /km² for collared and brown lemmings, respectively. Such values were not reached in collared lemming, although it was encountered twice in brown lemming during the study period.

Average summer population change was $-0.5\% \pm 0.5\%$ for collared lemmings and $0.8\% \pm 0.4\%$ for brown lemmings over the seven years of the study (when using only population estimates based on CMR, these values were $-0.8\% \pm 0.7\%$ and $0.1\% \pm 0.4\%$, respectively). Summer lemming population change was negatively associated with the estimated daily predation rate by avian predators, although not significantly (for collared lemming, $r = -0.41$, $P = 0.37$, $df = 5$; brown lemming, $r = -0.44$, $P = 0.32$, $df = 5$; Fig. 8). The association was stronger when using only data points derived from CMR, although still not significant (for collared lemming, $r = -0.74$, $P = 0.16$, $df = 3$; brown lemming, $r = -0.63$, $P = 0.37$, $df = 2$; Fig. 8).

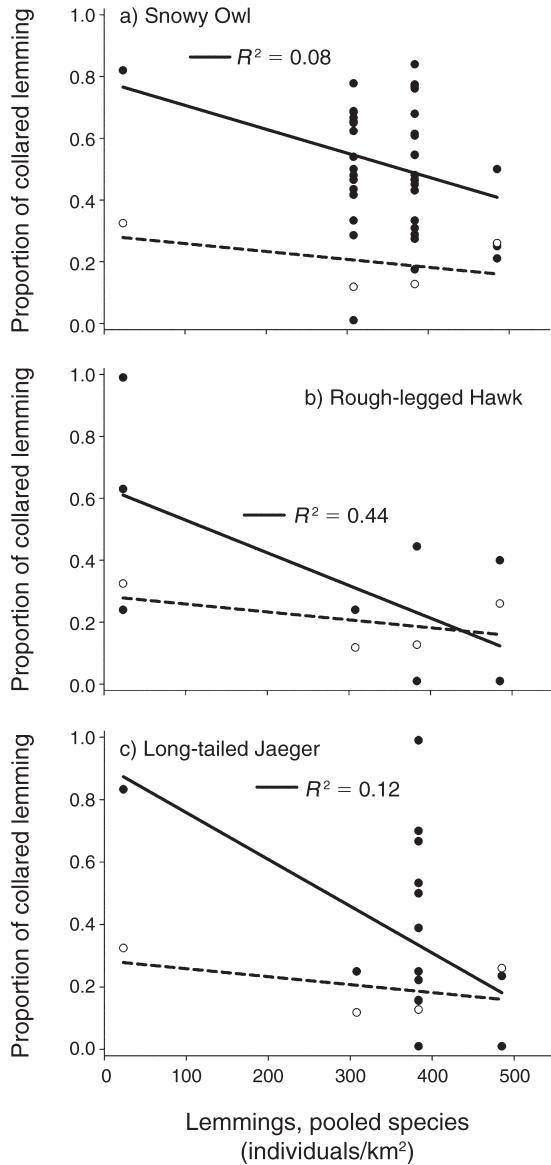


FIG. 4. Proportion of collared lemmings in the diet of the three main avian predators (solid circles and solid lines) and proportion of collared lemming in the overall lemming population (open circles and dashed lines) in relation to the density of lemming (both species combined) in early summer on Bylot Island, Canada (2004–2010).

DISCUSSION

As expected, the main avian predators (Snowy Owl, Rough-legged Hawk, and Long-tailed Jaeger) responded to local variations in lemming density by exhibiting strong numerical responses without any obvious time lag. In contrast with our second hypothesis, we did not detect any clear increase in consumption rates of brown or collared lemmings by the three main predator species with an increase of each respective prey density, except for consumption of brown lemmings by Rough-legged Hawk in response to variations in this prey species. Our

ability to detect a functional response by these predators was, however, limited by the relatively narrow range of prey density over which consumption rate could be measured in the field. Nevertheless, measured predation pressure by the dominant avian predators, Snowy Owls, Rough-legged Hawks, and especially Long-tailed Jaegers, suggests that it has the potential to limit lemming populations during the snow-free period on Bylot Island, which supports our third hypothesis. These observations are in accordance with previous studies

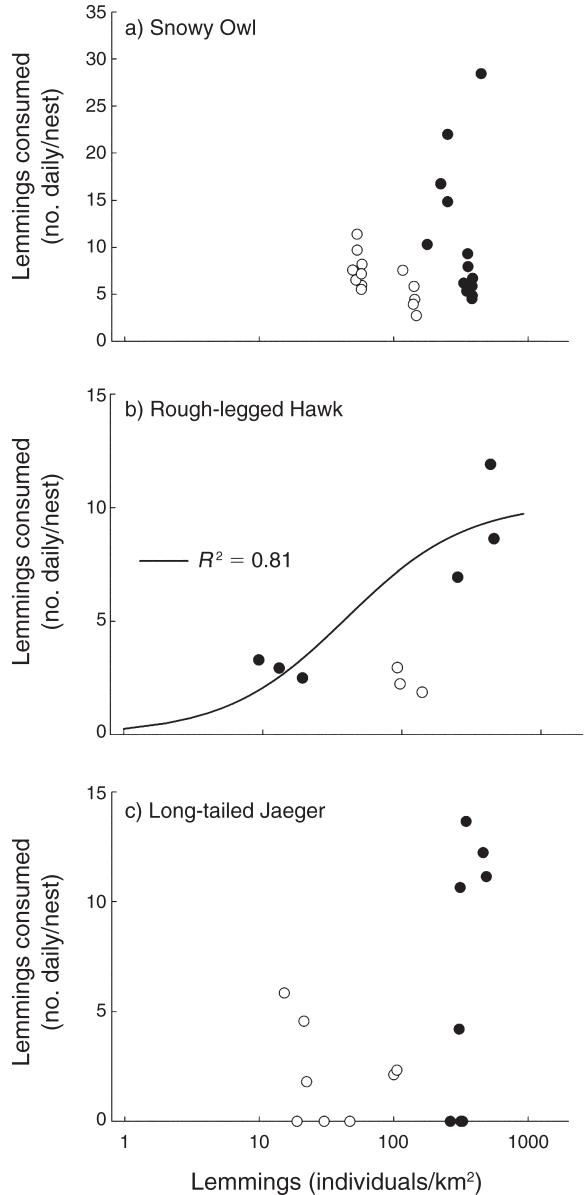


FIG. 5. Daily consumption rate by breeding pairs of the main avian predators in relation to daily density of brown and collared lemmings on Bylot Island, Canada (2007–2010). Open circles represent collared lemmings, whereas solid circles and the solid line represent brown lemmings. Significant relationships are shown.

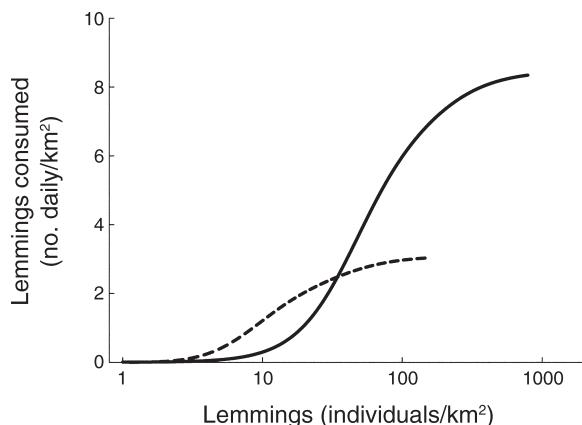


FIG. 6. Total daily lemming consumption by the three main avian predators in relation to the density of each lemming species in early summer on Bylot Island, Canada (dashed line represents collared lemmings while solid line represents brown lemmings; 2004–2010).

conducted in the central Canadian Arctic where the collared lemming was apparently continuously maintained at low density by predators during summer time (Reid et al. 1995, 1997).

Even though up to six avian predators may occur at our study site, our analysis focused primarily on the three most abundant species. Peregrine Falcons, Glaucous Gulls, and Parasitic Jaegers are additional predators known to prey upon lemmings to some extent during the breeding season (Pitelka et al. 1955, Gilchrist 2001, White et al. 2002, Legagneux et al. 2012), but none of them showed any aggregative numerical response to lemming densities and their densities were relatively low, except for the Glaucous Gull (Figs. 2 and 3). Failure to include these species in our estimation of the overall predation rate should not have changed much our conclusions on predation patterns. Nonetheless, it probably rendered our evaluation of the impact of predators on lemming populations somewhat conservative.

Despite the very high potential growth rate of the species, lemming populations remained fairly stable or decreased during the summer in most years, which is consistent with the high predation pressure recorded at our study site. Although the small sample size and the methods used to estimate population size at low density limited our ability to detect statistically significant relationships, the summer population change of both lemming species appeared negatively associated with the estimated predation intensity by avian predators. However, several other factors may contribute to the variability in summer population change, and longer time series would be needed to confirm such trends. Spatial heterogeneity in predation pressure and population growth rate at the landscape scale may contribute to variation in lemming population change. Moreover, predation rate by other predators (especially arctic fox

and stoat) can be a major source of annual variation in summer population change because these species also have the potential to strongly influence lemming population dynamics (Gilg et al. 2006, Bilodeau 2013).

A combination of factors may contribute to the high lemming predation rates by avian predators that we observed during the snow-free period. First, the open landscape and scant cover characteristic of the tundra environment may provide few refuges for small mammals during the snow-free period, thereby increasing their vulnerability to predation (Ims and Andreassen 2000). Second, the diverse suite of predators present on the tundra and their associated diverse hunting behaviors may further increase the vulnerability of lemmings. Finally, subsidies acquired from adjacent ecosystems or the presence of alternative prey species (Henden et al. 2010, Gauthier et al. 2011, Therrien et al. 2011, Giroux et al. 2012) may help to maintain the populations of some predators at higher levels than autochthonous resources would allow in this relatively low productivity environment. However, the latter phenomenon is not unique to Bylot Island and may actually be widespread across the Arctic, especially in North America (Gauthier et al. 2011).

Overall, the collared lemming suffered a higher predation rate than the brown lemming and its population generally declined during the summer (i.e., negative growth rate). Proportion of collared lemmings in the diet of the three main avian predators decreased when lemming density increased, most likely because in years of high abundance, the brown greatly outnumbered the collared lemming. Nonetheless, the collared lemming was most often consumed in a greater

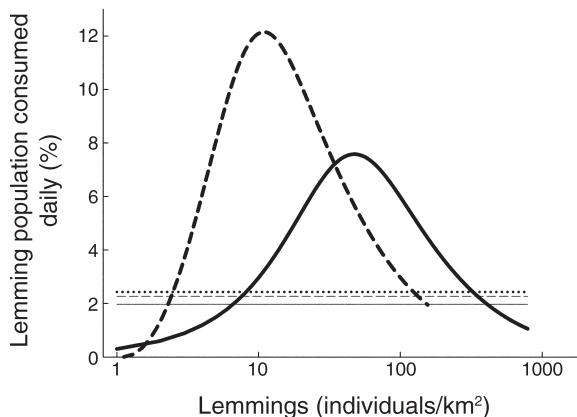


FIG. 7. Daily predation rate (percentage of the lemming population consumed) by avian predators in relation to the density of each lemming species in early summer on Bylot Island, Canada (dashed thick line represents collared lemmings, while solid thick line represents brown lemmings; 2004–2010). The horizontal lines represent various estimates of maximum daily potential growth rate of collared lemming (dashed thin line = 2.27%), brown lemming (solid thin line = 1.97%), and lemming spp. (dotted line = 2.44%; see *Materials and methods: Total responses*).

proportion than their relative availability in the overall lemming population, suggesting a selection toward this species. Those differential predation rates may be a key factor explaining the divergent population dynamic observed in these two species when they occur in sympatry (Gruyer et al. 2010, Krebs et al. 2011). Indeed, on Bylot Island, the collared lemming seldom reaches densities higher than 125 individuals/km² in contrast to Greenland, where it is the only lemming species present and where densities can be as high as 1000 individuals/km² in a peak year (Gilg 2002, Gilg et al. 2003). Our results suggest that the two lemming species are influencing the other population, either through direct competition (Morris et al. 2000), or perhaps more likely indirectly via apparent competition due to shared predators (Holt 1977), with the collared lemming apparently being more vulnerable to avian predation. By attracting large densities of avian predators during population outbreaks, the brown lemming would contribute to further depress collared lemmings and keep their populations at relatively low densities.

Our conclusions are limited to the range of lemming densities encountered during the study period. A legitimate question to ask is whether lemmings could escape from this apparent regulation by avian predators at low to intermediate density and become limited by other factors like food resources, as suggested in other studies (Pitelka and Batzli 2007). The numerical aggregative responses that we recorded for the main avian predators eventually leveled out, as evidenced by the asymptotic curves observed in most species, possibly due to territoriality. Because lemming reproduction starts under the snow and predation by birds is likely to be weak when the snow cover is present, lemmings could reach densities in early summer that are already beyond the range over which limitation by avian predators could occur. This is apparently not the case in collared lemmings as densities have never exceeded ~125 individuals/km² at our study site. However, brown lemmings densities up to 1000 individuals/km² or more have previously been recorded at our study site (Bilodeau et al. 2013a), which is beyond the value up to which limitation by avian predators occurred in this study (up to 325–410 individuals/km²). If brown lemming density exceeds such threshold in early summer in some years, this could allow them to maintain positive population growth during the summer despite the high consumption rate of avian predators. Therefore, the role of avian predation in the regulation of lemming population dynamic could be modulated by factors influencing their population growth rate during the long winter period from October to May (e.g., quality of snow cover; Bilodeau et al. 2013a). On the other hand, it is also possible that avian predators could still increase their numerical reproductive responses, and hence, their predation pressure if resource levels were higher. Indeed, over the range of lemming density recorded during the study period, the three main avian predators apparently

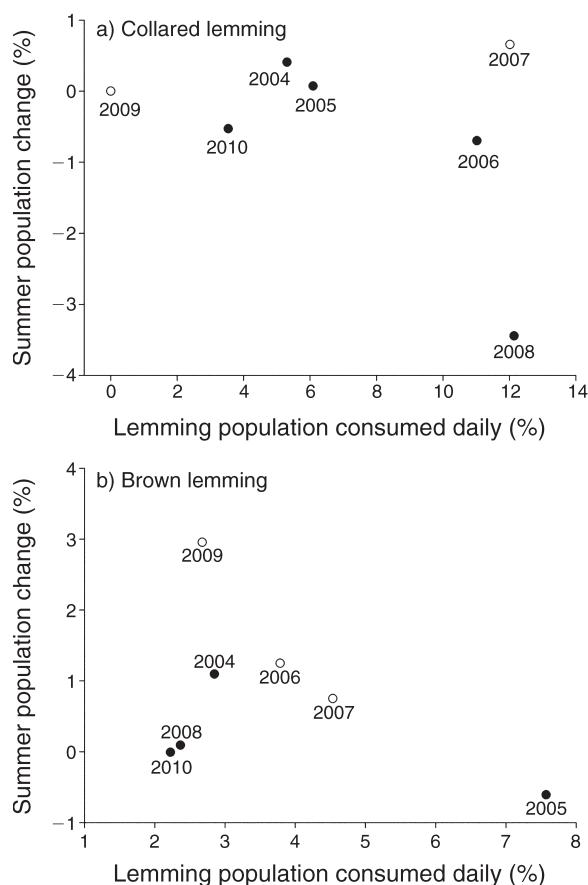


FIG. 8. Relationship between summer population change and estimated predation rate (percentage of the lemming population consumed daily) by avian predators for (a) collared lemmings and (b) brown lemmings on Bylot Island, Canada (2004–2010). Open circles represent estimates using minimum number alive (MNA), and solid circles represent estimates using capture–mark–recapture (CMR; see *Materials and methods*).

did not reach their maximum reproductive capacity and the average fledgling numbers per nest that we recorded during years of high lemming abundance were lower than the maximum reported for those species (Parmelee 1992, Bechard and Swem 2002, Wiley and Lee 1998). Finally, mammalian predation was not taken into account and any lemmings consumed by predators such as the arctic fox and the stoat should be additive to those taken by avian species. Using a mass balance model, Legagneux et al. (2012) recently showed that the combined consumption rate of avian and mammalian predators was sufficient to limit at low density the annual population of collared lemming at our study site.

In conclusion, the combined predation pressure exerted without delay by avian predators is likely sufficient to limit lemming populations at low levels during the snow-free period over a wide range of densities in the Canadian Arctic. This situation may thus be similar to the ones previously reported for collared lemmings in Greenland (Gilg et al. 2006) and

voles in the boreal forest (Korpimäki 1985, Korpimäki and Norrdahl 1989, 1991a, Ims and Andreassen 2000). Our study adds to the growing evidence that mobile avian predators, in combination to resident mammalian predators, may drive the population dynamics of small mammals in many parts of the tundra (Reid et al. 1997, Gilg et al. 2003, Ims et al. 2011, Legagneux et al. 2012).

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