



RESEARCH ARTICLE

Resource partitioning among avian predators of the Arctic tundra

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Abstract

1. Interspecific competition can play a key role in structuring ecological communities. The Arctic tundra is a low productivity ecosystem supporting simple food webs, but several predators often feed on the same prey species, lemmings, known for their large-amplitude population fluctuations.
2. We examined mechanisms involved in reducing intra-guild competition and allowing coexistence of four avian predators (snowy owls, glaucous gulls, rough-legged hawks and long-tailed jaegers) feeding on a pulsed resource (brown and collared lemmings). We compared the size and species of prey consumed by predators to see if resource partitioning occurred. We also verified if spatial segregation in nesting areas could be another mechanism allowing coexistence. Finally, we tested if the absence of the snowy owl, a dominant and irruptive species, triggered a competitive release on the smallest predator, the jaeger, with respect to prey size and nesting area used.
3. We monitored the breeding of predators and lemming abundance over a 14-year period on Bylot Island, Canada. We mapped their nesting sites and collected regurgitation pellets to recover lemming mandibles, which were used to infer prey species and size.
4. The size of lemmings consumed varied among species with the largest predators consuming the largest lemmings and the smallest predators consuming the smallest lemmings. All predators consumed more collared than brown lemmings compared to their availability although owls and jaegers consumed relatively more brown lemmings compared to gulls and hawks. Jaegers consumed larger lemmings in the absence of owls than in their presence, suggestive of a short-term competitive release. We found moderate to low overlap in nesting areas among predators and no evidence of their expansion in the absence of owls, suggesting that spatial distribution is caused by species-specific habitat preferences.
5. The main mechanism to partition food resources among these avian predators is spatial segregation, and secondarily prey size and species. However, we found evidence that food competition is still present and leads to a niche shift in the smallest predator of the guild. Interspecific competition may thus be a pervasive force in simple, low productivity food webs characterized by pulsed resources.

KEYWORDS

diet, interspecific competition, jaeger, lemming, nesting territory, owl, prey size, raptors

1 | INTRODUCTION

The importance of interspecific competition in ecological communities is a long-standing debate in ecology (Dhondt, 2012). Some argue that interspecific competition is a key factor structuring ecological communities when resources are limited and shared among several consumers (Hardin, 1960; Hutchinson, 1959; MacArthur & Levins, 1967; Schoener, 1983). In contrast, others argue that the role of competition in communities is limited, especially when resources are varying temporally (Connell, 1983; Wiens, 1977). Several studies have examined how temporal fluctuations in resources affect the strength of competition but with contrasting results as some found that resource pulses promote species coexistence while others found that they increase competition (Chesson & Warner, 1981; Ostfeld & Keesing, 2000; Yang et al., 2008). Experiments have shown that species sharing the same resource in the same environment need to differentiate their niche to coexist or they will go extinct (Gause, 1934; MacArthur & Levins, 1967). Therefore, considerable efforts have been devoted to determine the mechanisms used by species to reduce competition and allow coexistence.

Species can coexist by changing their foraging technique, foraging sites, habitat or reproductive phenology (Ashmole, 1968; MacArthur, 1958). Various studies have unravelled the mechanisms through which multiple consumers sharing prey can minimize interspecific competition, for instance by partitioning resources or foraging areas. A classic example is the Serengeti ecosystem where many predators differentiate their diet by selecting one or a few prey species based on size (Sinclair et al., 2003). Another case is the resource partitioning by desert seed-eating ants and rodents based on seed size (Brown & Davidson, 1977; Davidson, 1977). Specialization on various prey types to avoid competition among coexisting raptors has also been documented (Gerstell & Bednarz, 1999; Poole & Bromley, 1988; Restani, 1991). However, very few studies have examined how multiple predators sharing only one or two main prey species could coexist in an ecosystem characterized by a low productivity and large resource pulses, a situation where strong interspecific competition could be expected.

The Arctic tundra is a low productivity ecosystem with minimal habitat structuring that supports relatively simple food webs (Krebs et al., 2003; Legagneux et al., 2014). In the high Arctic, several species of mammalian (foxes, mustelids) and avian (raptors, seabirds) predators often feed primarily on only one or two species of lemmings (Gilg et al., 2006; Legagneux et al., 2012). The most common avian predators of lemmings in the Canadian Arctic include two specialist species, the snowy owl *Bubo scandiacus* and the rough-legged hawk *Buteo lagopus*, a semi-specialist species, the long-tailed jaeger *Stercorarius longicaudus*, and a generalist species, the glaucous gull *Larus hyperboreus*. Lemmings are well known for their large amplitude, multi-annual population fluctuations where abundance can vary 100-fold or more between peaks and lows, which can be considered a resource pulse (Ehrich et al., 2020; Krebs, 2011). A diverse array of top predator species feeding on one or two highly fluctuating prey species are conditions that should lead to intense

interspecific competition. Examining how these species can coexist together in the simple tundra ecosystem is of special interest considering that predator–prey interactions appear to be a driver of lemming fluctuations in many parts of the Arctic (Fauteux et al., 2016; Gilg et al., 2003; Therrien, Gauthier, Korpimäki, et al., 2014).

We examined mechanisms involved in reducing intra-guild competition for limited resources among four common avian predators of the Arctic tundra. The main prey of these predators in the Canadian Arctic are two rodent species, the brown *Lemmus trimucronatus* and the collared lemming *Dicrostonyx groenlandicus*. We first hypothesized that these predators partition the resource by specializing on prey of different size and different species. Accordingly, we predicted that the body mass of lemmings consumed would be proportional to the predator body size, with larger species consuming larger lemmings and vice versa. We also examined if spatial segregation due to species-specific preference in nesting habitat could be another mechanism allowing coexistence. In this system, the jaeger and the owl are the two species that overlap the most in their habitat use but the owl is only present at the study site in years of peak lemming abundance (Therrien, Gauthier, Korpimäki, et al., 2014; Therrien, Gauthier, Pinaud, et al., 2014). We therefore hypothesized that the absence of the largest predator, the snowy owl, would trigger a short-term competitive release on the smallest predator, the long-tailed jaeger. We predicted that in years when snowy owls are absent, (a) the size of lemmings consumed by the long-tailed jaeger would increase, but not the size of prey consumed by the rough-legged hawk and the glaucous gull, and (b) the spatial distribution of jaeger territories would expand into areas normally occupied by owls, but it will stay constant for gulls and hawks.

2 | MATERIALS AND METHODS

2.1 | Study site and species

Fieldwork was conducted during the breeding season (May–August) in the Qarlikturvik Valley of Bylot Island (Nunavut; 73°08'N 80°00'W) in the Canadian high Arctic over a 58 km² area (Figure 1; Gauthier et al., 2011). The study area is composed of a large glacial valley with a mixture of wet meadows and mesic tundra in lowlands. The valley is surrounded by rolling hills and low-elevation plateaus near the sea and more mountainous areas upstream. Streams and rivers running through surrounding hills and plateaus have created gullies, narrow valleys and ravine with frequent outcrops and small cliffs. The mesic tundra is dominated by prostrate shrubs and a sparse cover of forbs and graminoids, whereas wet tundra is mainly composed of graminoids growing through a thick moss layer in fens.

Snowy owls are an irruptive and highly nomadic species and their summer diet is almost exclusively composed of lemmings (Therrien, Gauthier, Korpimäki, et al., 2014; Therrien, Gauthier, Pinaud, et al., 2014). Mean body mass is 1,700 g for males and 2,150 g for females (Richards & Gaston, 2018; J.-F. Therrien, unpubl. data). Rough-legged hawks also feed predominantly on

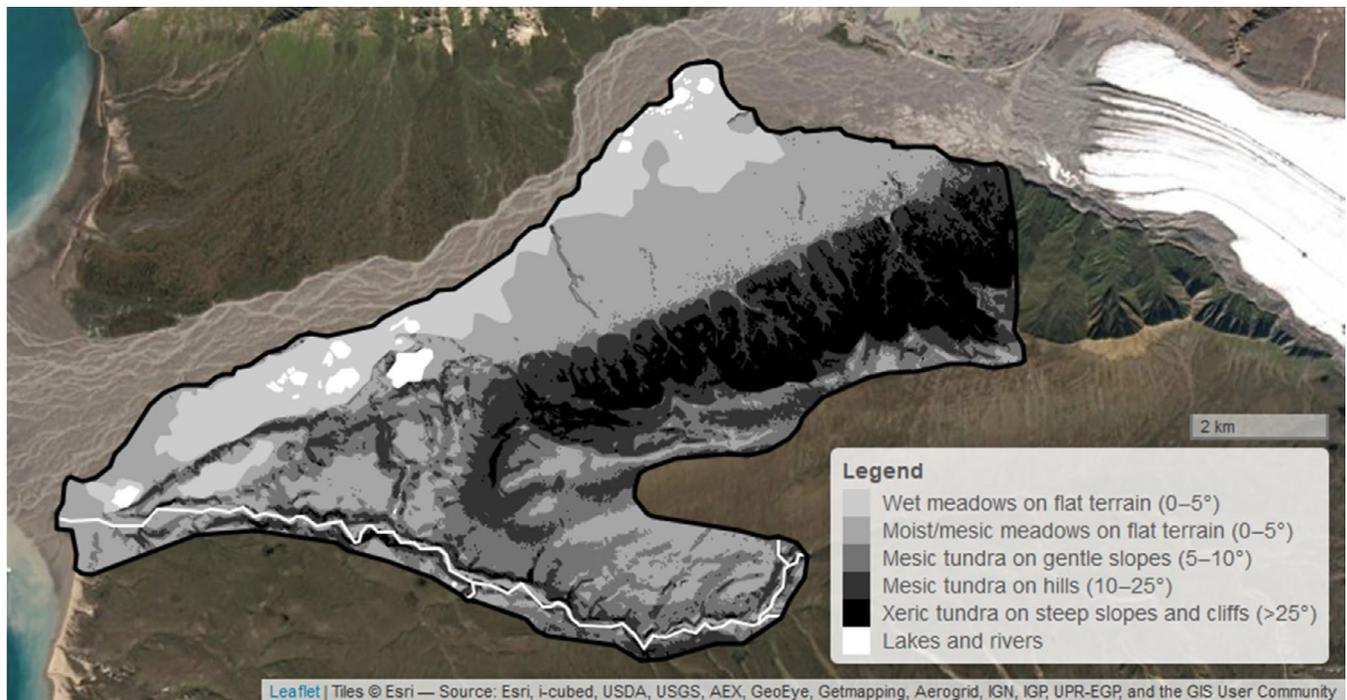


FIGURE 1 Main habitat types found in the 58-km² study area (Qarlikturvik Valley, Bylot Island, Nunavut; delimited by the thick black line) according to the wetness of the terrain and steepness of slopes. Digital elevation model (DEM) used to create the map is from Porter et al. (2018) and basemap from ESRI (2020)

lemmings and their breeding effort is related to annual abundance of small mammals (Beardsell et al., 2016). Their mean body mass is 950 g for males to 1,200 g for females (Richards & Gaston, 2018; J.-F. Therrien, unpubl. data). Long-tailed jaegers are seabirds breeding on the tundra in summer where they rely heavily on lemmings but also on some other prey (small birds, arthropods; Maher, 1970). Their mean body mass is 290 g for males and 320 g for females (Seyer et al., 2019) and their breeding effort is also related to lemming abundance (Maher, 1970). Glaucous gulls have a more diversified diet than the other species and includes lemmings, bird eggs and young, fish and invertebrates (Gauthier et al., 2015). The mean body mass is 1,700 g for males and 1,350 g for females (G. Gauthier, unpubl. data, Richards & Gaston, 2018). Other avian predators present at the study area are the peregrine falcon *Falco peregrinus*, the gyrfalcon *Falco rusticolus* and the parasitic jaeger *Stercorarius parasiticus* but they occur at low density and feed only occasionally on lemmings (Fauteux et al., 2016). Two mammalian predators are also present, the Arctic fox *Vulpes lagopus* and the ermine *Mustela erminea*, and both feed heavily on lemmings (Gauthier et al., 2011).

Only two rodent species are present at the study site, the brown lemming and the collared lemming and they are similar in size [adult brown lemmings, 51 ± 14 g ($M \pm SD$), $N = 1,450$; adult collared lemmings 57 ± 12 g, $N = 155$; Gauthier, 2020]. The brown lemming is the most abundant species and shows large-amplitude fluctuations of abundance every 3–4 years, whereas collared lemmings show weak amplitude population fluctuations (Fauteux et al., 2015; Gruyer et al., 2008). Brown lemmings typically prefer moist grass and sedge

habitats in wet and mesic tundra, whereas collared lemmings tend to prefer drier habitats, mostly mesic and xeric habitat, but can also be found in wet habitat (Morris et al., 2000; Naughton, 2012).

2.2 | Nest monitoring and pellet analysis

The breeding activity of avian predators was studied from 2004 to 2017. Nest searches were carried annually to find all breeding pairs in the study area. Linear transects spaced out by 400 m were surveyed in lowlands and gentle slope areas to locate jaeger and gull nests, and survey routes along ridges in hilly terrain were systematically walked for owls and hawks in their potential breeding habitat. Because gulls and hawks are often faithful to their old nesting structures, previously used nest sites were revisited.

Active nests were georeferenced and visited every 1–2 weeks until hatching. Fresh regurgitation pellets were collected at a subsample of nests or nearby perching sites in the breeding territory. At the first visit, old pellets and prey remains were removed from the nest and discarded to collect only fresh pellets during the following visits. Pellets were placed in paper bags and air-dried for 2 weeks or dried in an oven for 48 hr before dissection. Overall, we collected and analysed 176 pellets of snowy owls, 327 pellets of glaucous gulls, 239 pellets of rough-legged hawks and 402 pellets of long-tailed jaegers. Pellets were not collected for all four species every year, except in 2008, because nests of some species were scarce or failed early in some years or because of reduced field effort.

Pellets were dissected to extract intact lemming mandibles and we identified them to species based on Naughton (2012). We measured the ramus–molar tooththrow (RMT) as described in Schmidt et al. (2020) of either the left or right mandibles of each lemming found depending on which side was the most numerous in each pellet. The body mass of lemmings consumed was estimated from their RMT measurement based on the equations provided by Schmidt et al. (2020) for Nunavut. Because those equations overestimated the body mass of lemmings with very large mandibles, we truncated estimates to a maximum value of 105 g for brown lemmings ($N = 2$) and 118 g for collared lemmings ($N = 4$).

2.3 | Lemming monitoring

We live-trapped lemmings annually in two permanent 11-ha grids located in the centre of the study area, one in wet tundra habitat and one in mesic habitat (Fauteux et al., 2015). Each grid had 144 trapping stations (100 from 2004 to 2006) separated by 30 m according to a Cartesian plane, and one Longworth trap was set at each station. Each trap was visited every 12 hr for 3–4 consecutive days during three trapping sessions in June, July and August (see Fauteux et al., 2015, for details). We identified all captured lemming to species, weighed them, and individually tagged them.

Lemming densities were estimated with spatially explicit capture–recapture analyses with the *secr* package (Efford, 2020; see details in Fauteux et al., 2015) for each trapping period and grid. We assumed that trapped lemmings were representative of the population of prey available for predators in years when pellets were collected. However, we recognize that density estimates were based on only two trapping grids and may not capture all spatial variability especially with respect to the relative abundance of each species. To avoid pseudo-replication, we only considered the body mass of an individual the first time it was trapped.

2.4 | Spatial analysis

We mapped habitat types in the study area based on Duclos et al. (2006) and Porter et al. (2018). Habitat types were wet meadows and moist/mesic tundra, both on flat terrain (0–5° slopes), mesic tundra on gentle slopes (5–10°), mesic tundra on hills (10–25°) and xeric tundra on the steepest slopes (>25°; Figure 1).

We estimated the area used by each predator species within the study area based on the location of nests found. We estimated the nesting area of each species using the adaptive local convex hull polygon (*a*-LoCoH) method (Getz et al., 2007). The *a*-LoCoH is based on the minimum convex polygon method in combination with a non-parametric kernel method (see Appendix S1 for more details on the method). We used the 90% isopleth to delimit the core area used for nesting by each species across years, hereafter called the nesting area. We delimited the area used by each species of predators by combining the nests found in the years of presence of owls (2004,

2008, 2010, 2014) and the years of absence of owls (2005–2007, 2009, 2011–2013, 2015–2017). We estimated the overlap in the area used for nesting by each pair of species in years with and without owls. We also calculated the annual density of nests for each species over the entire study area and within the nesting area of each species as defined above.

To estimate if the presence of an owl nest influenced territory settlement by jaegers, we used two approaches. First, we created buffer zones of 500 and 1,000 m around each owl nest and counted the number of jaegers nesting in these zones when owls were nesting. We selected the previous or following year, when owls were absent, and counted the number of nests in the same buffer zones. For this analysis, we did not consider years when no jaeger nest was found to avoid a false exclusion effect. We then estimated the proportion of all jaeger nests found annually in the study area that were located within these buffer zones. Second, we measured the annual displacement of jaeger nests between years with and without owls. To do so, we measured the distance between each owl nest and all jaeger nests within a 1,000-m radius of owl nests that year. We measured again the distance from the position of these owl nests and all jaeger nests found within the same radius in the previous or the following year when owls were absent.

We also determined the influence of owl nests on the annual displacement of individual jaeger nests using a sample of marked birds (see Seyer et al., 2019, for details). We only used the nests of individuals for which we knew their location in more than 1 year, excluding cases with a gap of >2 years between nest locations. We first used jaeger nests located <1,000 m from an owl nest to measure the distance between their nest in the year of owl presence and in the previous or following year. Second, we used the same method to calculate the displacement of jaeger nests located >1,000 m from an owl nest.

2.5 | Statistical analyses

To determine if there were differences in body mass of lemmings consumed among the predators and with available lemmings (i.e. trapped), we used linear mixed-effect models (LMMs) based on a restricted maximum likelihood approach (REML) from the package *nlme* (Pinheiro et al., 2018). For all models, we used the nest ID as random factor because more than one pellet was collected at each nest. For the lemmings available, we used trapping grid and year as a single random effect (i.e. each combination of grid and year was assigned a different ID). We tested for differences in body mass of lemmings consumed and available (both species combined) in the presence of owls (M1, Table S2.1) and in their absence (M2). A limitation of our analysis is that pellets of each species were not collected in all years (see Table S2.2). To examine if pooling years could be a source of bias, we repeated the previous analysis for the single year (2008) that we collected pellets from all four species (model M1a). We also tested for a difference in body mass of lemmings consumed in the presence and absence of owls for each

of the other avian predators (M3, M4, M5, Table S2.1). Finally, we compared the body mass of available lemmings for years with and without owls (M6, Table S2.1). We repeated the previous analysis only for the years when pellets were collected for each predator separately. We calculated the marginal R_m^2 (for fixed effects) and the conditional R_c^2 (for fixed and random effects) based on Nakagawa and Schielzeth (2013). We evaluated normality for fixed and random effects and homoscedasticity visually with Q-Q plot and residuals in relation to fitted values plot respectively. For all models, we ln-transformed lemming body mass to obtain a normal distribution.

We used a stepwise model selection procedure to select the best fitted log-linear model to compare the proportion of brown versus collared lemmings in the prey consumed by the different avian predators in years with and without owls. We started from the saturated model including the three main effects (lemming species, predator species and owl presence) and we did a backward selection based on AIC (Burnham & Anderson, 2002). We performed separate analyses to compare the proportion of brown lemmings consumed by the predators versus those available: one in the years of owl presence and the other in the years of owl absence.

We compared nest density for the entire study area and within the estimated nesting area of each species between predator species and years with and without owls using a linear model. We used a two-sided *t* test to compare the number of jaeger nests found within a 500-m or a 1,000-m radius around an owl nest or the proportion of these nests among all nests found to the number or proportion in the year before or after owl presence. To compare jaeger nest displacement in the presence versus absence of owls, we used a LMM based on a REML approach. Since some jaeger nests were within a 1,000-m radius of more than one owl nest, we used the nest ID as a random factor. To compare the inter-annual nest displacement of marked jaegers, we used a LMM with the band number (individual

ID) as a random effect. We did all the analyses using the software R (R Core Team, 2019).

3 | RESULTS

3.1 | Resources partitioning

We measured a total of 534 mandibles, 283 in years with snowy owls and 251 in years without (Table S2.3). Over a 14-year period, lemming abundance was high during 7 years and low during the other 7 years, with annual densities varying from 2.5 to 6.5 lemmings/ha and from 0 to 0.5 lemmings/ha respectively. Owls were found nesting in the study area during 4 years (2004, 2008, 2010 and 2014) but were absent in 3 other years (2011, 2015 and 2016) when lemming densities were high.

In the presence of owls, the mean mass of lemmings consumed by the three largest predators (owls, gulls and hawks) was similar, although it tended to be higher in gulls, and was heavier than those available (i.e. live-trapped; Table 1, model M1; Figure 2A). In contrast, jaegers consumed lemmings lighter than those available and those eaten by all other predators. In the absence of owls, the mass of lemmings consumed differed again between jaegers and hawks but not between jaegers and gulls, and all predators consumed lemmings heavier than those available (Table 1, model M2; Figure 2B). When restricting the analysis to 2008, the pattern was similar though fewer significant differences were found, potentially due to smaller sample size (Table S2.4; Figure S2.1).

When comparing species individually, the body mass of lemmings consumed by jaegers was higher in absence than in the presence of owls [43.7 g (35.8, 49.2) vs. 33.5 g (27.5, 37.8), *M* (95% CI) respectively; Table 1, model M3] and the trend was similar for hawks but not statistically significant [63.9 g (46.4, 77.9) vs. 56.6 g (43.1, 66.9);

TABLE 1 Slope parameters (β) and their 95% confidence intervals (CI) for models M1 to M6. Response variables (body mass of lemmings consumed or available) are detailed in Table S2.1. Nest ID was used as random factor for all the models. R_m^2 : Marginal R-squared for fixed effects. R_c^2 : Conditional R-squared for fixed and random effects. σ_i^2 : Variance of the random effect intercept. σ_r^2 : Variance of the random effect residuals

Model no ^a	Explanatory variable	β	Low CI	High CI	R_m^2	R_c^2	σ_i^2	σ_r^2
M1	Owl	0.433	0.235	0.632	0.143	0.305	0.043	0.184
	Gull	0.638	0.412	0.864				
	Hawk	0.335	0.090	0.580				
	Jaeger	-0.227	-0.430	-0.025				
M2	Gull	0.351	0.153	0.549	0.134	0.208	0.015	0.160
	Hawk	0.503	0.315	0.691				
	Jaeger	0.171	0.031	0.311				
M3	Owl presence	-0.264	-0.490	-0.037	0.059	0.441	0.100	0.146
M4	Owl presence	-0.113	-0.452	0.226	0.014	0.348	0.069	0.135
M5	Owl presence	0.348	0.134	0.562	0.134	0.161	0.006	0.192
M6	Owl presence	0.057	-0.091	0.205	0.004	0.077	0.014	0.181

^aReference groups were as follows: M1 and M2: Lemming available; M3, M4, M5 and M6: Owl absent.

FIGURE 2 Body mass (g) of lemmings consumed by different predator species (square) or available (live-trapped lemmings; circle) (A) in the presence of owls (model M1) and (B) in the absence of owls (model M2; Table 1). Estimated means and 95% CI calculated from linear mixed-effect models (LMMs) were back-transformed to match the scale of the original data. Means with the same letters do not differ significantly

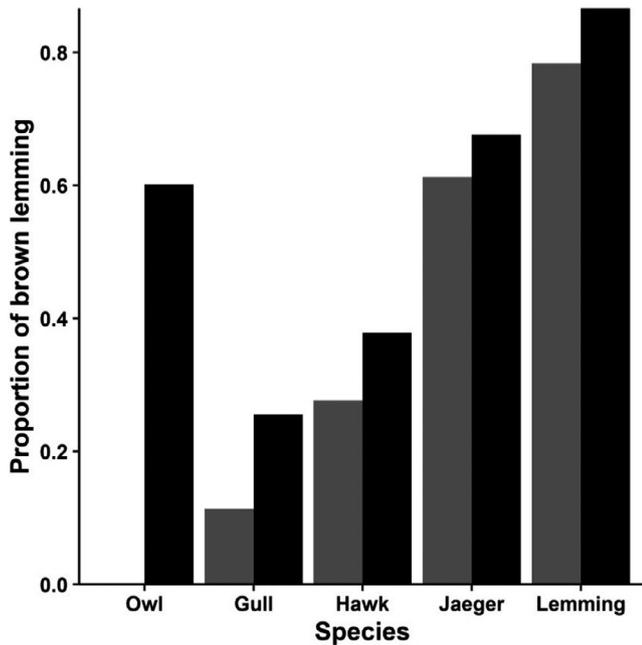
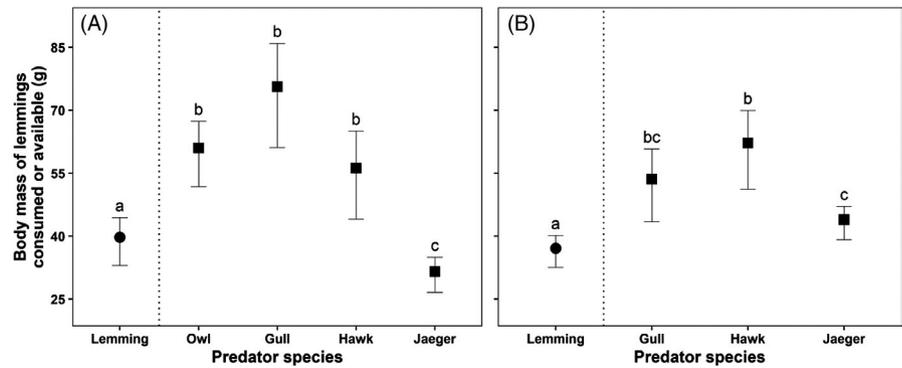


FIGURE 3 Proportion of brown versus collared lemmings in the diet of different predator species and in the lemmings available (live-trapped lemmings) in the presence of owls (black) or in the absence (grey)

Table 1, model M4]. Lemmings consumed by gulls were lighter in the absence than in the presence of owls [52.1 g (42.7, 58.8) vs. 73.5 g (61.6, 81.9); Table 1, model M5]. Finally, the body mass of lemmings available did not differ much between years without and with owls [37.2 g (32.4, 40.5) vs. 39.2 g (34.8, 42.3) respectively; Table 1, model M6]. We found the same results when we restricted the previous analysis only to years when pellets were collected for each species (Table S2.5).

All predators consumed both lemming species (Figure 3). The preferred model examining the effect of predator species and owl presence on the proportion of lemming consumed retained all two-way interactions between lemming species, predator species and owl presence (Table S2.6). Jaegers, hawks and gulls consumed slightly more brown than collared lemmings in years when owls were present (interaction lemming \times owl presence; Table 2; Figure 3). The proportion of brown lemmings consumed by jaegers was higher than that by hawks or gulls, and higher in hawks

TABLE 2 Slope parameters (β) and their 95% confidence intervals (CI) from the log-linear analysis comparing the proportion of brown versus collared lemmings in the prey consumed by three avian predators in the presence or absence of owls. Reference levels are collared lemming, hawks and owl absent

Explanatory variable	β	CI
Brown lemming	-0.953	[-1.424, -0.507]
Gull	-0.229	[-0.642, 0.177]
Jaeger	0.191	[-0.167, 0.553]
Owl presence	-0.709	[-1.152, -0.283]
Brown lemming \times Gull	-0.764	[-1.462, -0.094]
Brown lemming \times Jaeger	1.359	[0.860, 1.876]
Brown lemming \times Owl presence	0.447	[-0.001, 0.903]
Gull \times Owl presence	0.693	[0.113, 1.282]
Jaeger \times Owl presence	-0.275	[-0.794, 0.246]

than in gulls (interactions lemming \times predator species, Table 2). When owls were present, the proportion of brown lemmings they consumed was similar to jaegers and hawks but higher than gulls (Table S2.7). Regardless of the presence or absence of owls, all predators consumed brown lemmings in lower proportion than their availability, and conversely for collared lemmings (interactions lemming \times predator species; Table S2.7).

3.2 | Spatial partitioning

We found 216 nests in years of owl presence (jaeger: 122, hawk: 16, gull: 42, owl: 36), and 211 nests in their absence (jaeger: 91, hawk: 15, gull: 105). Nest density over the whole study area varied according to the predator species and owl presence (interaction species \times owl presence: $F_{2,29} = 8.19$, $p = 0.002$; Table 3). Nest density of jaegers and hawks was much higher in the presence of owls but not for gulls. When restricting the analysis to the nesting area used by each species, nest density did not differ between the years of owl presence or absence for all species ($F_{1,29} = 0.12$, $p = 0.72$; interaction: $F_{2,29} = 5.62$, $p = 0.58$; Table 3). However, the gull nest density within their nesting range was about 10 times higher than the other species ($F_{3,29} = 79.0$, $p < 0.001$).

	Study area		Nesting area	
	Owl present	Owl absent	Owl present	Owl absent
Snowy owl	0.17 ± 0.05	NA	0.88 ± 0.23	NA
Glaucous gull	0.21 ± 0.03	0.20 ± 0.02	11.05 ± 1.92	12.37 ± 1.16
Rough-legged hawk	0.09 ± 0.03	0.03 ± 0.01	1.00 ± 0.30	1.16 ± 0.43
Long-tailed jaeger	0.62 ± 0.13	0.18 ± 0.07	1.37 ± 0.23	0.70 ± 0.27

TABLE 3 Nest density ($M \pm SE$) of predators within the whole study area and only within the nesting area (nest/km²) in the years of presence ($N = 3$ years) and absence ($N = 8$) of owls (NA, not applicable)

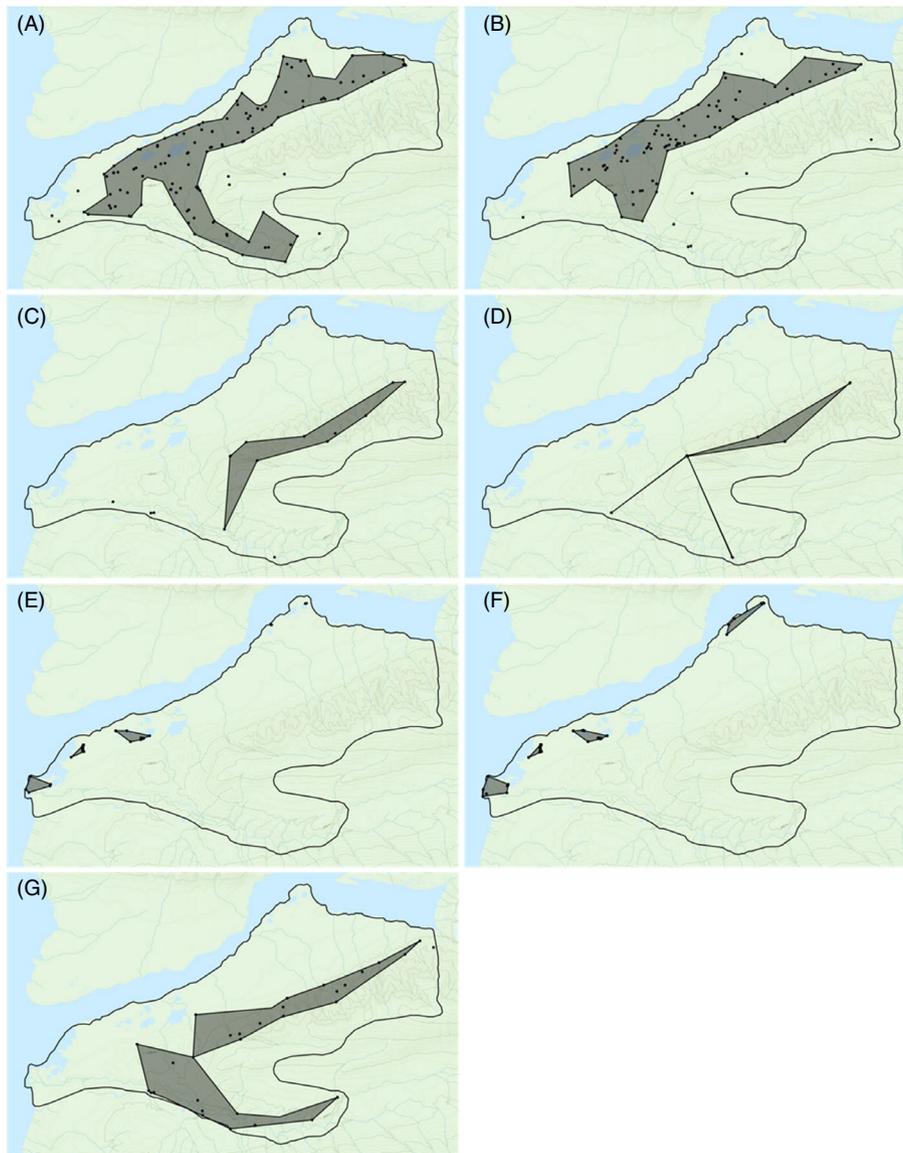


FIGURE 4 Local convex hull (LoCoH) polygons of the area covered by 90% of the nests (defined as the nesting area; grey shading) of long-tailed jaeger (A, B), rough-legged hawk (C, D), glaucous gull (E, F) and snowy owl (G) in the years of presence (left panel) and absence of owls (right panel). The black dots represent the position of each nest (some nest may overlap between years). The outer black line polygon represents the borders of the study area

In years with owls, the nesting area covered 17.2 km² for jaegers, 4.0 km² for hawks, 0.5 km² for gulls and 10.6 km² for owls (Figure 4). The habitat and topography of these nesting areas differed among species (Table S2.8). Gulls used predominantly wet meadows associated with lakes on flat terrain; hawks mainly used xeric tundra on steep slopes, cliffs and to a lesser extent mesic tundra on hills; jaegers used mostly moist/mesic meadows on flat terrain; and owls used almost equally moist/mesic meadows on flat terrain and mesic tundra on gentle slopes and hills. Almost 30% of the nesting area of owls overlapped with that of jaegers and 9% with the hawks while

17% of the nesting area of jaegers and 24% of hawks overlapped with that of owls (Table 4). In the absence of owls, the extent of the nesting areas was reduced for jaegers (12.9 km²) and hawks (1.6 km²) but not for gulls (0.9 km²; Figure 4). The nesting habitat of each species remained similar in those years (Table S2.8) and the nesting area of jaegers did not substantially overlap with other species (Table 4).

We found no difference between years with and without owls in the number or proportion of jaeger nests located within a 500-m radius around owl nest locations (Table 5). With a 1,000-m radius, the number of jaeger nests was lower in the absence than in the presence

TABLE 4 Overlap between the nesting areas of each species in the presence/absence of owls. Table should be read as the % of the nesting area of the species in row overlapped by the nesting area of the species in column (NA, not applicable)

	Long-tailed jaeger	Rough-legged hawk	Glaucous gull	Snowy owl
Long-tailed jaeger	–	0.2/<0.1	0.9/1.3	17.1/NA
Rough-legged hawk	0.8/0.2	–	0/0	24.4/NA
Glaucous gull	31.7/17.9	0/0	–	0/NA
Snowy owl	27.9/NA	9.2/NA	0/NA	–

TABLE 5 Comparison of the abundance of long-tailed jaeger nests around snowy owl nests between years of owl presence and absence. Radius: radius of the buffer zone around owl nests. Number of nest is the absolute count of nest. Proportion of all the nests found annually located within the buffer zone

Radius (m)	Method	Owl present		Owl absent		t test	
		M	SE	M	SE	t_6	p
500	N of nest	1.5	0.9	1.0	0.4	0.52	0.62
	Proportion of nests	0.07	0.04	0.07	0.03	-0.05	0.96
1,000	N of nest	9.0	1.1	3.8	1.3	3.18	0.02
	Proportion of nests	0.37	0.10	0.25	0.07	0.98	0.37

of owls, but the proportion of nests remained the same (Table 5). We found no difference in the distance between owl and jaeger nests within the 1,000-m radius around owl nests when comparing years with and without owls ($F_{1,49} = 0.26$, $p = 0.61$). Finally, the mean distance between nest locations of the same individual jaegers in different years was 325 m ($N = 36$, $SE = 49$) for those located >1,000 m away from an owl nest and 483 m ($N = 10$, $SE = 143$) for those nesting <1,000 m, a non-significant difference ($F_{1,13} = 1.05$, $p = 0.32$).

4 | DISCUSSION

Our 14-year study allowed us to gain a better understanding of the intensity of interspecific competition and of mechanisms promoting coexistence among a guild of avian predators exploiting temporally fluctuating resources in a low productivity environment. The irruptive behaviour of one predator, the snowy owl, in response to resource pulses created the conditions for a short-term natural competitive release experiment. We showed that resource partitioning according to prey body size and, to a lesser extent, prey species was a mechanism that reduced competition but it was modulated by the presence or absence of the dominant predator, the snowy owl. We also found that spatial segregation according to habitat was an important mechanism to minimize competition but that segregation changed little in the presence or absence of the largest competitor. Finally, the smallest predator of the guild was apparently affected the most by competition.

4.1 | Resource partitioning based on prey size and species

Even though the four avian predators in our system all feed on lemmings, each of them specialized on prey of different size and used

the two lemming species differently. As we hypothesized, larger predators generally consumed larger lemmings and this effect was most pronounced in the smallest predator, the long-tailed jaeger. Owls and jaegers overlapped in their habitat use and both fed mostly on brown lemmings contrary to hawks and gulls, which consumed mostly collared lemmings. It is therefore not surprising to observe a short-term competitive release on jaegers when owls, the largest and most dominant predator, are absent. Indeed, jaegers consumed lemmings that were on average smaller than those available in the presence of owls but heavier than those available when owls were absent. This clearly suggests a strong competition between these two species and a negative effect of the presence of owls on resources use by jaegers.

We observed weak resource partitioning based on prey size among the three largest predators but we found differences in lemming species consumed. Although all predators consumed collared lemmings in greater proportion than their relative availability, as also noted by Therrien, Gauthier, Korpimäki, et al. (2014), this proportion was highest in gulls, intermediate in hawks and lowest in owls. The high consumption of collared lemmings by hawks can be explained by their preference to nest in more xeric habitat, where collared lemmings should be more prevalent than brown lemmings (Morris et al., 2000; Naughton, 2012). However, the proportion of collared lemming consumed by gulls is surprisingly high considering that they breed mainly in wet meadows, the preferred habitat of brown lemmings. Glaucous gulls are generalist predators that feed on a wide range of prey and habitats (Gauthier et al., 2015; Samelius & Alisauskas, 1999) and our results suggest that they may often hunt away from their nest, in mesic habitat. The fact that all predators consumed more collared than brown lemmings compared to their availability is consistent with the idea of a greater vulnerability of the former to predation (Reid et al., 1995; Therrien, Gauthier, Korpimäki, et al., 2014), which is

possibly due to behavioural differences (Morris et al., 2019) since both species are of similar size.

Temporal segregation in resource use is another mechanism that can reduce interspecific competition. In the guild of avian predators studied by Poole and Bromley (1988) in the Canadian Arctic, interspecific variation in the timing of breeding, especially between common ravens *Corvus corax* and gyrfalcons, reduced temporal overlap of the chick-rearing periods and thus attenuated competition when resource demand is highest. In our system, timing of breeding is similar for all species except for owls that breed earlier. However, because of their lengthy breeding season, their brood-rearing period largely overlaps with the three other species. Therefore, temporal segregation in resource use is weak as the period of highest food requirement is largely synchronous among species. Moreover, except for gulls that partially switch from lemmings to geese after chick hatching (Gauthier et al., 2015), the diet composition for the three other predators is dominated by lemmings throughout the summer (Hakala et al., 2006; Maher, 1970; Therrien, Gauthier, Korpimäki, et al., 2014).

4.2 | Spatial resource partitioning

The four avian predators generally used different habitats for nesting and the overlap in nesting area was moderate to small. All these species are territorial during the breeding season and their foraging activity predominantly occurs in their breeding territory (Holt et al., 2020; Maher, 1970; Pokrovsky et al., 2020) except perhaps gulls, which range over a larger area during breeding (Gauthier et al., 2015). The use of different nesting habitats may thus be a primary mechanism allowing these species to feed on the same prey and reduce competition in an environment where vertical habitat structuring is absent. In avian predators, species that overlap the most in their nesting habitat should overlap the least in their diet (Pokrovsky et al., 2020; Restani, 1991). In agreement with this, the largest overlap in nesting area used among the four predators was between jaegers and gulls, the two species that differed the most in the lemming species used.

Jaegers and hawks showed some overlap in nesting area with owls. Wiklund et al. (1998) suggested that interference competition between snowy owls and rough-legged hawks could explain their mutual avoidance observed across a range of study sites in Siberia. We found no evidence for this as both species bred in good numbers in high lemming years. The diversity of landscape present in our study area and the tendency for each species to use different nesting habitats may have facilitated this coexistence. Moreover, rough-legged hawks in North America tend to be site faithful and reuse the same territory (Beardsell et al., 2016; Bechard & Swem, 2002) whereas in Siberia they tend to be more nomadic (Pokrovsky et al., 2020).

Contrary to our initial prediction, we found no evidence that owls excluded jaegers from potential breeding habitat even though both predators feed mostly on brown lemming. The settlement pattern

of jaegers was similar and they used approximately the same area regardless of the presence or absence of owls. Because jaegers do not reuse old nests, the position of the nesting site is a new decision every year. Nonetheless, the presence of a large and close competitor did not affect the distribution of nesting jaegers contrary to what was observed in a guild of forest owls (Kajtoch et al., 2015, 2016). The current distribution pattern of jaegers appears to be governed primarily by habitat preference rather than interference competition although spatial segregation with owls may have evolved in response to past competition. Although spatial partitioning may be an important mechanism to reduce food competition among these avian predators, the reduction in prey size consumed by jaegers when owls are present indicate that competition is still present between these two species, possibly due to their partial overlap in habitat use. This also suggests that competition may be mostly by exploitation with owls preying on large lemmings, which in turn force jaegers to rely on smaller prey.

Overlap in nesting areas among gulls, jaegers and hawks tended to decrease in the absence of owls, which was largely a consequence of jaegers and hawks having reduced nesting areas in those years. This is likely because lemming abundance was lower in the years of owl absence than presence, and thus the breeding effort of these two species was reduced. Nonetheless, the reduction of overlap in nesting areas of these species in years of low lemming abundance could be an additional mechanism reducing food competition when the resource is most limiting.

4.3 | Competition in fluctuating environments

Numerous studies have reported intense interspecific competition, either by interference or exploitation, in various raptor guilds (Gerstell & Bednarz, 1999; Hakkaraïnen et al., 2004; Restani, 1991; Wiklund et al., 1998). The arctic tundra is rather unique in having several sympatric avian predators feeding mostly on the same prey, lemmings, a pulsed resource with large inter-annual fluctuations in abundance. In accordance with Wiens (1977), and Lack (1946) in the case of raptors, we found that intensity of competition is dynamic and varied as resources fluctuated temporally. However, contrary to the conventional wisdom, we found that competition was more intense when the resource was abundant rather than scarce (Schoener, 1983; Wiens, 1977). This occurs because snowy owls, the largest and most dominant predator, are present in the system only when lemmings are abundant and other species (jaegers, hawks) increase their breeding effort in those years. Therefore, resource pulses increase interspecific competition by attracting more species and higher densities due to the high mobility of avian predators (Therrien, Gauthier, Korpimäki, et al., 2014). Interestingly, under these conditions, predators consumed a larger spectrum of lemming size than when they are scarce even if the size of available lemmings remains the same. Thus, as competition increases, resource partitioning leads to a greater breadth of

resource exploitation, as reported by Finke and Snyder (2008) in an insect consumer community.

Spatial segregation in nesting areas through species-specific habitat preferences appears to be the primary mechanism allowing the coexistence of predators in our system, and secondarily a differential use of resources according to species and size. Due to its importance in promoting coexistence in this low productivity ecosystem, it is possible that species-specific habitat preference may be a ghost of competition between these predators in the distant past (Dhondt, 2012; Rosenzweig, 1981). Despite spatial and resources partitioning, the smallest species of the guild appears to suffer from asymmetric exploitative competition and is forced to shift its feeding niche by relying on smaller prey size than what they would consume in the absence of its strongest competitor. However, we do not have data to evaluate the consequences of this shift in resource use on the reproductive success of jaegers. Nonetheless, our study shows that interspecific competition could be a pervasive force in a relatively simple and low productivity arctic food web where avian predators play a prominent role (Therrien, Gauthier, Korpimäki, et al., 2014) and result in a niche shift for some species.

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AUTHORS' CONTRIBUTIONS

Y.S. and J.-F.T. collected the data in the field and conducted the laboratory analyses; Y.S. conducted the statistical analyses and wrote the manuscript with the assistance of G.G., D.F. and J.-F.T. All contributed to the revision of the manuscript and gave the final approval for publication.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available on the NordicanaD website <https://doi.org/10.5885/45400AW-9891BD76704C4CE2> (Gauthier, 2020); <https://doi.org/10.5885/45591AW-F9B906CC647948E0> (Gauthier et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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