# Anthropogenically-induced population increases in sympatric breeding arctic geese incur apparent competition consequences

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## Abstract

Populations of Lesser Snow Geese *Anser caerulescens caerulescens* and Cackling Geese *Branta hutchinsii* have increased substantially since the mid-20th century because of their utilisation of agricultural crops as a food resource on their wintering grounds. In contrast, Atlantic Brant Geese *Branta bernicla hrota*, which specialise in feeding on submerged marine vegetation in winter, have not capitalised on the availability of agricultural crops to the same extent. On the breeding grounds, Atlantic Brant are also adversely affected by multiple forms of competition from other sympatrically-nesting goose species. There has however been little research on apparent competition between these three species. Apparent competition occurs whenever the presence of one species leads to a reduced population density of another species when they share a generalist predator. To determine whether apparent competition stemming from higher goose nest densities might be a functional mechanism in limiting Atlantic Brant Goose reproduction, we monitored artificial nest survival in high, medium, and low goose nest densities at East Bay, Southampton Island, Nunavut, Canada in July 2015. Eggs in artificial nests located in high-density plots had the lowest survival probabilities compared to those in medium- and low-density plots. These results support the hypothesis that the increase in nest densities resulting from anthropogenically-induced population increases of sympatric native competitors could induce decreased breeding success and a cumulative decline in numbers of nesting Atlantic Brant via apparent competition.

**Key words:** artificial nests, nest density, predation, survival, waterfowl.

Apparent competition occurs when the presence of one species leads to a reduced population density of another species when they share a generalist predator (Holt 1977). Theoretically, predators can be attracted to foraging areas of high densities of one prey, and if an alternative prey is more accessible or more vulnerable, it may suffer increased predation risk (Holt & Kotler 1987). Apparent competition may be further exacerbated when one species population increases as a result of human influence on their environment (*e.g.* subsidised feeding or climate change impacts on food availability and environmental stochasticity; Robinson *et al.* 2002; DeCesare *et al.* 2010; DeMars *et al.* 2023). In the arctic, predator-prey relationships are relatively simple and driven primarily by trophic interactions between Arctic Foxes *Vulpes lagopu*, lemmings *Lemmus trimucronatus* and *Dycrostonyx groenlandicus* and nesting birds (Gauthier *et al.* 2004; Giroux *et al.* 2012; McKinnon *et al.* 2013), so the population explosion of one prey species (*e.g.* Lesser Snow Geese *Anser caerulescens caerulescens*) can have serious consequences on alternative prey such as shorebirds (McKinnon *et al.* 2013; Flemming *et al.* 2019).

Populations of mid-continent Lesser Snow Geese increased from a few million to *c.* 15 million between the 1960s and 2015 with consequences that resonated throughout ecosystems (Fox & Leafloor 2018a; Rosenfeld *et al.* 2021). Numbers of mid-continent Cackling Geese *Branta hutchinsii* increased from *c.* 400,000 to *c.* 3.6 million (Fox & Leafloor 2018a) and the breeding range of Ross's Geese *Anser rossii* also expanded over the same period (Moser 2001). The increases in abundance of these species at annual rates of 6–7% was associated with: (1) increased use of agricultural foods on migration and wintering grounds resulting in higher survival rates, (2) lower harvest rates, and (3) benefits of climate change, specifically a warming arctic and earlier springs (Batt 1997; Abraham *et al.* 2012; Juhasz *et al.* 2020). The negative implications of Lesser Snow and Cackling Goose population expansions on vegetation communities in their subarctic and arctic staging and nesting grounds are well known (Jefferies *et al.* 2003; Ward *et al.* 2005; Jefferies *et al.* 2006; Abraham *et al.* 2012; Flemming *et al.* 2019).

The Atlantic Brant *B. b. hrota* is a small arctic goose that coinhabits its Canadian arctic nesting grounds with Lesser Snow, Cackling and Ross's Geese but has a very different life history strategy. This species specialises in feeding on submerged marine aquatic vegetation (sea lettuce *Ulva* sp. and *Enteromorpha* sp.) and Common Eelgrass *Zostera marina* in winter, which did not permit the population expansions associated with those that feed primarily on agricultural crops (Ladin *et al.* 2014; Fox & Abraham 2017; Abraham *et al.* 2020). Most Atlantic Brant nest in the Foxe Basin, Nunavut, Canada and they winter around coastal New Jersey and New York, USA. The size of the wintering population has been fluctuating for a long-time with a slow decline in numbers from 2008–2015 and a steadier decline since 2017 (Fox & Leafloor 2018b; U.S. Fish & Wildlife Service 2020, 2022). Furthermore, the mean percentage of juveniles in the population has been only 17% per year between 2012 and 2015 compared to 22% per year between 1975–2011 (Fox & Leafloor 2018b; Roberts *et al.* 2021). A possible explanation for such a low proportion of juveniles is reduced reproductive success due to limiting factors on the nesting grounds. For example, Southampton Island's East Bay, on the southern end of the Foxe Basin, supported a nesting colony with, at minimum, 455 nesting Atlantic Brant pairs in 1979 as well as large numbers of Lesser Snow Geese ($n$ = 250) and a small number of Cackling Geese ($n$ = 35; Abraham & Ankney 1986). In 2010, 2014 and 2015, however, only 75, 44 and 78 Atlantic Brant nests were discovered in the same nesting area, which suggested that breeding opportunities may be limited on the island (Nissley 2016).

Nissley (2016) found evidence that increased numbers of Lesser Snow Geese and Cackling Geese may be detrimental to nesting Atlantic Brant through pre-emptive interference and exploitative competition, especially between Cackling Geese and Atlantic Brant, for nesting locations. Exploitative competition is direct competition for resources (*e.g.* food), interference competition involves aggressive behavioural interaction (*e.g.* displacement from nesting or foraging sites), and pre-emptive competition is a form of exploitative competition where individuals occupy a space (*e.g.* nesting sites) and prevent its use by others (van Riel *et al.* 2007). In this particular case, pre-emptive competition manifests as Lesser Snow or Cackling Geese occupying Atlantic Brant nest habitat, interference competition manifests as more general aggression by Lesser Snow and Cackling Geese toward Atlantic Brant, and both interference and exploitative competition manifest as habitat degradation and food depletion through Lesser Snow and Cackling Geese decreasing the standing biomass of sedges *Carex* sp. (Abraham *et al.* 2020) which is the preferred food of the Atlantic Brant (Nissley 2016). Pre-emptive and interference competition likely reduce the number of nests initiated, whilst interference and exploitative competition reduce nest success and brood survival.

The three species all overlap in their nesting habitats, but Atlantic Brant and Cackling Geese overlap to a greater degree than Atlantic Brant and Lesser Snow Geese, as the Lesser Snow Geese tend to nest in upland locations more than the other species (Abraham & Ankney 1986). Lesser Snow and Cackling Geese are larger in size and arrive on the breeding grounds *c.* 1–2 weeks before Atlantic Brant. Lesser Snow Geese also have larger absolute fat reserves on arrival, accumulated during migration, so have a greater tendency towards capital breeding (which permits a prompt start to the breeding season), although they do use a mix of capital and income breeding strategies (Klassen *et al.* 2006). The smaller-bodied Brant has less capacity to store fat reserves and thus typically follow an income breeding strategy, with food foraged on the breeding grounds typically contributing most of the energy required for egg production (Ankney 1984; Vangilder *et al.* 1986; Schmutz *et al.* 2006; Lübcker *et al.* 2023). In warm years, Lesser Snow and Cackling Geese, which migrate sooner than Brant, can access higher quality nesting and post-hatch foraging sites sooner (Raveling

1978; Dickey *et al.* 2008). For instance, earlier nest initiation dates in warmer years have been associated with higher survival rates and clutch sizes in Cackling Geese (Kellett & Alisauskas 2011). In cold years, however, emergence of these resources from beneath the snow and ice is delayed, causing later nest initiation or potentially nesting failure for species that arrive early and are unable to gain the body condition needed to breed successfully during the short arctic summer (Cooke *et al.* 1984; Abraham & Ankney 1986). By arriving later, the Atlantic Brant effectively have a bet-hedging strategy, whereby they will consistently find food and nesting sites upon arrival. Hence, in warm years, Atlantic Brant may be outcompeted but in cold years they are more likely to have readier access to resources.

Global climate change is predicted to increase in severity and exhibit a greater frequency of short-term extreme climate events but also reduced snow cover (Coumou & Rahmstorf 2012; IPPC 2021). Therefore, the outcompeted and declining Atlantic Brant are potentially an indicator species for negative ecosystem impacts associated with climate change. The later nesting phenology of Atlantic Brant puts them at risk of increased terrestrial Arctic Fox depredation once the earlier species vacate nesting areas to move to brood rearing areas and the Atlantic Brant remain the only goose species with eggs. While pre-emptive, interference, and exploitative competition have been documented among geese at East Bay (Nissley 2016), it is unknown whether an increase in the numbers of Lesser Snow Geese and Cackling Geese has encouraged increased mesocarnivore predation and thus exposed the local population of Atlantic Brant to apparent competition. Apparent competition could happen if predators are disproportionately drawn to higher densities of Lesser Snow and Cackling Geese nests and broods, which could theoretically reduce nest success and brood survival of other species, such as Atlantic Brant, Common Eiders *Somateria mollissima* and shorebirds.

Deployment of artificial nests is one method of studying the potential impact of predation and has been used reliably in earlier arctic goose studies (Bêty *et al.* 2001; Lecomte *et al.* 2008). To determine whether apparent competition could be a functional mechanism in limiting Atlantic Brant Goose breeding success, we conducted an artificial nest depredation trial, in which artificial nests simulated goose nests, and survival probabilities for high, medium, and low nest density scenarios were calculated. Previous studies have investigated apparent competition of Snow Geese with other species (McKinnon *et al.* 2013; Lamarre *et al.* 2017), but none involved colonies with multiple goose species or Atlantic Brant. We hypothesised that depredation rates in high nest density areas would be higher than in areas with nests at low and medium density.

## Methods

### Study area

Research was conducted in the East Bay Migratory Bird Sanctuary, Southampton Island, Nunavut, Canada. The study area extended west to 82.031°W and east to 81.770°W (Fig. 1). East Bay Migratory Bird Sanctuary is a tundra habitat dominated by

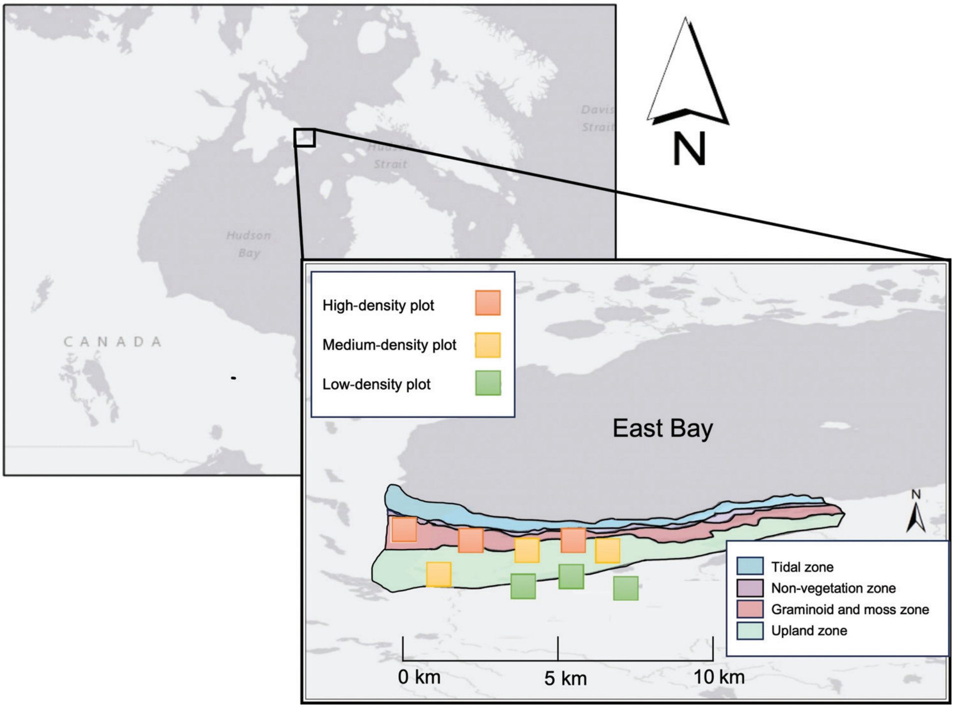

**Figure 1.** Study area on the south shore of East Bay, Southampton Island, Nunavut, Canada. Most of the Lesser Snow Geese, Cackling Geese and Atlantic Brant nested from the tide line to *c.* 3 km inland. Colours represent nest habitat zones that were searched: light blue = tidal, purple = non-vegetated, red = graminoid and moss dominated, and green = upland. Squares indicate the location of the study plots and the nesting density of migratory geese in each plot: high ($\geq$ 30 nests/km$^2$, average = 30.2 nests/km$^2$, purple), medium (5–10 nests/km$^2$, average = 15.2 nests/km$^2$, yellow), and low-density plots (1–2 nests/km$^2$, average = 1 nest/km$^2$, green). Ten artificial nests with 1–2 chicken eggs were also put in place for each plot, to measure egg predation rates in areas with high, medium and low nesting density.

ponds and lakes. It includes four general zones: tidal, non-vegetated (rock dominated), graminoid (with sedges *Carex subspathacea* and *C. aquatilis*, Fisher's Tundragrass *Dupontia fisheri* and moss vegetation), and upland areas (dominated by Entire-leaved Mountain Avens *Dryas integrifolia* and Dwarf Willow *Salix herbacea*). All three species of geese co-exist across the study area, primarily in the graminoid and moss zone and the non-vegetated zone with Lesser Snow Geese and Cackling Geese also occurring in the bordering upland zone (see Nissley 2016 for nesting locations). These saltmarsh plant communities have been affected by the grazing and grubbing activity of both Lesser Snow Geese and Cackling Geese in recent decades, resulting in significant loss of plant species biodiversity and abundance, exposure of peat, hypersalinity and soil compaction (Abraham *et al.* 2012, 2020).

## Artificial nest protocol

In 2015, peak Lesser Snow Goose, Cackling Goose and Atlantic Brant hatching occurred between 14–23 July and we conducted our artificial nest experiment 11–12 days earlier, from 2–11 July 2015. Densities of all nesting goose species therefore were at a maximum during our study. Nest searching was completed prior to the start of the experiment so nest densities were known. Using the Garmin programme Basecamp (Garmin licensed software), we established artificial nests in high (≥ 30 nests/km$^2$; mean ± s.e. = 30.2 ± 7.1 nests/km$^2$, $n$ = 3 plots), medium (5–15 nests/km$^2$; mean ± s.e. = 15.2 ± 2.9 nests/km$^2$, $n$ = 3 plots) and low-density plots (1–2 nests/km$^2$; mean ± s.e. = 1.0 ± 0.0 nests/km$^2$, $n$ = 3 plots). High-density plots were composed of 73% Cackling Goose, 23% Lesser Snow Goose and 4% Atlantic Brant nests. Goose densities for each species were relatively uniform across the high nest density area, although Atlantic Brant and Cackling Geese were more common in the east and Lesser Snow Geese were more common in the west. Medium-density plots were composed of 74% Cackling Goose, 25% Lesser Snow Goose and 1% Atlantic Brant nests. Low-density plots were composed of 50% Cackling Goose, 50% Lesser Snow Goose and 0% Atlantic Brant nests.

The plots were randomly distributed across these three habitat zones used as nesting areas by the geese (*i.e.* excluding the tidal zone). However, the general pattern was that high-density plots were in the more coastal moss and graminoid zone, whereas the medium and low-density plots were slightly further inland (Fig. 1). All nine plots measured ≥ 1 km$^2$, each plot was separated from all other plots by 1 km, and there were with three replicates per density level. Using the Basecamp program (Garmin Inc.), we generated 10 random points within each plot which determined the artificial nest locations.

We followed a modified version of the Arctic Wildlife Observatories Linking Vulnerable EcoSystems (ArcticWOLVES) artificial nest monitoring protocol (McKinnon *et al.* 2008). To construct a nest, five members of the research team located the randomly generated nest locations with a hand-held GPS unit over a 2-day period and used local vegetation to construct a simulated (realistic) goose nest. Two chicken eggs were placed in each nest. Chicken eggs have reliably been used in previous artificial nest studies which focused on predation of arctic geese (Bêty *et al.* 2001; Lecomte *et al.* 2008). Latex gloves were worn during nest construction and daily checks of the nests were minimised to reduce human scent around the nest site. A labelled popsicle stick was placed 5 m north of each artificial nest and the coordinates (latitude and longitude) of the nest were logged on a hand-held GPS unit. Establishing all artificial nests during the first 2 days of the experiment provided a uniform start across the three density levels. They were checked after 12, 24 and 72 h, then at 6 and 9 days, or until 90% of the nests had failed (McKinnon *et al.* 2008). At each artificial nest check, the level of depredation was recorded as partial (1 egg depredated), complete (2 eggs depredated), or none (both eggs present). Any other relevant details regarding the nest were also recorded.

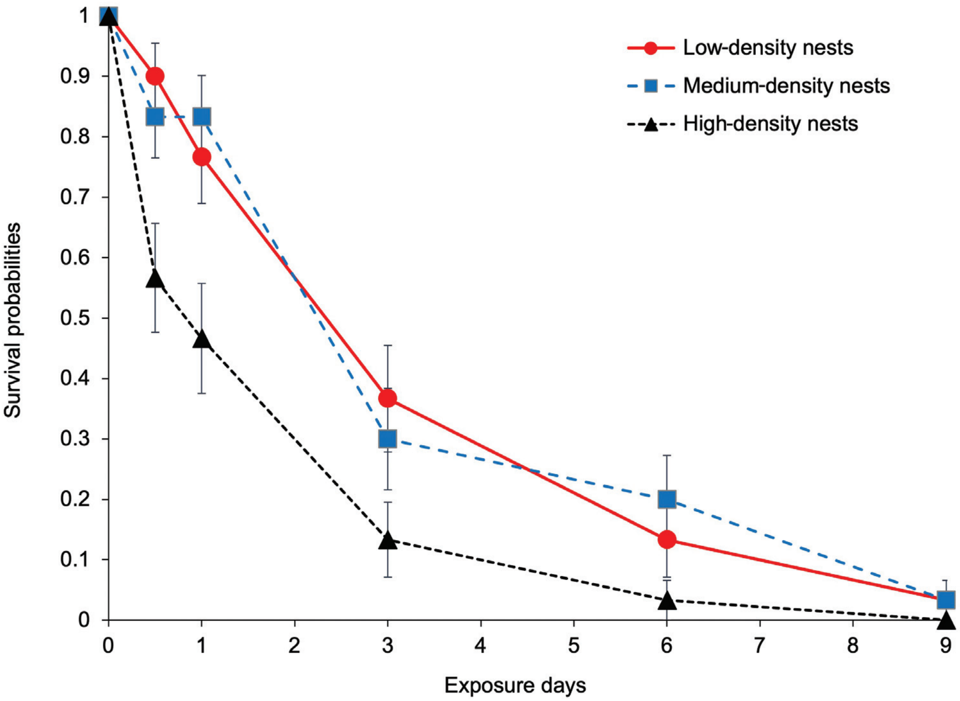

**Figure 2.** Survival probabilities for artificial nests placed in high ($\geq 30$ nests/km$^2$, black fine dotted line with triangle points), medium (5–10 nests/km$^2$, blue coarse dotted line with square points) and low nesting density (1–2 nests/km$^2$, red solid line with circular points), for up to 9 exposure days after the construction of the artificial nests on East Bay, Southampton Island, Canada, 2–11 July 2015.

Mammalian predators tended to carry off the eggs or eat the entire clutch of eggs, while avian predators typically broke the egg open at the nest and left egg fragments, allowing us to identify whether the predator was avian or mammalian. We also searched for faeces that would indicate fox presence (McKinnon *et al.* 2008). If the nest was fully depredated, the popsicle stick was removed, and the nest was no longer included in nest checks. Depredation probabilities were calculated following Kaplan and Meier (1958) using nest success (had 1 or 2 eggs) or failure (had 0 eggs) and the timing of complete depredation. We compared pairwise survival across goose density levels using a log rank Mantel-Cox chi-square test ($\alpha \leq 0.05$).

## Results

While most nests across all plots failed by day 9, the rate of failure differed with density, with artificial nests in high-density plots being depredated more rapidly. Mammalian predation (*e.g.* by Arctic Fox or Polar Bear *Ursus maritimus*, identified from trail cameras in a companion study; Nissley 2016) accounted for 91% of nest failure and avian (Herring Gull *Larus argentatus*) predation accounted for the remainder. The nest survival for high-density locations went from 0.567 at 12 h to 0.467 at 24 h, 0.133 at 72 h, 0.033 at 6 d and 0.000 at 9 d. Survival for medium-density went from 0.833 at 12 h and 24 h to 0.300 at 72 h, 0.200 at 6d and 0.033 at 9 d. Survival for low-density went from 0.900 at 12 h to 0.767 at 24 h, to 0.367 at 72 h, 0.133 at 6 days and 0.033 at 9 days. Because fewer than 10% of artificial nests remained at 9 days, a final check at 12 days was not conducted. Survival within the high-density plots was significantly lower than for both the medium- ($\chi^2_1 = 8.82$, $P < 0.01$) and low-density plots ($\chi^2_1 = 7.58$, $P < 0.01$). Cumulative nest survival recorded for the medium- and low-density plots did not differ significantly ($\chi^2_1 = 0.09$, $P = 0.77$, n.s.). The time to nest failure was also associated with the distance of the nests from the shoreline, a function of the higher goose nest densities being closer to the shore (linear regression: $F_{1,88} = 7.29$, $P = 0.01$, Fig. 3).

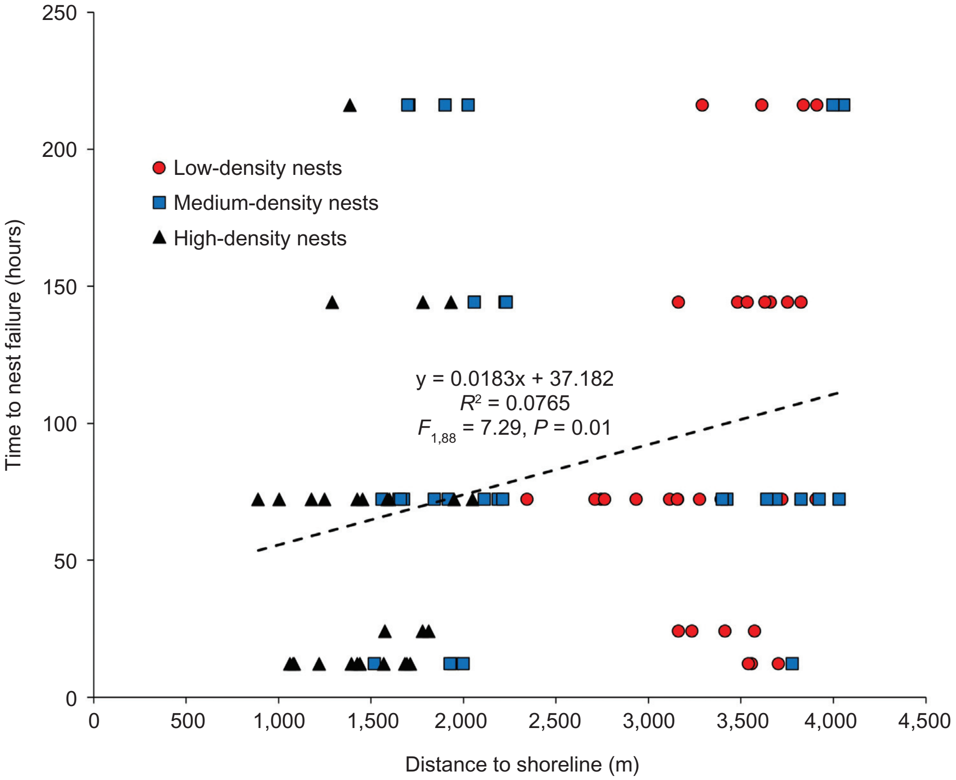

**Figure 3.** Time to nest failure as a function of the distance to the shoreline for artificial nests placed in high (≥ 30 nests/km$^2$, black triangle points), medium (5–10 nests/km$^2$, blue square points) and low nesting density (1–2 nests/km$^2$, red circular points), for up to 9 exposure days after the construction of the artificial nests on East Bay, Southampton Island, Canada, 2–11 July 2015.

## Discussion

Our artificial nest experiment demonstrated an effect of goose nest density on depredation probability, supporting the hypothesis that apparent competition may be adversely affecting Atlantic Brant nesting at this study site. Apparent competition is known to be a driving force in ecological systems and has been shown to play a role in influencing the population dynamics of species (Holt & Kotler 1987; Bonsall & Hassell 1997). Researching potential apparent competition in a simple arctic system allowed us to test for the impacts of apparent competition across different nesting densities while limiting the confounding effects of habitat variation.

Lesser Snow Goose and Cackling Goose populations have increased at East Bay (Abraham & Ackney 1986; Abraham *et al.* 2020). Atlantic Brant nests suffered high depredation and low nest success rates in the 2014 (17%) and 2015 (5%) breeding seasons (Nissley 2016), as opposed to an 86% success rate in 1979 and 65% in 2010 (Abraham & Ackney 1986; K. Abraham & C. Sharp, unpubl. data). While higher densities and communal breeding strategies can improve nest defence in geese, it also likely allows foxes to maximise searching efficiency, which gives them the greatest energy input with lowest expenditure.

Spatial position in a goose colony could influence nest defence strategies and thus the relative effect of apparent competition and nest depredation. Low-density Atlantic Brant colonies experienced high rates of depredation in a study by Raveling (1989), but neither Lesser Snow Geese nor Cackling Geese were mentioned as sharing colonies with Atlantic Brant in that study. Baldwin *et al.* (2011) showed higher nest success for Cackling Geese when they nested inside a Ross's Goose colony, compared to those outside colonies, likely because of the benefits of group nest defence. However, Cackling Goose nest success decreased drastically when there were more than 20 Ross's Goose nests within 30 m and predation was extremely high in the densest areas, so there is a point at which high-density is detrimental even when group defence is occurring (Ims & Fuglei 2005). Unlike the Cackling Geese in Ross's Goose colonies, Atlantic Brant rarely nest in the upland environment where Lesser Snow Geese nest. Instead, they nest on the periphery or outside the high-density portions of the Lesser Snow Goose colony in the graminoid moss zone closer to the shore, so they could be affected differently by group defence. Of note, higher densities of nests were also seen closer the shoreline, thus possibly maximising the predation efficiency of foxes travelling linearly through the goose colony parallel to the shore. It is therefore possible the goose nest success could be reduced by a combination spatial placement to shore, apparent competition and Arctic Fox movement patterns.

It is worth noting some limitations of this study. Effect sizes were not calculated because of small sample sizes. It would be beneficial for future studies to use larger sample sizes and calculate effect sizes, if possible. Additionally, observations at artificial nests are not always a perfect reflection of true predation risk, although the simple nature of the ecosystem in our experiment potentially increases its chances of accurately reflecting true nest predation risk (MacInnes 1962). It is also possible that the differences in between-site predation rates could be related to other factors such as habitat differences. Because the higher density nests, which suffered higher depredation, were closer to shore there could be additional interactive effects complicating independent apparent competition. While our results show evidence for an association between increased multi-species goose nest density and increased probability of depredation via apparent competition, we recommend future research into varying levels of goose densities and predation rates across various habitat types and years to account for trophic interactions between these variables.

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**Photograph:** Arctic Fox taking an egg from an Atlantic Brant Goose nest, caught on trail camera, by Clark Nissley.