1 High goose abundance reduces nest predation risk in a simple

2 rodent-free high-Arctic ecosystem

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Abstract

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Breeding geese are the preferred prey of the Arctic fox Vulpes lagopus in the high-Arctic Svalbard archipelago. According to the apparent competition hypothesis (ACH), less abundant prey species (e.g. ptarmigan, waders and small passerines) will experience higher predation rates when breeding in association with the more common prey (geese), due to spill-over predation by the shared predator. As many of these less abundant species are endemic and/ or red-listed, increased predation can have negative repercussions on their populations. We used a one-year baited artificial nest study to assess relative nest predation risk on Svalbard Rock Ptarmigan Lagopus muta hyperborea, small waders (Purple Sandpiper Calidris maritima, Dunlin Calidris alpina, plovers Charadrius spp., and phalaropes Phalaropus spp.) and Snow bunting Plectrophenax nivalis in two study locations contrasted by nesting density of Arctic breeding geese (Pink-footed Goose Anser brachyrhynchus and Barnacle Goose Branta leucopsis). We predicted higher predation risk for the less abundant species in the study location with higher goose abundance. However, we found that relative nest predation risk was lower in the study location with higher goose abundance, thus being compatible with apparent mutualism and / or prey swamping mechanisms. Our results contrast with those from more structurally complex Arctic ecosystems and suggest that allochtonous subsidies from temperate ecosystems structure the predation pattern in this high-Arctic tundra ecosystem. **Key words:** Apparent competition, Arctic fox *V. lagopus*, artificial nest, predator, Pink-footed Goose, Svalbard

Introduction

Recent circumpolar studies have demonstrated that at high latitudes, predation can exert strong top-down control on small to medium-sized vertebrates and be a major driver of their population dynamics (Legagneux et al. 2012; Legagneux et al. 2014). In tundra ecosystems lacking lemmings and voles, key resources for predators are typically geese, seabirds and carrion from reindeer *Rangifer tarandus platyrhynchus* and seals (Jepsen et al. 2002; Fuglei et al. 2003; Eide et al. 2005; Eide et al. 2012; Giroux et al. 2012; McKinnon et al. 2013, 2014). The magnitude of such resources may be decisive in structuring predation patterns (Tombre et al. 1998; Jepsen et al. 2002; Fuglei et al. 2003; Roth 2003; Eide et al. 2012) including the level of predation on less preferred prey such as smaller ground-nesting birds (Bety et al. 2001; McKinnon et al. 2013, 2014).

Abundant prey availability may attract predators and can lead to increased predator

Abundant prey availability may attract predators and can lead to increased predator densities in proximity to prey (Giroux et al. 2012). According to the apparent competition hypothesis (Holt and Kotler 1987), an increase in the abundance of a predator's main prey (in time or space) can cause spill-over predation on alternative prey (Iles et al. 2013; McKinnon et al. 2013). However, the relationship is complex as high availability of main prey can also buffer predation on alternative prey, resulting in a positive relationship between the two (i.e. apparent mutualism (Abrams and Matsuda 1996; Abrams et al. 1998)). The occurrence of contrasting abundances of breeding geese in the valleys of Svalbard provide a setting in which to test the apparent competition hypothesis (Jepsen et al. 2002; Eide et al. 2005).

The terrestrial ecosystem in the Svalbard archipelago is one of the world's most simple vertebrate tundra food webs (Ims et al. 2014). The main terrestrial resident generalist predator and scavenger is the Arctic fox *Vulpes lagopus* (Frafjord 1993; Prestrud 1992).

Rodents are almost functionally absent in the ecosystem, apart from a small, local, geographically isolated population of sibling voles Microtes levis (Henttonen et al. 2001). In summer, the preferred food resource consists of eggs, chicks and adult Arctic-nesting geese (Pink-footed Goose Anser brachyrhynchus and Barnacle Goose Branta leucopsis). The increase in the populations of Pink-footed Goose (i.e. 15000 [1965] to 81500 [2012]; Madsen et al. 2016) and Barnacle Goose (i.e. 3000 - 4000 birds [1960's] to 35000 individuals [2008]; Mitchell et al. 2010) has been large and rapid. Seabirds (e.g. family Alcidae and Fulmar Fulmarus glacialis), remains of reindeer carcasses and occasionally newborn calves are typically secondary prey (Eide et al. 2005). In addition, Arctic fox V. lagopus can prey upon terrestrial ground nesting birds (Eide et al. 2005), many of which are of conservation concern due to their small populations in Svalbard. This includes the endemic Svalbard Rock Ptarmigan Lagopus muta hyperborea, locally red-listed waders living at the northern end of their range (Common Ringed Plover Charadrius hiaticula, Ringed Plover Charadrius hiaticula, Dunlin Calidris alpina, Sanderling Calidris alba, Red Phalarope Phalaropus fulicarius, Rednecked Phalarope Phalaropus lobatus, Ruddy Turnstone Arenaria interpres; Henriksen and Hilmo (2015)), and the only passerine, the Snow bunting *Plectrophenax nivalis* (Kovacs and Lydersen 2006). We expect these species to be incidental prey taken during the predator's search for preferred prey (see Cornell 1976), and for predation to be relatively limited due to their low abundances (Eide et al. 2005). In this one-year observational study, we used artificial nests to compare the relative

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In this one-year observational study, we used artificial nests to compare the relative nest predation risk on small to medium sized ground-breeding birds (Svalbard Rock Ptarmigan *L. muta hyperborea*, small waders [Purple Sandpiper *Calidris maritima* and the seven locally red-listed waders described above] and Snow bunting *P. nivalis*) between two valleys that differed in abundance of nesting geese. According to the apparent competition

hypothesis and McKinnon et al. (2013), we predicted higher predation rates on groundnesting birds in the study location with high abundance of nesting geese compared to the study location with low abundance of nesting geese due to increased spill-over predation by Arctic fox *V. lagopus*.

Methods

Study area

The high-Arctic archipelago of Svalbard, Norway (62 700 km²; 74-81°N, 15-30°E), has only 15 % of land covered with vegetation. Glaciers (60 %) and barren rocky ground (25 %) cover the remaining areas (Johansen et al. 2012). We conducted the study in the middle Arctic tundra zone of the largest island, Spitsbergen. The landscape is mountainous and moderately glaciated and continuous vegetation cover is only present in the valley bottoms and on the lower parts of the mountain slopes (Elvebakk 1999; Elvebakk 2005). The study sites are located in two adjacent open, u-shaped river valleys, *Adventdalen* and *Sassendalen* (78'15°N, 17'20° E; Fig. 1) which are characterized by differences in prey availability (Jepsen et al. 2002; Eide et al. 2004, 2005; see below for a description).

Prey resource landscapes and predator abundance

Former studies by Jepsen et al. (2002) and Eide et al. (2004, 2005) have characterized *Adventdalen* (termed 'prey-poor') as a poor prey resource landscape consisting mainly of reindeer, while *Sassendalen* (termed 'prey-rich') has richer prey resources consisting of both reindeer and geese (Fig. 1 and Table 1). The study locations have similar Svalbard reindeer *R. t. platyrhynchus* densities that show synchronous population dynamics (Aanes et al. 2003; Pedersen et al. 2014). Thus, we expect no significant differences between the study locations in the availability of reindeer carcasses as food for the Arctic fox *V. lagopus* (Jepsen

et al. 2002; Eide et al. 2005). The abundance and density of Arctic-nesting geese (Pink-footed Goose and Barnacle Goose) differ between the study locations. The prey-rich study location is an important breeding area for Pink-footed Goose in Svalbard, in cliff habitat (e.g. Nøisdalen cliff colony, area of 0.19 km²), there is a range of 25 - 55 nests per colony and in open tundra slope (e.g. Gåseflatene slope colony, area 0.76 km²) there is a range of 170 -230 nests per colony (see Anderson et al. 2015 for details and colony maps). In contrast, nesting geese are almost absent in the prey-poor study location (Mehlum et al. 1998; Eide et al. 2004, 2005; Wisz et al. 2008; Fig. 1). Both goose species incubate nests in June and most of the goslings have hatched around the beginning of July (Madsen et al. 2007) with posthatching aggregations forming along rivers and small lakes (Fox et al. 2009). Several large seabird cliff colonies are found in close proximity to the prey-rich study location (between 1 -- 7 km from the transects), while they are further away in the prey-poor study location (between 16 - 20 km from the transects) (for additional details see Eide et al. 2004; Fig. 1 and Table 1). Fulmar F. glacialis, Brünnich's Guillemot Uria lomvia, Little Auk Alle alle and Puffins Fratercula arctica dominate these colonies. While all of these species are potential prey for the Arctic fox V. lagopus, Eide et al. (2005) found that geese, eggs, goslings and adult individuals were the preferred prey to seabirds and reindeer carcasses. In the absence of geese, seabirds were preferred to reindeer.

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Diet studies of Arctic fox *V. lagopus* scats have documented that foxes also prey on Svalbard Rock Ptarmigan and smaller migratory birds such as waders and Snow buntings (Prestrud 1992; Eide et al. 2005). The ptarmigan is non-cyclic on Svalbard and has low breeding densities $(1.5 - 4.7 \text{ males / km}^2)$ across the study locations (Soininen et al. 2016). Among the eight wader species commonly breeding in Svalbard, seven are locally red-listed (listed in the introduction; see also Henriksen and Hilmo 2015 for a complete species list).

There is no information on abundances of Snow bunting or small waders within the two study locations; however, we expect them to occur in low densities due to the high-Arctic location of our study sites (Ims et al. 2014).

In terms of predator abundance in the two study locations, the Arctic fox *V. lagopus* den occupancy rate is slightly, but not statistically, higher in the prey-rich compared to the prey-poor study location (see Figure 4b in Eide et al. 2012; Table 1 for occupancy rates in 2012 study year). Currently, there is no knowledge about abundances of the avian predators, the glaucous gull (*Larus hyperboreas*) and skuas (*Stercorarius spp.*), which scavenge and prey upon the same resources as the Arctic fox *V. lagopus*.

Study design

We used an observational study design with artificial nests (cf. McKinnon et al. 2013) to assess nest predation rates along transects spanning from the valley bottom to the upper vegetation limit (altitude range; Adventdalen 110 – 384 masl., Sassendalen 3 – 182 masl., Fig. 2). Thus, the transects represented both a gradient in terms of vegetation productivity and type of nesting habitat (e.g. wetlands in the valley bottom, snow-bed/moss tundra in the foothills, heath and ridge vegetation on the slopes and rocks with sparse vegetation at the upper vegetation limit) for ground-nesting birds. We used 120 artificial nests deployed between 1st and 20th July 2012 to obtain spatial replication and controlled stratification that would not be possible using natural nests (McKinnon et al. 2010, 2013, 2014). This time-period covers the main breeding season for the most common ground-nesting birds in Svalbard (e.g. Svalbard Rock Ptarmigan *L. muta hyperborea*, Steen and Unander 1985; Snow bunting *P. nivalis*, Hoset et al. 2004; Purple Sandpiper *C. maritima*, Summers and Nicoll 2004). This type of study design provides information about spatial and temporal prevalence of egg-consuming predators, thus indicating relative predation-risk patterns for ground-nesting

birds from both mammalian and avian predators (e.g. Angelstam 1986; Storch 1991; Villard and Part 2004; Manzer and Hannon 2005; McKinnon et al. 2010).

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Based on a random start position, we placed 12 transects in each study location with five artificial nests in each transect (N = 60 artificial nests per study location; total N = 120; Fig. 1). In the prey-poor study location, we placed the 12 transects adjacent to each other on one side of a large glacial river due to difficulties involved in crossing the river. In the preyrich study location, we placed six transects on each side of a large glacial river which could act as a barrier for Arctic fox V. lagopus movement in summer. The overall mean distance between transects was 1190 m (range [932 – 2852 m]) and differed slightly between study locations (prey-poor, mean = 1099 m, range [932 – 1701 m]; prey-rich, mean = 1281 m, range [1004-2852 m]). The overall mean transect length was 911 m (range [99 - 1652 m]) and differed also slightly between study locations (prey-poor, mean = 994 m, range [99 – 1652 m], the lowest number is due to that only two nests were placed in this short transect due to topographical constraints; prey-rich, mean = 828 m, range [381 - 1401 m]). The artificial nests (n = 5) were deployed at equal distance intervals along a low to high elevation gradient of individual transects. Due to varying transect length the mean distance between two artificial nests was 239 m (range [99 - 558 m]).

We placed four of the artificial nests in vegetated habitats, while the fifth nest was placed in sparsely vegetated habitats with less than 25 % vegetation cover. Post fieldwork we assigned each artificial nest site a habitat type using the digital habitat map of Johansen et al. (2012) that defines 18 habitat classes (see Johansen et al. 2012, Table 2 for habitat classes). Prior to analysis, we reclassified the habitat types into four coarse habitat productivity categories assumed to be relevant for the breeding ecology of ground-nesting birds in the study areas. These were barren (original classes 4 - 6, 8, 17 and 18; n = 40), moist

(original classes 9, 12 and 15; n = 74), wet (original classes 10 and 11; n = 29) and dry (original classes 13, 14 and 16; n = 26) (Fig. 2). Since many of the plots were located in an unclassified habitat type (original class 7; n = 57), we added a fifth vegetation category 'not classified' to our habitat variable (Fig. 2).

Artificial nests

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Each nest consisted of two commercially produced common quail eggs Coturnix coturnix that were placed on the ground in a small, shallow hand-made nest cup to imitate nest characteristics of the most common bird species. We followed McKinnon et al. (2013) in assuming that exposure of eggs in artificial nests provided a measure of relative predation risk on small to medium-sized ground-nesting birds. To reduce human scent we wore latex gloves and rubber boots or plastic covered hiking-boots when handling the eggs, and we left only plastic covered equipment on the ground (Bowen 1976). We noted the GPS position of each nest and placed a small orange coloured wooden stick (7 mm in diameter, 2 - 5 cm above ground) 5 m above or below the nest in the direction of the transect line to aid nest relocation. We exposed the nests to predators for two consecutive trial periods of 10 days to account for potential temporal differences in predation rates. The nests were set out for the first time on 1st July, which coincided with the incubation period of the most common ground-nesting bird species (Svalbard Rock Ptarmigan, Steen and Unander 1985; Snow bunting, Hoset et al. 2004; purple sandpiper, Summers and Nicoll 2004). The nests were visited every 10 days (two visits) and we recorded a nest as predated when at least one of the eggs was missing, destroyed or distributed in the immediate surroundings of the nest site.

Statistical analysis

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We analysed relative nest predation risks using generalized linear mixed-effects models using a logit-link function and a binomial distribution for the response variable, probability of nest predation (Lewis 2004). Models were fitted in R (R Development Core Team 2010) using the lme4 package (Bates et al. 2015). We included *location* (prey-rich and prey-poor, period (two consecutive trial periods of 10 days from 1st – 20th July) and nesting habitat type (barren, moist, wet, dry and not classified) as fixed factorial predictor variables. Elevation (m.a.s.l.) of the artificial nest and habitat type were highly correlated and therefore we chose to only included habitat type in the statistical analyses (Fig. 2). Transect and plot were included as random variables with plot nested within transect to account for spatial variation that could not be attributed to habitat type. The full model contained the interaction between the fixed effects *location* × *period*, *location* × *habitat type* and the random effects transect and plot. We selected the best model using the Akaike's information criterion corrected for small sample size (AICc), ΔAICc and AICc-weights (Anderson and Burnham 2002). Where difference in \triangle AICc was < 2, we chose the simpler model for inference. We present estimates of effect sizes as odds ratios (OR) with 95 % confidence intervals (CI) for the predictor variables.

Results

Nest predation was consistently high in both study locations with more than half of all the artificial nests being predated (Table 2). A simple model including only the predictor variable *location* explained best the nest predation risks (Fig. 3, Table 3 - 4). There was no support for any effects of *period* or *habitat type* on predation rates. The probability of nest predation

was significantly higher in the prey-poor location (88 %), compared to the prey-rich location (62 %) (odds ratio [OR] prey-poor/ prey-rich = 4.6, 95 % CI = 1.5 - 14.2; Fig. 3).

Discussion

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Our results indicate that nest predation risk of ground-nesting birds (Svalbard Rock Ptarmigan L. muta hyperborea, small waders (listed in introduction) and Snow bunting P. nivalis) was lower in tundra landscapes with high abundances of geese, the preferred prey of Arctic fox *V. lagopus*. These results contrast with those from several structurally more complex Arctic ecosystems where presence of goose colonies led to elevated predation rates on other ground-nesting birds (Iles et al. 2013; McKinnon et al. 2013, 2014). Our results thus demonstrate the first indications that an allochtonous resource, in the form of abundant migratory geese from temperate ecosystems, influences nest predation risk in a tundra ecosystem lacking small rodents. Based on the apparent competition hypothesis and results from the study by McKinnon et al. (2013), we expected nest predation risk on ground-nesting birds to be higher in the prey-rich compared to the prey-poor study location. Our results indicated the opposite, with an almost five-fold decrease in relative nest predation rates in the prey-rich location and are therefore compatible with an apparent mutualism mechanism (Abrahams and Matsuda 1996), where less abundant alternative prey benefit from high abundances of main prey. Whether alternative prey benefit from being interspersed amongst the main prey of a shared predator is dependent on the functional and numerical response of the predator, as well as the relative abundance of the different prey species and their spatial and temporal distributions (Barraquand et al. 2015). The contrasting findings to McKinnon et al. (2013) may relate to differences in both abundance of main goose prey and spatial study scale, i.e. local (McKinnon et al. 2013) versus landscape scale (this study). McKinnon et al.'s (2013)

study placed the artificial nests in the centre of a large snow-goose colony (i.e. approx. 50 000 individuals, four nests were set out in each of 10 quadrats of 500 × 500 m with varying goose nest density). In our study, we dispersed the artificial nests along elevation gradients representing different types of ground-nesting bird habitats, in tundra landscapes that contained either no goose nests or colonies spread across the hill-slopes or on smaller cliffs (Anderson et al. 2015; see their Table 1). McKinnon et al.'s (2013) study suggested an aggregative search response of Arctic fox *V. lagopus* and indeed such behaviour might happen in our study area and be directly comparable. However, as the density of the goose nests is much lower in our study, the search response (and hence overspill predation) may be confined to sections of the landscape where geese are present (Jepsen et al. 2002). Thus, for ground-nesting birds that nest in low densities, a heterogenic aggregative search response of the Arctic fox *V. lagopus* may result in a reduction in the overall predation pressure on these species.

At the time of the study (1st - 20th July) many geese have already hatched their eggs, while many of the other ground-nesting birds are still incubating. Former studies have demonstrated that goose prey distribution can concentrate the aggregation of Arctic foxes *V. lagopus* to certain parts of the landscape where geese congregate such as flooded areas, small lakes and along river banks (Jepsen et al. 2002; Fox et al. 2009). Thus, the presence of goose family groups in these areas is likely to influence the spatial pattern of fox distribution. This may result in reduced time spent by the fox in the nesting habitats of other less common ground-nesting birds. Seabird colonies may also act in a similar way and reduce local predation pressure on other ground-nesting birds. As such, the short distance to bird cliffs in the prey-rich location may also have contributed to reduced nest predation rates on the ground-nesting birds in this location. In the prey-poor location, the high nest predation

may simply result from virtually no other prey present than ground-nesting birds in summer, which leads to high search effort by Arctic foxes *V. lagopus* for ground-nesting bird nests.

Additionally, potential differences in abundance of the bird predator communities (e.g. Glaucous gull *Larus hyperboreus* and skuas *Stercorarius spp.*) may contribute to this pattern as demonstrated by Iles et al. (2013) in a more complex ecosystem. While no information currently exists to evaluate this effect, the lack of both habitat and time period effects in our study indicate a continuous predation pressure from both Arctic fox *V. lagopus* and avian predators during the 2012 season.

Another plausible explanation for the lower predation risk in the prey-rich location is a prey swamping effect whereby high abundances of geese buffer predation of less abundant prey (Robertson 1995, Gauthier et al. 2004, Iles et al. 2013). This is documented in other Arctic ecosystems where goose-nesting colonies buffered predation on vulnerable tundra birds from e.g. Snowy Owls *Bubo scandiacus* (Gauthier et al. 2004). Indeed, such an effect from a temporally pulsed resource, such as goose nests and goose family groups, are most likely if they are dispersed across the landscape, as occurs in the Svalbard breeding Pinkfooted Goose *A. brachyrhynchus* populations rather than being highly concentrated spatially (Ims 1990).

There are many shortcomings of artificial nest studies, which may lead to a discrepancy between absolute predation rates of real and artificial nets. These include the lack of an incubating bird and associated nest defence, as well as the limited ability to identify predator species (reviewed in Moore and Robinson 2004). We argue, however, that as we use a standardised study design applied in other studies of relative predation risk in similar open habitats (see McKinnon et al. 2010, 2013, 2014), we capture the relative nest predation risk from the predator community on the less common prey species. We thus suggest that

experiments with artificial nests should be part of long-term monitoring efforts. Such an approach allows estimation of the inter-annual variability and climate-change related trends in nest predation rates in areas of different prey abundances. The monitoring should also include methods that enable identification of the nest predator species (mammalian versus avian egg predators; McKinnon et al. (2009)), as well as improved data on the abundance and distribution of the nests of geese and other ground-nesting birds. Implementation of the "Climate-Ecological Observatory for Arctic Tundra", which is an adaptive ecosystem-based long-term monitoring program covering our study regions (Ims et al. 2013), along with circumpolar initiatives such as "The Arctic Migratory Birds Initiative" (Johnston et al. 2015), are important steps to enhance the knowledgebase. This will advance our understanding of the interactive effects between the Arctic fox *V. lagopus*, avian predators / scavengers and goose abundance on terrestrial high-Arctic birds of conservation concern, thus, allowing for the effective appraisal of management actions that can reduce their vulnerability to extinction.

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444 Tables

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Table 1 Summary of prey and predator characteristics of the two study locations, the prey-poor inland resource landscape with low goose abundance and the prey-rich inland resource landscape with high goose abundance (Jepsen et al. 2002, Eide et al. 2004; see also Fig. 1.). We give also Arctic fox *Vulpes lagopus* den occupancy rates for the 2012 study year

STUDY LOCATION CHARACTERISTICS	PREY-POOR	PREY-RICH
Goose abundance (Eide et al. 2004; 2005, Wisz et al. 2008; GOOSEMAP¹))	Lower	Higher
Seabird colonies (Eide et al. 2004; NPI Seabird database ²⁾)	Longer distance from Arctic fox natal den	Shorter distance from Arctic fox natal den
	Mean = 13.5 km (± 4.32)	Mean = 8.69 km (± 3.79)
Access to other marine resources (Seal carcasses and pups on sea ice or at glacier fronts; Eide et al. 2012)	Longer distance from Arctic fox natal den	Shorter distance from Arctic fox natal den
Reindeer density and carcass availability (Jepsen et al. 2002; Eide at al. 2005, Pedersen et al. 2014)	Similar	Similar
Arctic fox den occupancy 1984-89 and 1997-2001- (Based on estimates from Eide et al. 2012; see Fig. 4b)	Lower	Higher
Arctic fox den occupancy 2012 (Fuglei unpublished)	N monitored dens = 10 N occupied dens = 4 (40 %)	N monitored dens = 10 N occupied dens = 4 (40 %)

^{448 1)} www.goosemap.nina.no 449 2) http://svalbardkartet.npd

²⁾ http://svalbardkartet.npolar.no/Viewer.html?Viewer=Svalbardkartet.

Table 2 Summary of artificial nest predation by study location (prey-rich = high goose abundance; prey-poor = low goose abundance; Fig. 1) and time period (period $1 = 1^{st} - 10^{th}$ July; period $2 = 10^{th} - 20^{th}$ July) the nests were available for predation. Total predation = the number of eggs depredated. Nest = the total number of artificial nests available for predation

	Prey-rich		Prey-	poor
	Period 1	Period 2	Period 1	Period 2
Total predation	30 (57 %)	35 (59 %)	43 (75 %)	51 (89)
Nest (n)	53	59	57	57

Table 3 Ranking of the five best generalized linear mixed-effect models for assessment of relative nest predation risk on small to medium-sized ground-nesting birds (e.g. Svalbard Rock Ptarmigan *Lagopus muta hyperborea*, small waders [Common Ringed Plover *Charadrius hiaticula*, Ringed Plover *Charadrius hiaticula*, Dunlin *Calidris alpina*, Purple Sandpiper *Calidris maritima*, Sanderling *Calidris alba*, Red Phalarope *Phalaropus fulicarius*, Red-necked Phalarope *Phalaropus lobatus*, Ruddy Turnstone *Arenaria interpres*; Henriksen and Hilmo (2015)] and the Snow bunting *Plectrophenax nivalis*) in the prey-rich (high goose abundance) and the prey-poor (low goose abundance) study locations.; Fig. 1). *Transect* and *plot* were always included as random effect variables in the models. Models were ranked according to Akaike's information criterion corrected for small sample size (AIC_c), differences in ΔAIC_c and ΔAIC_c. K = number of parameters estimated. The model in bold was used for inference

Model rank	Location	Period	Habitat	Location × Period	Location × Habitat	К	AICc	ΔAIC _c	AIC _{c weights}
1	Х	Х			-	5	256.12	0.00	0.50
2	X				-	4	256.38	0.26	0.44
3			Х	X	-	10	262.58	6.46	0.02
4	х	Х	Х		-	9	262.89	6.77	0.02
5	Х		Х		-	8	263.06	6.94	0.02

Table 4 Estimated effect sizes (on the logit scale) from the selected model describing artificial nest predation risks in the two study locations contrasted by prey resources (preyrich = high goose abundance; prey-poor = low goose abundance; Fig. 1). Coefficients for the random effect variables and residual variability are standard deviations. Residual degrees of freedom = 222

Explanato	ry variable	Estimate	SE	р
Fixed	Intercept (prey-rich location)	0.49	0.37	0.18
	Location (prey-poor location)	1.53	0.57	<0.01
Random	Transect × Plot	0.92		
	Transect	0.87		

Figures legends

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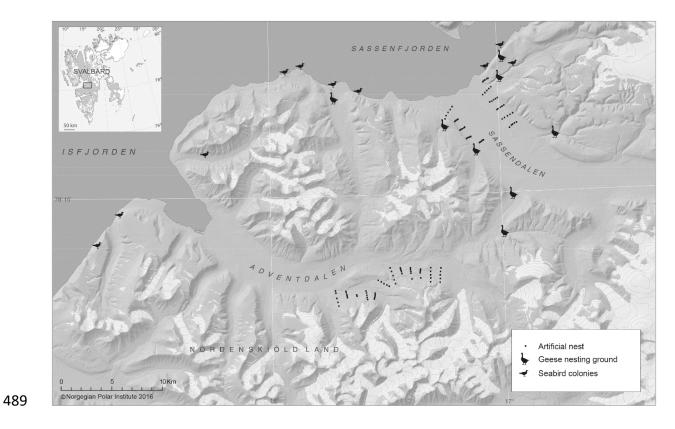
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Fig. 1 Location of the study area with the spatial design of the 24 transects for assessing relative nest predation risks in two study locations contrasted by prey resources (Adventdalen = prey-poor [low goose abundance]; Sassendalen = prey-rich [high goose abundance]; see Jepsen et al. 2002, Eide t al. 2004). The transects span along a vegetation productivity gradient from the valley bottom to the upper vegetation limit at higher elevations. Symbols indicate the distribution of goose breeding grounds and seabird colonies. The inset shows the study area on the Svalbard archipelago. The figure is modified after Eide et al. (2004; Fig. 1) Fig. 2 Habitat and altitude characteristics for assessing relative nest predation risk in the prey-poor and prey-rich study locations between 1st and 20th July in 2012. . The bar-plots (a c) show the proportion of the habitat types across: a) the prey-poor and prey-rich study locations; b) plots in the prey-poor study location; and c) plots in the prey-rich study location. The box-plots (d - f) show the altitude (m) across: d) the prey-poor and prey-rich study locations; e) plots in the prey-poor study location; and f) plots in the prey-rich study location.

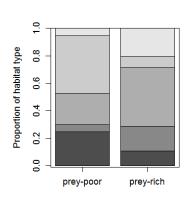
Figures

Fig. 1

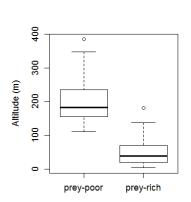


490 Fig. 2

a)



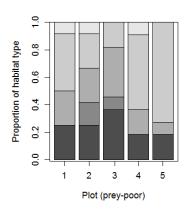
d)

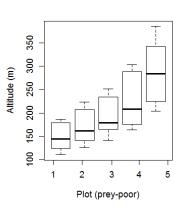


not classified
dry
wet
moist
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b)

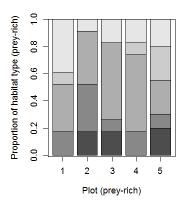
e)





c)

f)



150 Altitude (m) 100 20 Plot (prey-rich)

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