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RESEARCH ARTICLE

Nest association between two predators as a behavioral response to the low density of rodents

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ABSTRACT
Many birds nest in association with aggressive birds of other species to benefit from their protection against predators. We hypothesized that the protective effect also could extend to foraging resources, whereby the resultant resource-enriched habitats near a nest of aggressive raptors could be an alternative cause of associations between nesting bird species with non-overlapping foraging niches. In the Arctic, the Rough-legged Hawk (*Buteo lagopus*) and the Peregrine Falcon (*Falco peregrinus*) are 2 raptor species with non-overlapping food resources that have been reported to nest sometimes in close proximity. Since nesting Peregrine Falcons are very aggressive, they may protect the small rodent prey near their nests from predation, and Rough-legged Hawks could use these hot spots as a nesting territory. In 2 regions in low Arctic Russia we found that (1) the nesting territories of Peregrine Falcons were indeed enriched with small rodents as compared to control areas, (2) the probability of nest association between the 2 raptors increased when rodent abundance was generally low in the region where hawks did not use alternative prey, and (3) hawk reproductive success increased when nesting close to Peregrine Falcons. These results suggest that implications of aggressive nest site defense in birds in certain cases may involve more mechanisms than previously explored. A key ecological process in tundra, rodent population cycles, may explain the occurrence and adaptive significance of a specific behavior pattern, the nesting association between 2 raptor species.

Keywords: Arctic, nest association, Peregrine Falcon, raptors, Rough-legged Hawk, tundra

Asociación de nidos entre dos depredadores como respuesta comportamental a la baja densidad de roedores

RESUMEN
Muchas aves anidan en asociación con aves agresivas de otras especies para beneficiarse de su protección contra los depredadores. Hipotetizamos que el efecto protector también podría extenderse a los recursos alimenticios, por lo cual los hábitats resultantes con recursos adicionales cerca de los nidos de rapaces agresivas podrían ser una causa alternativa de asociación entre especies de aves anidando con nichos de forrajeo no superpuestos. En el Ártico, *Buteo lagopus* y *Falco peregrinus* son dos especies de rapaces con recursos alimenticios no superpuestos que han sido identificadas por anidar a veces de modo cercano. Debido a que los individuos anidando de *F. peregrinus* son muy agresivos, ellos pueden proteger de la depredación a las pequeñas presas de roedores cerca de sus nidos, y *Buteo lagopus* podría usar estos sitios "calientes" como territorios de anidación. En dos regiones del bajo Ártico de Rusia encontramos que (1) los territorios de anidación de *F. peregrinus* estuvieron de hecho enriquecidos con pequeños roedores en comparación a las áreas control, (2) la probabilidad de asociación de nidos entre las dos especies de rapaces aumentó cuando la abundancia de roedores fue generalmente baja en los lugares donde *B. lagopus* no usó presas alternativas, y (3) el éxito reproductivo de *B. lagopus* aumentó cuando anidó cerca de *F. peregrinus*. Estos resultados sugieren que, en ciertos casos, las implicancias de la defensa agresiva del sitio de anidación pueden incluir más mecanismos que los explorados previamente. Un proceso ecológico clave de la Tundra, como el ciclo de los roedores, puede explicar la existencia y la significancia adaptativa de un patrón de comportamiento específico, la asociación de anidación entre dos especies de rapaces.

Palabras clave: Ártico, asociación de nidos, *Buteo lagopus*, *Falco peregrinus*, rapaces, tundra

INTRODUCTION

Many birds nest in association with birds of prey or aggressive insects (Wiklund 1982, Bogliani et al. 1999, Quinn and Kokorev 2002, Quinn et al. 2003, Quinn and Ueta 2008). The main benefit of such an association is reduced predation for the protected species. However, other benefits have also been described, such as early warning of predators, lower parasitism, lower brood parasitism, and higher mating success (Larsen and Grundetjern 1997, van Kleef et al. 2007, Quinn and Ueta 2008). At the same time, protective species can prey on the protected ones, and the decision to nest close to these aggressive species is always a tradeoff between costs and benefits (Gotmark 1989, Quinn and Kokorev 2002). According to the review of Quinn and Ueta (2008), nest associations among birds are global in distribution and involve raptors, gulls, and waders as protective species, and waterfowl, waders, and passerine birds as protected ones. Nest associations including raptors as both protective and protected species have not been reported.

The minimum distance between raptor nests of different species in the Arctic ranges from 700 to 1,800 m for different species, except for the Rough-legged Hawk (*Buteo lagopus*). These hawks have been reported to nest as close as 50 m from Peregrine Falcons (*Falco peregrinus*) or Gyrfalcons (*Falco rusticolus*), whereas they prefer to nest at a minimum 700 m from the nests of Golden Eagles (*Aquila chrysaetos*) (Janes 1985, Bergo 1987, Poole and Bromley 1988, Kalyakin 1989, Sokolov 2002). Rough-legged Hawks are generally considered specialized small-rodent predators while Peregrine Falcons mostly feed on birds (Bradley and Oliphant 1991, Ellis et al. 2004). Thus, there is no trophic niche overlap between the 2 species.

We suggest that Rough-legged Hawks and Peregrine Falcons are nesting together because one or both parties benefit from such an association and not because they use a common patchily distributed resource. An alternative reason could be that they prefer the same nesting habitat. Indeed, both species like to nest on cliffs, but whereas this is the only nesting habitat for Peregrine Falcons, Rough-legged Hawks build nests in other habitats as well (Wiklund et al. 1998). In the study regions, Rough-legged Hawks nest on sand cliffs along the rivers and in the open tundra in equal numbers (Sokolov 2002, Pokrovsky et al. 2014). It seems thus unlikely that they would be forced to breed close to Peregrine Falcons because of a lack of other nesting sites. Peregrine Falcons are known to behave aggressively toward hawks nesting close to their nest; therefore, Rough-legged Hawks risk predation on themselves or their offspring when nesting near Peregrine Falcons (Kalyakin 1989). Rough-legged Hawks have been reported to avoid breeding close to Snowy Owls (*Bubo scandiacus*), a behavior that has been interpreted as avoidance of predation from the more aggressive owls (Wiklund et al. 1998). Consequently, it is likely that Rough-legged Hawks will only engage in nesting association with Peregrine Falcons if the benefit of such a behavior outweighs the predation risk.

We assume that nesting associations between Rough-legged Hawks and Peregrine Falcons result from a choice of the hawks. Peregrine Falcons have a high level of fidelity to nesting sites (Ratcliffe 1993). Rough-legged Hawks, on the contrary, are considered to be nomadic and may change nesting territory from year to year, although long-term nesting sites exist in some regions (Bechard and Swem 2002, Beardsell et al. 2016). At the same time, the nest-use probability among Rough-legged Hawks increased with rodent density (Beardsell et al. 2016), and nest association between Peregrine Falcon and hawk nests occurred mostly in years with a low density of small rodents (Kalyakin 1989, Sokolov 2002).

We propose 2 nonexclusive hypotheses to explain the suggested link between the Rough-legged Hawks' choice of a breeding site close to Peregrine Falcons and small-rodent density. First, during periods of low density of small rodents the risk of nest predation increases (Bêty et al. 2001, Ims et al. 2013) because predators such as Arctic foxes (*Vulpes lagopus*) and mustelids must rely on alternative prey. Thus, hawks nesting near Peregrine Falcons may benefit from their protection. Peregrine Falcons have a high level of aggressiveness indeed and are very efficient in protecting their nesting territories. This explains why Arctic goose species, especially Red-breasted Goose (*Branta rufficollis*), prefer them to Snowy Owls when establishing nesting associations (Quinn et al. 2003, Kharitonov et al. 2013). Quinn et al. (2003) studied the ability of several raptor species and gulls to repel Arctic foxes approaching their nests and found that Rough-legged Hawks were less likely than others to exclude this predator from their nesting territory. Besides the direct effect of protection, an association with a protective species could also indirectly benefit hawks by allowing the adults to spend more time searching for food. We call this the "defense hypothesis." The second hypothesis assumes that the protective effect of Peregrine Falcons extends to the hawk's preferred prey, small rodents. Thus, Peregrine Falcons could create a patch around their nest with zero or very low impact of predators. The density of small rodents inside exclosures that protect them from predators can increase up to 1.9 times because predation limits small-rodent population growth during the summer due to its negative impact on survival (Fauteux et al. 2016). Because of that, local patches with a high density of small rodents may be created around Peregrine Falcon nests. Such rodent "hot spots" can be expected to be attractive and beneficial to Rough-legged Hawks, especially in years when rodent abundance is generally low at the landscape level. We call this the "foraging hypothesis."

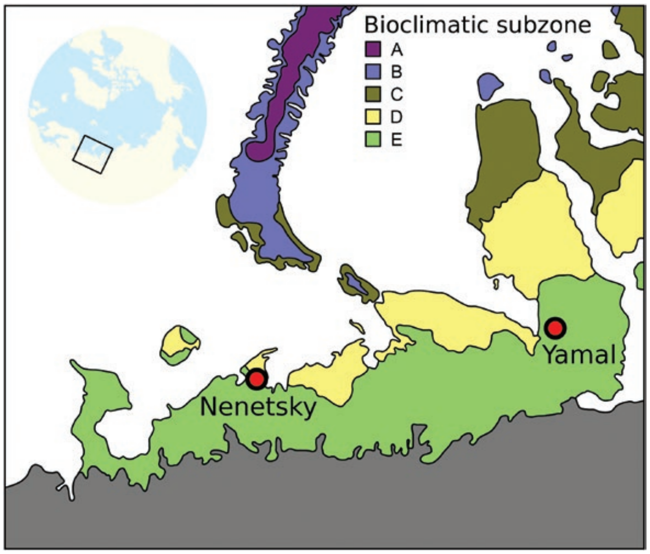

FIGURE 1. Map showing the locations of the study regions. See Table 1 for characteristics of each region. Bioclimatic subzones: A = High Arctic tundra, B = Arctic tundra: northern variant, C = Arctic tundra: southern variant, D = Northern hypo-Arctic tundra, E = Southern hypo-Arctic tundra (Walker et al. 2005).

In the present paper, we study the circumstances of breeding associations of Rough-legged Hawks and Peregrine Falcons in 2 low Arctic regions of Russia (Figure 1) and assess which of the 2 hypotheses outlined above may explain this phenomenon. Rough-legged Hawks have been shown to behave differently in the 2 study regions regarding their numerical and functional response to small-rodent density fluctuations. In one of the regions (Nenetsky Nature Reserve, hereafter "Nenetsky"), the hawks switched to alternative prey when small rodents were scarce and their breeding density did not depend on small-rodent abundance (Pokrovsky et al. 2014). In the other region (southern Yamal peninsula, hereafter "Yamal"), hawks behave as more strict small-rodent specialists feeding mostly on this preferred prey regardless of its abundance, and breeding density is strongly correlated with small-rodent abundance (Sokolov 2002, Fufachev et al. 2019; Figure 2). Given the contrast in the degree of specialization of Rough-legged Hawks in the 2 study areas and our 2 hypotheses, we make the following predictions. First, we test the prediction (Prediction 1) of the foraging hypothesis that the density of small rodents is higher around Peregrine Falcon nests than in a similar habitat without Peregrine Falcons. Second, we predict (Prediction 2) that if the foraging hypothesis is true then a relationship between the probability of Rough-legged Hawk–Peregrine Falcon nest association and density of small rodents would be likely in Yamal but not in Nenetsky. In Nenetsky, where Rough-legged Hawks switch to alternative prey when small rodents are scarce, they would not need to look for spots with a high density of small rodents, which may form around Peregrine Falcon nests. If, on the contrary, the defense hypothesis is true, then nesting association between Rough-legged Hawks and Peregrine Falcons would be more likely in years of low density of small rodents both in Yamal and Nenetsky, because in such years predation risk generally increases. Third, both of our hypotheses predict (Prediction 3) that breeding success of Rough-legged Hawks will be higher for pairs, which are in a nesting association with Peregrine Falcons independent of the study region.

MATERIAL AND METHODS

Study Regions and Study Species

Our research was carried out in 2 regions of the Russian Arctic: Nenetsky Nature Reserve (68°20′N, 53°18′E) in the Pechora river lowlands and "Erkuta" tundra monitoring site (68°12′N, 68°59′E) in the southern part of Yamal peninsula (Figure 1). Both study regions are situated in the low-shrub tundra zone of the low Arctic (Walker et al. 2005), which is characterized by numerous patches of willow (*Salix* spp.) thickets (~1.5 m high) mostly distributed along the river valleys. In both of them, the surrounding tundra landscape contains sand cliffs up to 40–50 m above sea level (Ehrich et al. 2012). In both regions, field observations were carried out from mid-June to mid-August; in Nenetsky in 2007–2011 and in Yamal in 2007–2015.

Peregrine Falcons and Rough-legged Hawks are the only raptors breeding there, although White-tailed Sea Eagles (*Haliaeetus albicilla*) and Northern Harriers (*Circus cyaneus*) are present in both areas in most years; single

TABLE 1. Abundance of Rough-legged Hawks, Peregrine Falcons, and small rodents in Nenetsky and Yamal.

Area	Years	Number of nests		Distance between hawk nest and nearest falcon nest (m)		Abundance of small rodents (animals per 100 traps per night)	Breeding success of Rough-legged Hawks (fledglings)	
		Hawk	Falcon	(min–max)	(mean ± 95% CI)	(min–max)	(min–max)	(mean ± 95% CI)
Nenetsky	2007–2011	36	21	501–5,507	2,181 ± 412	1.97–14.93	0–3	1.1 ± 0.3
Yamal	2008–2015	41[a]	63	351–7,962	2,433 ± 620	1.04–10.07	0–2	1.2 ± 0.5

[a] In Yamal, parameters of the distance between nests are based on 39 nests and parameters of breeding success are based on 16 nests (2008, 2012–2015)

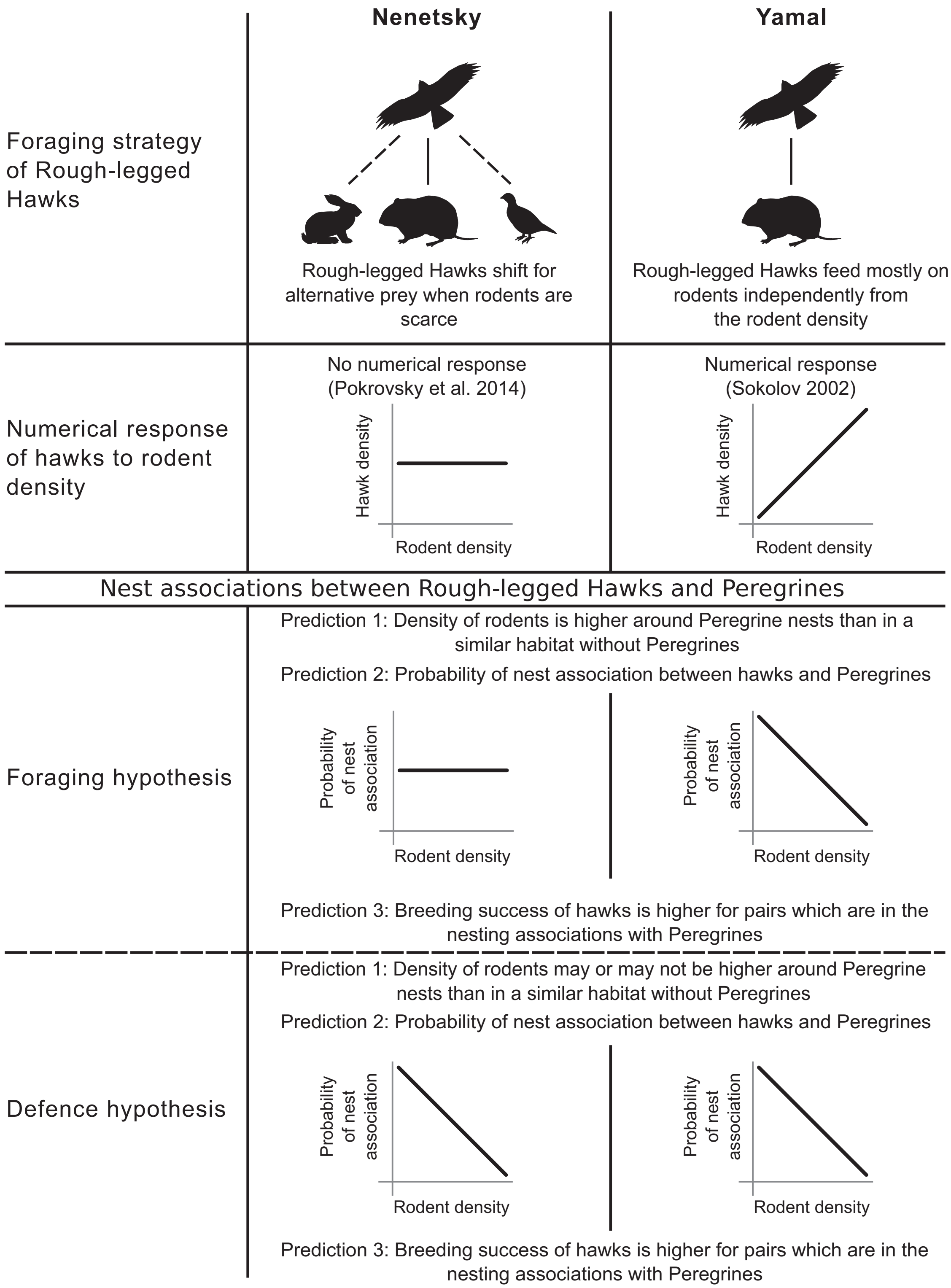

FIGURE 2. The difference in foraging strategy of Rough-legged Hawks in 2 regions leads to a difference in the numerical response of hawk density to rodent density and, thus, to a difference in nest association behavior.

nests of harriers were found in Yamal and in Nenetsky. Mammalian predators that could prey on raptor nests—such as foxes (*V. lagopus* and *V. vulpes*), stoats (*Mustela erminea*), and wolverine (*Gulo gulo*)—were regularly present in both regions (van Eerden 2000, Sokolov 2002). In Nenetsky, the small-rodent community is dominated by tundra voles (*Microtus oeconomus*) with a small share of collared lemmings (*Dicrostonyx torquatus*) and water voles (*Arvicola terrestris*) (Pokrovsky et al. 2014). In Yamal, the most abundant small rodents are narrow-headed voles (*M. gregalis*) and Middendorff's vole (*M. middendorffi*). In addition, collared lemmings as well as rare Siberian lemmings (*Lemmus sibiricus*) and northern red-backed voles (*Myodes rutilus*) occur (Sokolova et al. 2014). In both regions, the small-rodent cycles are of rather low amplitude.

Nest Association and Breeding Success

In both regions, we monitored an area of ~150 km^2 each year to search for Rough-legged Hawk and Peregrine Falcon nests and to register the nest association events. We observed an area, targeting river and lake banks, during walking excursions and using 8–10× binoculars. We used observations of the alarm behavior of adult birds as an indicator of the presence of a nesting territory. We registered coordinates of all nests using various models of Garmin GPS recorders. We used coordinates of the nests to calculate the linear distances between hawk and falcon nests. For each Rough-legged Hawk nest, we determined the distance to the nearest Peregrine Falcon nest. In total, we found 77 Rough-legged Hawk nests and 84 Peregrine Falcon nests (Table 1). The distance between hawk and nearest falcon nests varied between 351 and 7,962 m. Two nests with distances of 14,673 and 15,469 m were excluded from the analysis as outliers; these were situated outside the main study area in Yamal and it is possible that we did not find the nearest Peregrine Falcon nests.

We defined Rough-legged Hawk nests as associated with Peregrine Falcons when the distance between them was <1 km. We chose this distance based on information about Peregrine Falcons' home range, estimated based on telemetry in the same study region in Yamal (Sokolov et al. 2014), and on information about Rough-legged Hawks' home range estimated in the same study region in Nenetsky (I. Pokrovsky personal observation). Mean radius of the Peregrine Falcons' home range was 5.6 km; however, in the early stages of breeding, it averaged 1.7 km. Mean radius of the Rough-legged Hawks' home range was 1.6 km. Thus, nests located at a distance of 1 km or less would have a strong home range overlap and could be defined as nests in an association. Because this distance was chosen quite arbitrarily, we also carried out the analysis setting the cutoff for nests in association at 750 m and 1.5 km from each other. After that, for each year we scored each hawk nest with respect to whether it was in association with Peregrine Falcons or not. Overall, 16 Rough-legged Hawk nests were located within 1 km of a Peregrine Falcon nest of which 8 were in Nenetsky and 8 in Yamal (for 750 m and 1.5 km, see Appendix Table 3).

We estimated Rough-legged Hawk breeding success as the number of fledglings (young that reached 35 days of age; ~4 days before average fledging time) per territorial pair. In Nenetsky, we estimated breeding success during all 5 yr and in Yamal during 2007–2008 and 2012–2015. Breeding success among Rough-legged Hawks was higher for the nests located in the river valley than in the open tundra landscape (Sokolov 2002, Pokrovsky 2012). Thus we also recorded nest location as river valley or open tundra to control for this variable in the analysis. Breeding success was estimated for 52 Rough-legged Hawk nests: 36 nests observed in Nenetsky and 16 nests in Yamal (for number of these nests in different habitat types see Appendix Table 4).

Abundance of Small Rodents at the Landscape Level and Near Peregrine Falcon Nests

In both regions, we estimated abundance indices for small rodents at the landscape level, near Peregrine Falcon nests, and at associated control locations. Small-rodent abundance at the landscape level was evaluated using snap trapping on 36 permanent plots covering 3 widespread habitat types (meadows at the edge of willow thickets and 2 types of tundra). In Yamal in 2012–2015, the number of study plots was increased to 54. Spatially, we arranged the plots as triplets as far as possible given landscape constraints, with one plot in each of the three habitats in each triplet (see Ehrich et al. [2012] for details about the habitats and design). Rodent trapping was done using the small quadrate method (Myllymäki et al. 1971). We placed 3 snap traps in each corner of 15 × 15 m plots for 2 successive nights at the end of June and in the middle of August and baited them with raisins and rolled oats. In total, in Nenetsky and in Yamal in 2007–2011 the yearly abundance indices were thus based on 864 traps per night per session in each region (36 plots × 12 traps × 2 nights), and on 1,296 traps per night (54 plots × 12 traps × 2 nights) for Yamal in 2012–2015. We used an index averaged over all habitats and both trapping sessions to reflect the relative abundance of small rodents in a particular summer. The number of small rodents caught per year varied between 1.97 and 14.93 animals per 100 traps per night (all species pooled) in Nenetsky and between 1.04 and 10.07 in Yamal (Table 1).

Abundance indices for small rodents near Peregrine Falcon nests and at associated control locations were estimated in Nenetsky in 2009–2011 and in Yamal in 2016. In Nenetsky, we placed snap traps around the nest and ~500 m from the nest at a control location (Appendix Figure 6). This distance corresponds approximately to the distance at which Peregrine Falcons stop alarming when we were leaving their nests, and thus where the impact of their defense is likely to decrease (Quinn and Kokorev 2002, Quinn et al. 2003). In all other aspects such as relief (sand cliff), vegetation, and slope exposition the control locations were chosen to be as similar as possible to the Peregrine Falcon nesting sites. In each location, in the middle of August, we placed 50 snap traps on an area of approximately 700–900 m^2 at 3–5 m from each other for 2 successive nights (resulting in 100 trap nights per site). For nests (and associated controls) located on river banks, we placed traps on the slope of the river, covered by meadows and willow thickets. For nests located on the seashore (as well as on the associated control locations) we placed traps in the surrounding tundra where shrubby and hummocky habitats dominated. As for the regular trapping, all traps were baited with raisins and rolled oats. In Yamal, snap trapping was carried out directly around the nest and at 3 control locations for each nest, which were chosen at approximately 500, 1,000, and 1,500 m from the nest. However, for one of the nests in Yamal, we could not find any suitable habitat at 500 m distance; therefore, the closest control location was established 200 m from the nest. Trapping was carried out in the same way in Yamal as in Nenetsky.

Data Analysis

We analyzed the relationship between small-rodent abundance and distance from the Peregrine Falcon nest (Prediction 1) using a generalized linear mixed-effects model (GLMM) with the number of rodents caught as the response variable and a Poisson distribution. Location (falcon nest/control plot) and region (Nenetsky or Yamal) were included as fixed effects. Nesting event (i.e. nest site and year) was included as a random effect to account for the design of the experiment, where each nest was paired with one or several control sites that were chosen to be as similar as possible. To account for overdispersion, observation was included as additional random effect.

The relationship between the occurrence of nesting association and small-rodent density (Prediction 2) was analyzed using a general linear model (GLM) with the proportion of the Rough-legged Hawk nests in association as the response variable and a binomial error distribution. Region (Nenetsky or Yamal) and the logarithm of the yearly average small-rodent trapping index (number of animals caught per 100 trap nights) were used as explanatory variables. We included an interaction between these 2 variables to estimate the difference between 2 regions according to our prediction.

The predicted relationship between Rough-legged Hawk breeding success and location of the nest in a hawk–falcon nest association (Prediction 3) was analyzed using a generalized linear model (GLM) with the number of fledglings per nest as the response variable, a log link, and a Poisson distributed error. The explanatory variables were a factor for in/out of the nest association (750, 1,000, and 1,500 m), region (Nenetsky or Yamal), the average small-rodent trapping index for the whole summer (log transformed), and the habitat where a Rough-legged Hawk nest was located (in the river valley or in the open tundra). Six candidate models were compared. All models included nest association, as this is the focal parameter in our study. First we compared 3 models with each of the nest association variables (750, 1,000, and 1,500 m). Then we used the nest association variable with most support (1,500 m) to extend the models to include an interaction with region, log small-rodent abundance, and habitat (Appendix Table 5). The candidate models were compared using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and a model was considered better than another when the difference in AIC_c was larger than 2.

All analyses were carried out using R 3.4.3 (R Development Core Team 2018). The function *glmer* from the package *lme4* (Bates et al. 2015) was used for GLMM, the function *glm* for GLM, and the function *aictab* from the package *AICcmodavg* (Mazerolle 2019) for AIC_c. Results are reported as means ± 95% CI.

RESULTS

We conducted estimation of abundance indices for small rodents around 18 Peregrine Falcon nests and at 28 associated control locations. Thirteen nests and 13 control locations were in Nenetsky (2009–2011) and 5 nests and 15 control locations in Yamal (2016). In Nenetsky, the nests were found within 5 nesting sites, which were located in 2 different habitats: on sand cliffs along the shore of Korovinskaya Bay and in the river valleys in the inland tundra. In Yamal, 4 nests were situated on high river banks on sandy cliffs, whereas the last one was located on a sand cliff on the shore of a lake. In total, we caught 230 small rodents near the nests and at associated control locations. In Nenetsky, 90% of all small rodents were tundra voles; in Yamal 98% of all small rodents were narrow-headed voles. In Nenetsky, in the seashore habitat over all 3 yr, we trapped only one collared lemming near the nest and no rodents on the control locations. In the river valley habitat, we caught on average 15 (95% CI: 12.06–18.44, estimated based on the Poisson distribution) rodents around the nests and 5.2 (95% CI: 3.51–7.33) rodents around the control locations (Figure 3). In Yamal, we caught an average of 9.6 (95% CI: 7.08–12.73) rodents around the nests and 4.08 (95% CI: 3.02–5.40) at the control locations (Figure 3). According to the GLMM, the number of small rodents increased by a factor of 3.23 (95% CI: 1.66–6.62) around Peregrine Falcon nests compared to control locations (Appendix Table 6 and Figure 3).

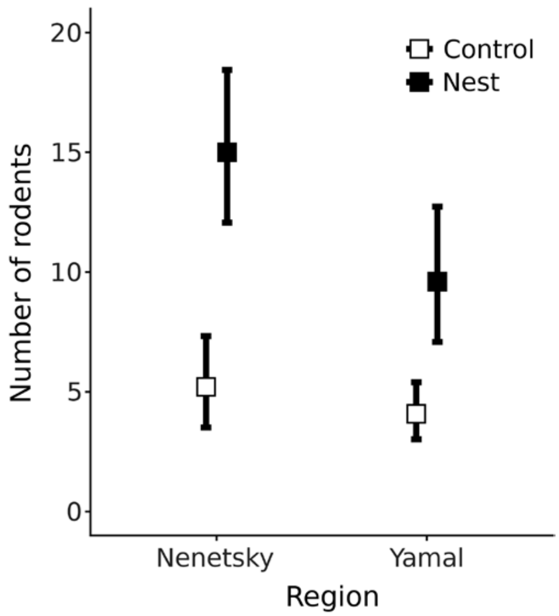

FIGURE 3. The number of small rodents caught per 100 trap nights in the immediate vicinity of Peregrine Falcon nests and at control locations (>500 m). Error bars = 95% CI (estimated based on a Poisson distribution). See Appendix Table 6 for model output.

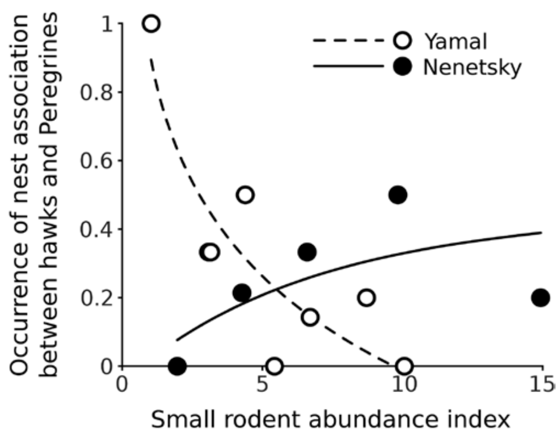

FIGURE 4. The relationship between Rough-legged Hawk and Peregrine Falcon nest association occurrence and rodent abundance. See Table 2 for the model output and Appendix Tables 7 and 8 for the model output for the distances 750 and 1,500 m.

As predicted by the foraging hypothesis (Prediction 2; Figure 2), occurrence of nesting association in Yamal decreased with an increase in small-rodent abundance, whereas that was not the case in Nenetsky (Figure 4). The binomial model of occurrence of nest associations between the 2 raptors revealed a significant interaction between rodent abundance and region (Table 2). Carrying out the same analysis with a cutoff for nest association at distances of 750 m and 1,500 m provided qualitatively similar results (Appendix Tables 7 and 8).

TABLE 2. The relationship between the occurrence of the Rough-legged Hawk and Peregrine Falcon nest associations and rodent abundance. Intercept: Yamal is the intercept for the reference level Yamal. Rodents is the slope for Yamal. Nenetsky is the difference between the 2 intercepts (for Yamal and Nenetsky). Nenetsky/Yamal is the difference between the 2 slopes: for Nenetsky and for Yamal. Effect sizes are on the logit scale. For the plot of the model, see Figure 4

Explanatory variable and interactions	Estimate	SE	*z* value	*P* value
Intercept: Yamal	2.09	1.53	1.37	
Rodents	−2.19	0.97	−2.25	0.025
Nenetsky	−4.18	1.99	−2.09	0.036
Nenetsky/Yamal	2.63	1.16	2.27	0.023

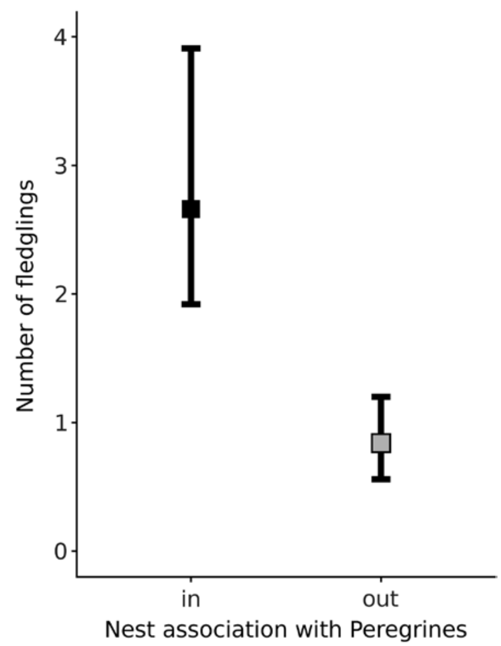

FIGURE 5. The relationship between the Rough-legged Hawk breeding success and location of the nest in or out of association with Peregrine Falcons. Error bars = 95% CI (estimated based on a Poisson distribution). See Appendix Table 9 for the model output.

The number of Rough-legged Hawk fledglings varied between 0 and 3 with little difference between areas in the mean number of fledglings per nest (Table 1). The general linear model, which received the most support from AIC_c, included only nest association (with a cutoff distance of 1,500 m; Appendix Table 5). The 2 models with shorter cutoff distances received lower support from AIC_c (difference in AIC_c 2.14 for 750 m and 4.07 for 1,000 m). This was also the case for the models that included region, small-rodent abundance, and habitat. According to the best model, the number of fledglings was higher with a factor of 1.82 (CI: 1.08–3.07) in the nests that were in association with Peregrine Falcons (Appendix Table 9 and Figure 5), in accordance with

Prediction 3 (Figure 2). The interaction between nest association and region was not supported by our data.

DISCUSSION

Here we showed that the protective effect of Peregrine Falcon nest defense could extend to foraging resources of Rough-legged Hawks and that this could be an alternative cause of nest associations between these 2 species. We observed Rough-legged Hawks breeding well within Peregrine Falcons' nesting territory in both study areas in agreement with what had been reported in earlier literature (Poole and Bromley 1988, Kalyakin 1989, Sokolov 2002). As assumed by the foraging hypothesis, the abundance of small rodents was in general higher around Peregrine Falcon nests than in similar habitats without a Peregrine Falcon nest (Figure 3). The occurrence of nest association between Rough-legged Hawks and Peregrine Falcons increased with low abundance of small rodents but this was the case only in Yamal (Table 2, Figure 4). Thus, because of the difference between the study regions (Figure 2), our data are in agreement with the foraging hypothesis. In general, nest defense is the main reason for establishing nesting associations among bird species (Quinn and Ueta 2008), and we cannot exclude that nest defense might also play a role for Rough-legged Hawks, notably in Nenetsky. However, for the hawks, nestling predation represents only about 0–10% of all cases of nestling mortality, while lack of food is one of the most frequent reasons for unsuccessful breeding and could be the cause of up to 90% of all nestling mortality (Kalyakin 1989, Potapov 1997, Pokrovsky et al. 2012). Low nest predation rate in Rough-legged Hawks also suggests that predation by Peregrine Falcons could hardly counteract nest defense benefits of breeding in association. While it is clear that Rough-legged Hawks could use "hot spots" of small rodents around Peregrine Falcon nests, there could be several possible underlying mechanisms for the nest association.

The most convincing mechanism of nest association formation is that Rough-legged Hawks choose to nest in a location with a high density of small rodents, which has been formed by Peregrine Falcons around their nesting site, suggesting rodents are the main factor. Alternatively, Peregrine Falcons themselves could be a factor for Rough-legged Hawks to nest in close vicinity. Previous studies have shown that hawks use rodent scent marks to assess the breeding area (Koivula and Viitala 1999). Also, according to our data, in some years in Yamal Rough-legged Hawks nested close to the Peregrine Falcon breeding area, while Peregrine Falcons were absent in this particular year on their nesting site. This evidence suggests that the main factor for Rough-legged Hawks to associate their nest with Peregrine Falcons might be enhanced rodent density around the nests of Peregrine Falcons and not the Peregrine Falcons themselves. An interesting question in this respect is whether the high density of small rodents could be maintained over several years on the breeding site of Peregrine Falcons, or whether it is forming each year starting at the moment when Peregrine Falcons arrive at their territory during spring migration. We have no firm evidence of long-term (over winter) persistence of high rodent densities near Peregrine Falcon nests. However, we could suggest this persistence due to the results of the trapping sessions around the Peregrine Falcon nests and control locations. The density of small rodents was indeed higher close to the nests of Peregrine Falcons than at 500 m from the nest in all cases except 2 (Appendix Figures 7 and 8). These 2 cases (one in Yamal and one in Nenetsky) occurred on nests whose locations had changed relative to the previous year. By chance, control plots in these 2 cases were placed close to the location where the nest was situated in the previous year. These observations could mean that Peregrine Falcons might form a local high density of rodents that could exist not only during the breeding season but last at least until the next spring when Rough-legged Hawks could use them during habitat selection.

The well-known aggressive behavior of Peregrine Falcons (Quinn et al. 2003) is another factor suggesting that Rough-legged Hawks use the density of small rodents to assess their habitat and not the presence of Peregrine Falcons themselves when they establish a nest in the association. In Yamal and in Nenetsky during all the years we observed 7 nest associations with a very close distance between the nests (357–567 m). Such an association could be formed only if Rough-legged Hawks established first on the nesting site. Peregrine Falcons would likely not tolerate hawks building a nest in such close proximity to their nest. It is also interesting to compare our results to the study of Wiklund et al. (1998) suggesting that Rough-legged Hawks avoid nesting in the proximity of Snowy Owls, another highly aggressive Arctic raptor. In contrast to Peregrine Falcons, Snowy Owls arrive very early to the breeding grounds and establish territories around the first snow-free patches available for nesting (Holt et al. 2015). They are thus already present when Rough-legged Hawks would choose their territory. This avoidance makes the defense hypothesis a less likely explanation for the breeding association observed here. However, Snowy Owls are specialized small-rodent predators, thus an association based on the foraging hypothesis would not be expected. Therefore, our results suggest 3 conditions for Rough-legged Hawks to form a nest association: (1) hawks should come earlier than Peregrine Falcons to the nesting region, (2) hawks should have no sufficient abundance of alternative prey in the nesting region, and (3) there should be a high density of rodents around the nest of Peregrine Falcons.

Peregrine Falcons can facilitate a local high density of rodents around their nests only if they nest in suitable habitat. Nests of Peregrine Falcons in Nenetsky were situated on sandy cliffs in 2 different habitats: on the seashore (covered by dwarf shrub tundra) and on the river banks. Tundra voles are the dominant species of small rodents in Nenetsky, and they prefer meadows and willow thickets along the rivers as habitat. Therefore, except for one lemming, it was to be expected that we caught no voles around the seashore nests or at their control locations. On the river bank, Peregrine Falcon home ranges are surrounded by meadows and willow thickets, and in these cases, there were more voles around the nests than at the control locations. While not all Peregrine Falcon nest sites are located in suitable habitat for small rodents, it is clear that some of these sand cliffs could be attractive for Rough-legged Hawks as the only snow-free place by the time of their arrival. In that case, we could observe nest association even in the regions where Rough-legged Hawks are known to use alternative prey or even in the regions where rodents are absent, like on Kolguev Island. The postulated underlying mechanisms for the nest association formation implies that appearance of Peregrine Falcons in close proximity to Rough-legged Hawks is unexpected for them. Thus, one could ask whether it is profitable for the hawks, or whether it is commensalism or even an ecological trap.

Breeding success of Rough-legged Hawks increased when nesting close to Peregrine Falcons. The difference between nests in and out of nest association was ~0.5 fledgling and the variation in these groups was very high. We could not conclude that nesting in association with Peregrine Falcons could give Rough-legged Hawks an important gain in reproductive output. At the same time, that allows them to nest in years with a low rodent density. In the systems with higher rodent cycle amplitudes, formation of high density around the Peregrine Falcon nests could be even more pronounced. Local patches of high rodent density could be formed not only by birds but also by humans, which could chase away terrestrial predators specialized on rodents.

To conclude, here we presented a new explanation for the formation of nest association, which could be relevant for other species and systems. Nest association could be formed not only as a result of the attractiveness of one species to another one but indirectly through the changes of the environment by one of the species including humans. The studied phenomenon shows us one of the numerous ways birds, and raptors in particular, can adapt to the unstable tundra environment and compensate for resource depletion.

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Ethics statement: No specific permissions were required according to §44 and §6 of the Federal Law of the Russian Federation No. 52 from 24.04.1995 (last update 03.08.2018) "On Wildlife" to carry out the work for this study. There were no Special Protected Natural Territories in our study area (described in section "Study area," including coordinates), and our activities (described above) did not include withdrawal of investigated species from nature. In Nenetsky, the work was carried out in agreement with the Nenetsky Nature Reserve in a buffer zone. All our protocols met the ABS/ASAB guidelines for the ethical treatment of animals. Snap trapping was used vs. live trapping because live trapping requires inspection of the traps every 2 hr and such frequent visits to the Peregrine Falcon nests are potentially harmful to them.

Author contributions: IP, DE, IF, RAI, OK, AS, NS, VS, and NGY conceived the study and collected the data. IP and DE analyzed the data. IP, DE, RAI, and NGY wrote the paper with the assistance of IF, OK, AS, NS, and VS.

Data depository: Analyses reported in this article can be reproduced using the data provided by Pokrovsky et al. (2019).

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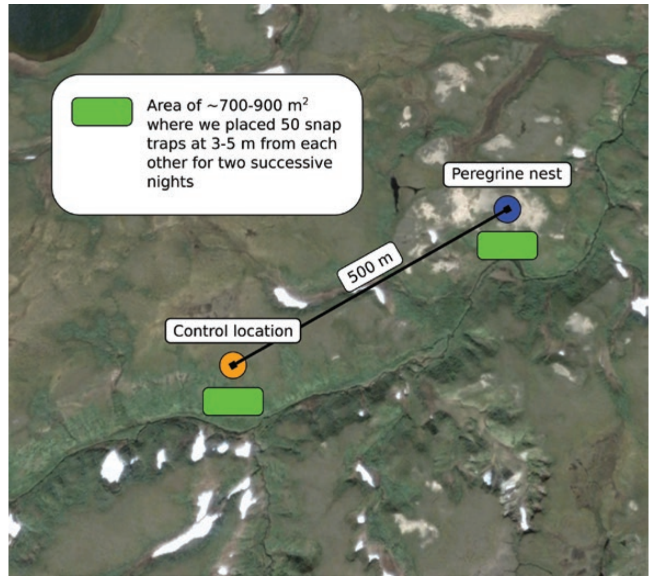
APPENDIX TABLE 3. Number of Rough-legged Hawk nests associated with Peregrine Falcon nests for different cutoff distances.

Distance (m)	Nenetsky	Yamal	Total
750	5	6	11
1,000	8	8	16
1,500	11	17	28

APPENDIX TABLE 4. Number of the Rough-legged Hawk nests associated with Peregrine Falcon nests for different habitats.

Nest association	Habitat		Total
	River valley	Open tundra	
For 750 m			
In nest association	6	2	8
Out of nest association	16	28	44
For 1,000 m			
In nest association	8	5	13
Out of nest association	14	25	39
For 1,500 m			
In nest association	11	10	21
Out of nest association	11	20	31



APPENDIX FIGURE 6. Example of Peregrine Falcon nest and associated control location and area where we placed 50 snap traps 3–5 m apart for 2 successive nights.

APPENDIX TABLE 5. Results of the AIC_c for 6 candidate models. Response variable: the number of fledglings per nest, a log link, and a Poisson distributed error. The explanatory variables: a factor for in/out of the nest association (750, 1,000, and 1,500 m = "Association750," "Association1000," and "Association1500," respectively), region (Nenetsky or Yamal–"Region"), the average small-rodent trapping index for the whole summer (log transformed–"Rodents"), and the habitat where the Rough-legged Hawk nest was located (in the river valley or in the open tundra–"Location").

Model	*k*	AIC_c	ΔAIC_c	w_i	Σw_i	LL
Association1500	2	135.94	0.00	0.53	0.53	–65.85
Association750	2	138.08	2.14	0.18	0.71	–66.92
Association1500*Region	4	139.69	3.75	0.08	0.79	–65.42
Association1500*Location	4	139.91	3.97	0.07	0.87	–65.53
Association1000	2	140.01	4.07	0.07	0.94	–67.88
Association1500*Rodents	4	140.17	4.23	0.06	1.00	–65.66

APPENDIX TABLE 6. Results of the generalized linear mixed-effects model (GLMM) with the number of rodents caught as the response variable and a Poisson error distribution. Location (Peregrine Falcon nest/control) and region (Nenetsky or Yamal) are fixed effects. Effect sizes are on the log scale.

Explanatory variable and interactions	Estimate	SE	*z* value	*P* value
Intercept	0.77	0.84	0.92	
Location	1.17	0.33	3.51	<0.001
Region	–1.65	1.07	–1.54	0.123

APPENDIX TABLE 7. Rough-legged Hawk and Peregrine Falcon nest association occurrence (calculated for 750 m cutoff distance) relative to the region and the rodent abundance. Intercept: Yamal is the intercept for the trend line for Yamal. Rodents is the slope for Yamal. Nenetsky is the difference between 2 intercepts (for Yamal and Nenetsky). Nenetsky/Yamal is the difference between 2 slopes: for Nenetsky and for Yamal. Effect sizes are on the log scale.

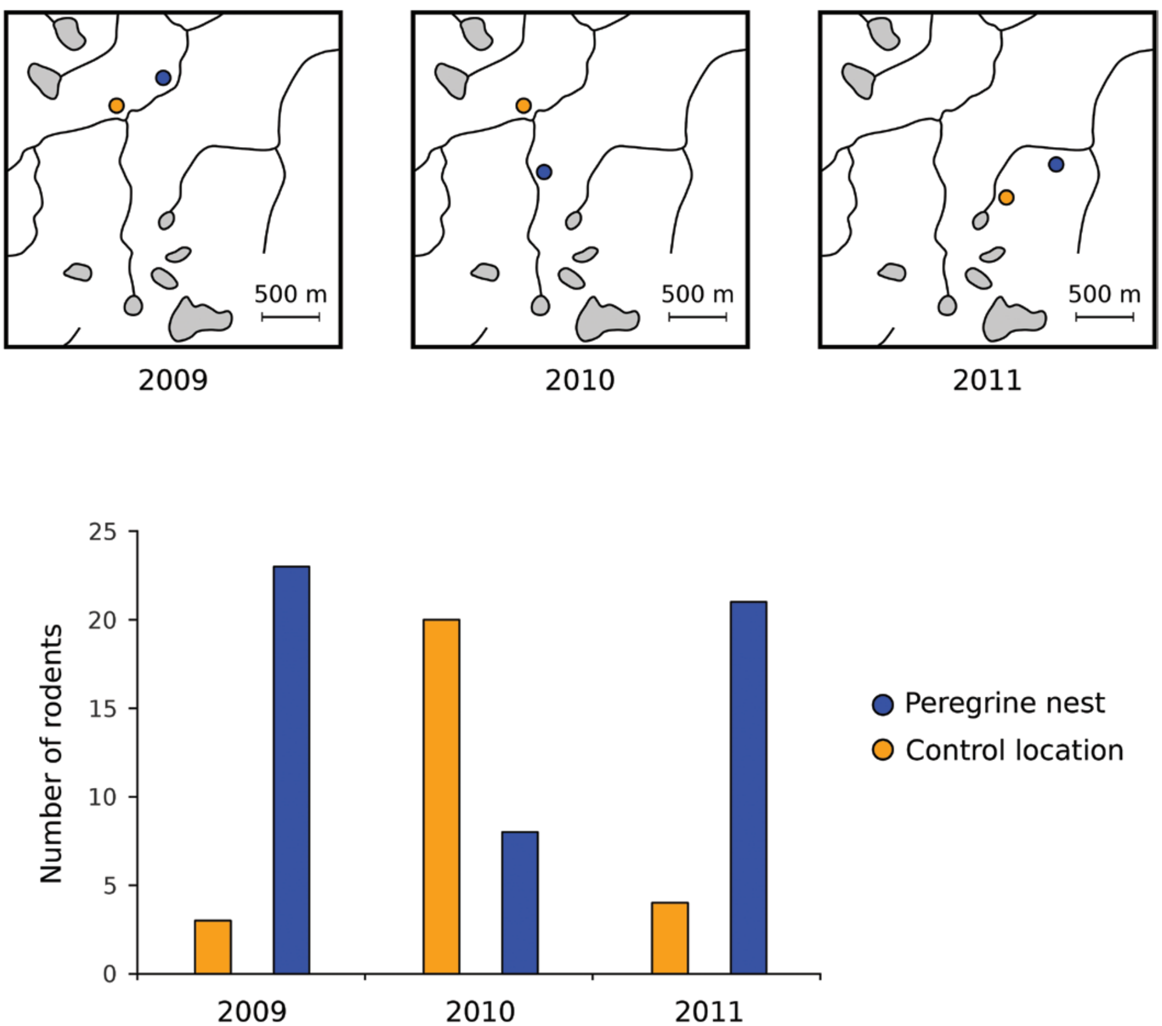
Explanatory variable and interactions	Estimate	SE	*z* value	*P* value
Intercept: Yamal	2.29	1.76	1.31	
Rodents	–2.62	1.18	–2.21	0.027
Nenetsky	–5.25	2.39	–2.20	0.028
Nenetsky/Yamal	3.21	1.41	2.28	0.023

APPENDIX TABLE 8. Rough-legged Hawk and Peregrine Falcon nest association occurrence (calculated for 1,500 m cutoff distance) relative to the region and the rodent abundance. Intercept: Yamal is the intercept for the trend line for Yamal. Rodents is the slope for Yamal. Nenetsky is the difference between 2 intercepts (for Yamal and Nenetsky). Nenetsky/Yamal is the difference between 2 slopes: for Nenetsky and for Yamal. Effect sizes are on the log scale.

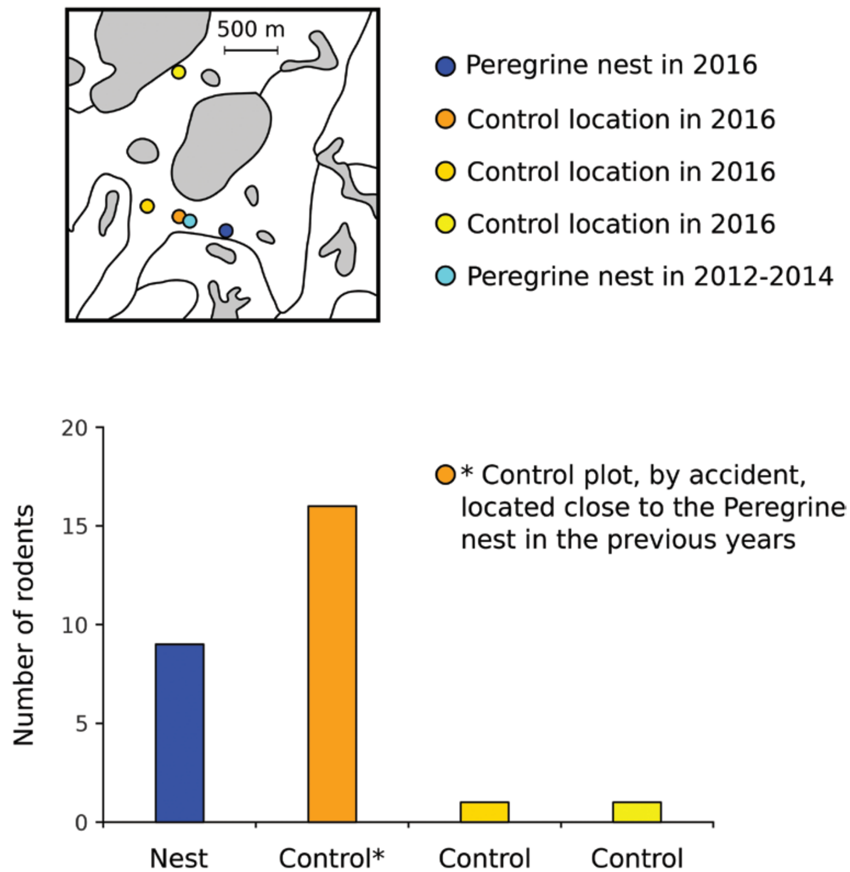
Explanatory variable and interactions	Estimate	SE	*z* value	*P* value
Intercept: Yamal	2.57	1.37	1.88	
Rodents	−1.69	0.77	−2.20	0.028
Nenetsky	−4.13	1.77	−2.33	0.020
Nenetsky/Yamal	2.09	0.95	2.19	0.029

APPENDIX TABLE 9. Breeding success of Rough-legged Hawks depending on association with Peregrine Falcons ("in" or "out"; 1,500 m cutoff distance). Explanatory variables: Intercept:out = breeding success in the nests out of association, Association.in = breeding success in the nests in association. Estimates are on the log scale. See also Figure 5.

Explanatory variable	Estimate	SE	*z* value	*P* value
Intercept:out	−0.176	0.196	−0.897	
Association.in	0.597	0.264	2.262	0.0237



APPENDIX FIGURE 7. Density of rodents around one of the Peregrine Falcon nests and associated control locations in Nenetsky, where during one year (2010) the control plot, by accident, was located close to the nest of Peregrine Falcons in the previous years.



APPENDIX FIGURE 8. Density of rodents around one of the Peregrine Falcon nests and associated control locations in Yamal where one of the control plots, by accident, was located close to the nest of Peregrine Falcons in the previous years.