

Nest association between two predators as a behavioural 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 birds species with non-overlapping foraging niches. In the Arctic, Rough-legged Hawks and Peregrine Falcons are two raptor species with non-overlapping food resources that have been reported to nest sometimes in close vicinity. Since nesting Peregrines 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 two regions in the low arctic Russia we found that: 1) the nesting territories of Peregrines were indeed enriched with small rodents as compared to control areas; 2) the probability of nest association between the two 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 Peregrines. 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, the rodent cycles, may explain the occurrence and adaptive significance of a specific behaviour pattern, the nesting association between two raptor species.

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

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 trade-off 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 1800 meters 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 peregrinu*) 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 Peregrines mostly feed on birds (Bradley and Oliphant 1991, Ellis et al. 2004). Thus, there is practically no trophic niche overlap between the two species.

We suggest that Rough-legged Hawks and Peregrines are nesting together because one or both parties benefit from such an association and not because they use a common patchy distributed resource. An alternative reason could be that they both prefer the same nesting habitat. Indeed, both species like to nest on cliffs, but whereas this is the only nesting habitat of Peregrines, 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 Peregrines because of a lack of other nesting sites. Peregrines are known to behave aggressively towards hawks nesting close to their nest; therefore, Rough-legged Hawks risk predation on themselves or their offspring when nesting near the Peregrines (Kalyakin 1989). Rough-legged Hawks have been reported to avoid breeding close to Snowy Owls (*Bubo scandiacus*), a behaviour 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 Peregrines if the benefit of such a behaviour outweighs the predation risk.

We assume that nesting associations between Rough-legged Hawks and Peregrines result from a choice of the hawks. Peregrines 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 and hawk nests occurred mostly in years with a low density of small rodents (Kalyakin 1989, Sokolov 2002).

We propose two non-exclusive hypotheses to explain the suggested link between the Rough-legged Hawks' choice of a breeding site close to Peregrines and small rodent density. First, during 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 Peregrines may benefit from their protection. Peregrines have a high level of aggressiveness indeed and are very efficient in protecting their nesting territories. This explains why arctic geese species, especially Red-breasted Geese (*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 Peregrines extends to the hawk’s preferred prey, small rodents. Thus, Peregrines could create a patch around their nest with zero or very low impact of predators. The density of small rodents inside exclosures which 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 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’.

In the present paper, we study the circumstances of breeding associations of Rough-legged Hawks and Peregrines in two low arctic regions of Russia (Figure 1) and assess which of the two hypotheses outlined above may explain this phenomenon. Rough-legged Hawks have been shown to behave differently in the two 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 two study areas and our two 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 nests than in a similar habitat without Peregrines. Second, we predict (Prediction 2) that if the ‘foraging hypothesis’ is true then a relationship between the probability of hawk-Peregrine 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 nests. If, on the contrary, the ‘defense hypothesis’ is true, then nesting association between Rough-legged Hawks and Peregrines would be more likely in years of the 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 Peregrines independent of the study region.

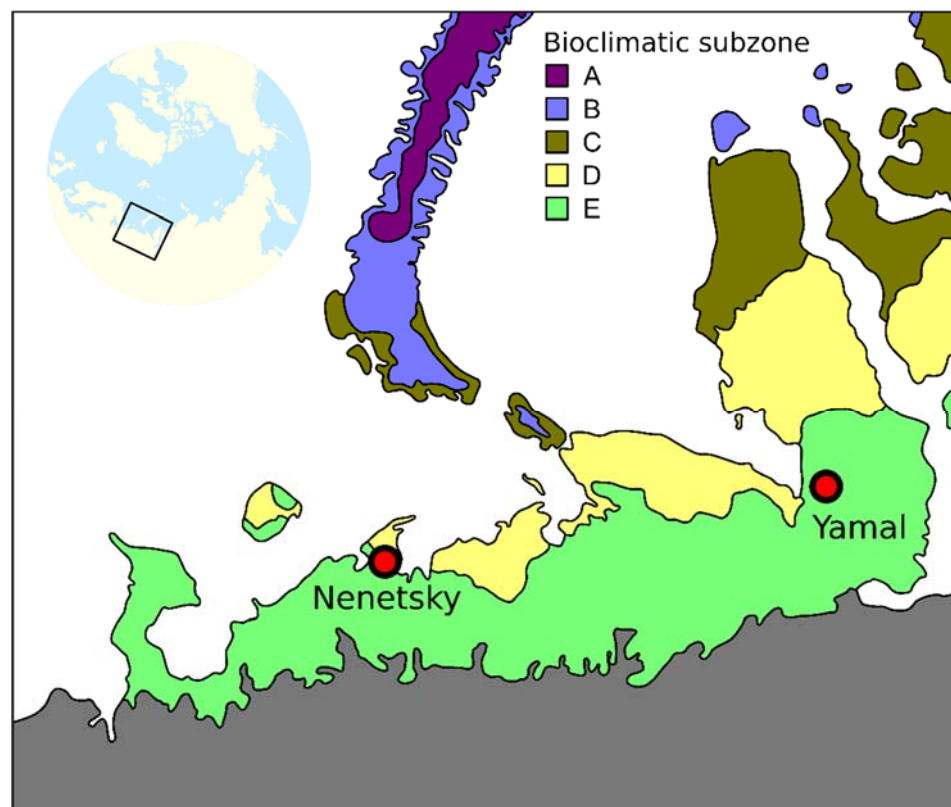


Figure 1. The map of the study regions locations. See Table 1 for characteristics of each region. Bioclimatic subzones: A – High Arctic tundra, B – Arctic tundra: northern variant, C – Arctic tundra: southern variant, D – Northern hypo-Arctic tundra, E – Southern hypo-Arctic tundra (Walker et al. 2005).

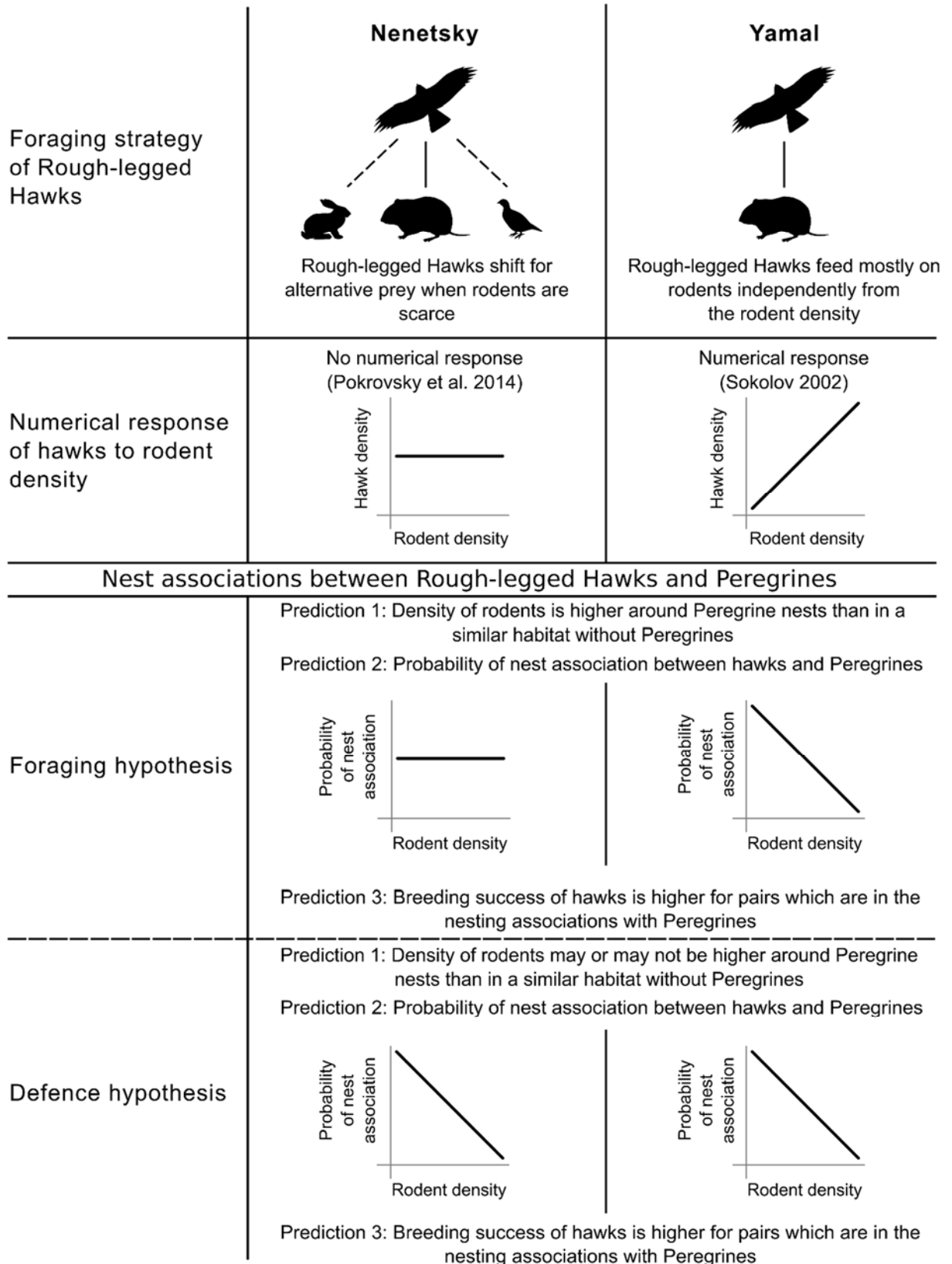


Figure 2. The difference in foraging strategy of Rough-legged Hawks in two regions leading to the difference in the numerical response of hawk density to rodents density and thus to the difference in nest association behaviour.

MATERIAL AND METHODS

Study regions and study species

Our research was carried out in two 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 thickets (ca. 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.

Peregrines 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 nests of harriers were found in Yamal and in Nenetsky. Mammalian predators that could prey on raptors nests – such as foxes (*V. lagopus* and *V. vulpes*), stoats (*Mustela erminea*) and wolverine (*Gulo gulo*) – were regularly present in both regions (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 ca. 150 km² each year, to search for Rough-legged Hawk and Peregrine nests and to register the nest association events. We observed an area, targeting river

and lake banks during walking excursions and using 8-10 X binoculars. We used observations of the alarming behaviour 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 hawks and Peregrines nests. For each Rough-legged Hawk nest, we determined the distance to the nearest Peregrine nest. In total, we found 77 Rough-legged Hawk nests and 84 Peregrine nests (Table 1). The distance between hawk and nearest Peregrines 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 thus possible that we did not find the nearest Peregrine nests.

Table 1. Abundance of Rough-legged Hawks, Peregrines and rodents in Nenetsky and Yamal.

Area	Years	Number of nests		Distance between hawk and nearest Peregrines nests (m)		Abundance of small rodents (animals per 100 traps/night)	Breeding success of Rough-legged Hawks (fledglings)	
		hawks	Peregrines	min – max	mean ± 95% CI		min – max	mean ± 95% CI
Nenetsky	2007-2011	36	21	501 – 5507	2181 ± 412	1.97 – 14.93	0 – 3	1.1 ± 0.3
Yamal	2008-2015	41 ^a	63	351 – 7962	2433 ± 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 (2012-2015)

We define Rough-legged Hawk nests as associated with Peregrines when the distance between them was less than 1 km. We chose this distance based on information about Peregrines' home range, estimated based on telemetry in the same study region in Yamal (Sokolov et al. 2014) and on information about Rough-legged Hawk home range estimated in the same study region in Nenetsky (Pokrovsky et al., unpublished data). Mean radius of the Peregrines home range was 5.6 km, however, in the early stages of breeding it was 1.7 km on average. Mean radius of Rough-

legged Hawk 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 cut off 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 Peregrines or not. Overall, 16 Rough-legged Hawk nests were located within 1 km of a Peregrine nest of which eight were in Nenetsky and eight in Yamal (for 750 m and 1.5 km see Appendix Table 1).

We estimated Rough-legged Hawk breeding success as the number of fledglings (young that reached 35 days of age – ca. 4 days before average fledging time) per territorial pair. In Nenetsky, we estimated breeding success during all five years and in Yamal – in 2007-2008, 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 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 for different habitat type see Appendix Table 2).

[Abundance of small rodents at the landscape level and near Peregrine nests](#)

In both regions, we estimated abundance indices for small rodents at the landscape level, near Peregrine nests and at the associated control locations. Small rodent abundance at the landscape level was evaluated using snap trapping on 36 permanent plots covering three widespread habitat types (meadows at the edge of willow thickets and two 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 quadrat method (Myllymäki et al. 1971). We placed three snap traps in each corner of 15x15 m plots for two 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/night per session in each region (36 plots X 12 traps X 2 nights), and on 1,296 traps/night (54 plots X 12 traps X 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/nights (all species pooled) in Nenetsky and between 1.04 and 10.07 in Yamal (Table 1).

Abundance indices for small rodents near Peregrine 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 approximately 500 meters from the nest at a control location (Appendix Figure 1). This distance corresponds approximately to the distance at which Peregrines 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 nesting sites. In each location, in the middle of August, we placed fifty snap traps on an area of ca. 700-900 m² at 3-5 m from each other for two 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 three control locations for each nest, which were chosen at approximately 500, 1000 and 1500 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 the small rodent abundance and distance from the Peregrine 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 (Peregrine 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 two variables to estimate the difference between two regions according to our prediction.

The predicted relationship between Rough-legged Hawk breeding success and location of the nest in a hawk – Peregrine 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, 1000, and 1500 meters), 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 parameters in our study. First we compared three models with each of the nest association variables (750, 1000, and 1500 meters). Then we used the nest association variable with most support (1500 meters) to extend the models to include an interaction with region, log small rodent abundance and habitat (Appendix

Table 3). The candidate models were compared using Akaike's Information Criterion corrected for small sample sizes (AICc) and a model was considered better than another when the difference in AICc was larger than 2.

All analyses were carried out using R 3.4.3 (R Development Core Team 2017). 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 AICc. Results are reported as means \pm 95% CI.

RESULTS

We conducted estimation of abundance indices for small rodents around the 18 Peregrine nests and at 28 associated control locations. Thirteen nests and 13 control locations were in Nenetsky (2009-2011) and five nests and 15 control locations – in Yamal (2016). In Nenetsky, the nests were found within five nesting sites, which were located in two different habitats: on sand cliffs along the shore of Korovinskaya Bay and in the river valleys in the inland tundra. In Yamal, four 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 associated control locations. In Nenetsky, 90% of all small rodents were tundra voles and in Yamal 98% of all small rodents were narrow-headed voles. In Nenetsky, in the seashore habitat over all three years, 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 in average 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 a Peregrine nests compared to control locations. (Appendix Table 4, Figure 3).

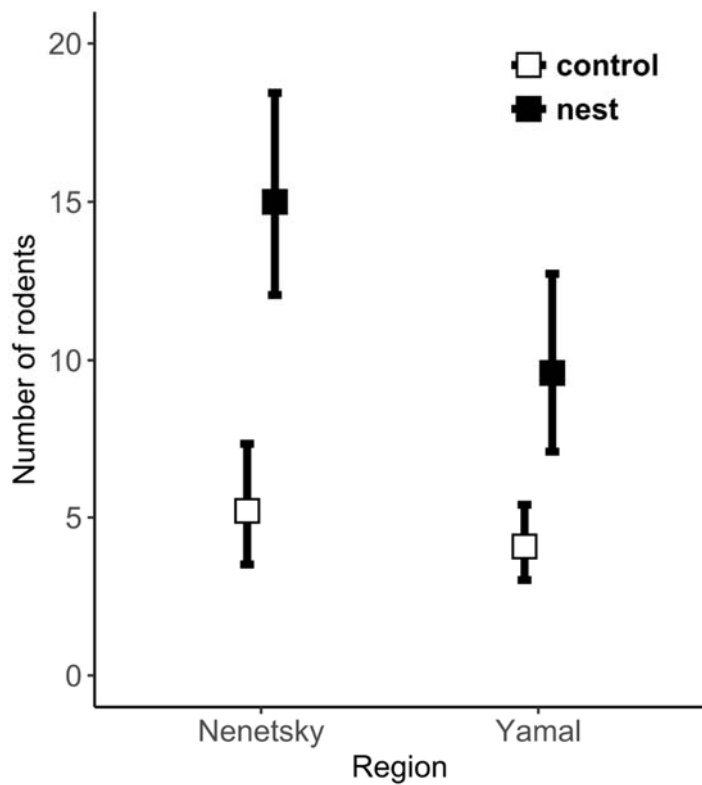


Figure 3. The number of small rodents caught per 100 trap nights in the immediate vicinity of Peregrine nests and at control locations (>500 m). Error bars – 95% CI (estimated based on a Poisson distribution). See Appendix Table 4 for model output.

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 two raptors revealed a significant interaction between rodent abundance and region (Table 2). Carrying out the same analysis with a cut off for nest association at distances of 750 m and 1500 m provided qualitatively similar results (Appendix Table 5 and 6).

Table 2. The relationship between the occurrence of the Rough-legged Hawks and Peregrines nest association and the rodent abundance. ‘Intercept: Yamal’ – the intercept for the reference level Yamal. ‘Rodents’ – the slope for Yamal, ‘Nenetsky’ – the difference between the two intercepts (for Yamal and Nenetsky). ‘Nenetsky/Yamal’ – difference between the two 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	Std. Error	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

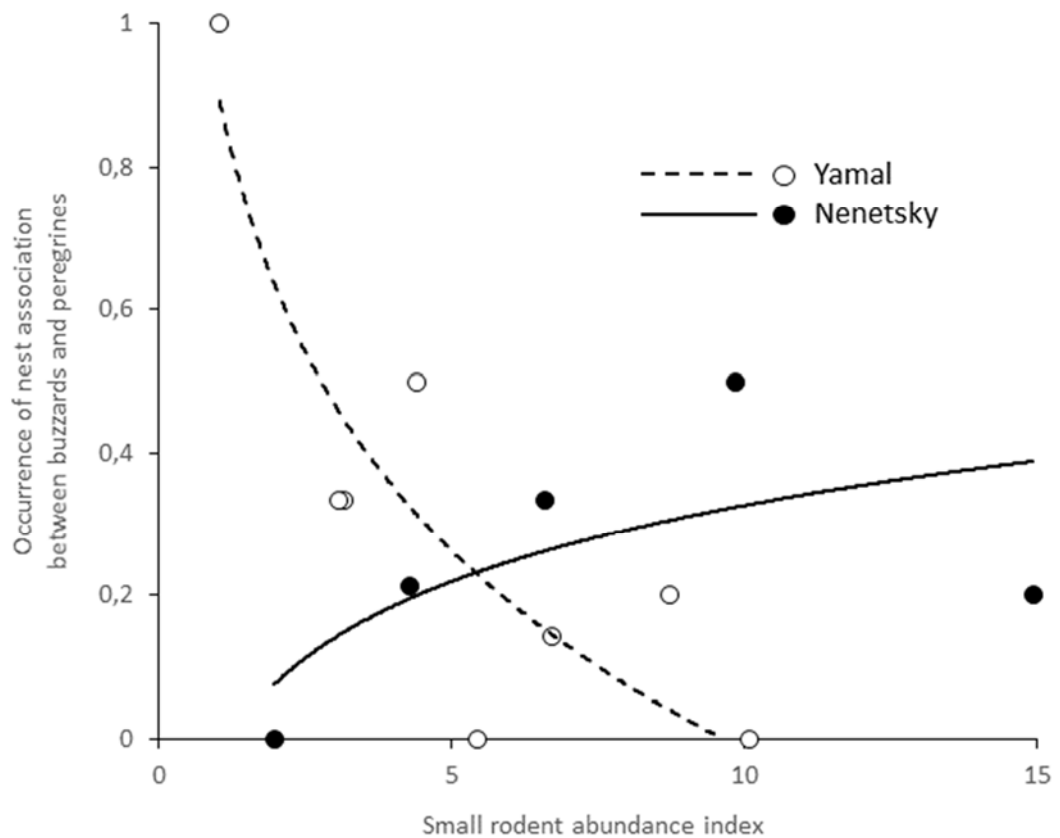


Figure 4. The relationship between Rough-legged Hawk and Peregrine nest association occurrence and the rodent abundance. See Table 2 for the model output and Appendix Tables 5 and 6 for the model output for the distances 750 and 1500 meters.

The number of Rough-legged Hawk fledglings varied between zero and three and there was little difference between areas in the mean number of fledglings per nest (Table 1). The general linear model, which received the most support from AICc, included only nest association (with a cut off distance of 1500 m) (Appendix Table 3). The two models with shorter cut off distances received lower support from AICc (difference in AICc 2.14 for 750 m and 4.07 for 1000 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, which were in association with Peregrines (Appendix Table 7, Figure 5), in accordance with prediction 3 (Figure 2). The interaction between nest association and region was not supported by our data.

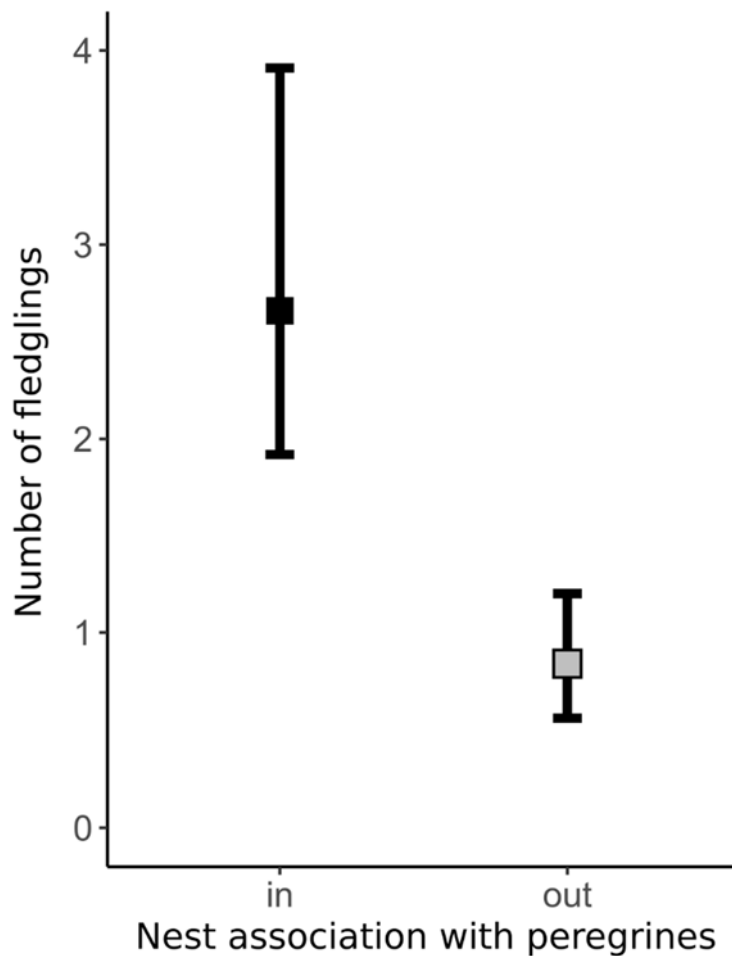


Figure 5. The relationship between the Rough-legged Hawk breeding success and location of the nest in or out of association with Peregrines. Error bars – 95% CI (estimated based on a Poisson distribution). See Appendix Table 7 for the model output.

DISCUSSION

Here we showed that the protective effect of Peregrine Falcons nest defense could extend to foraging resources of Rough-legged Hawks and that this could be an alternative cause of nest associations between these two species. We observed Rough-legged Hawks breeding well within Peregrines 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 nests than in similar habitats without a Peregrine nest (Figure 3). The occurrence of nest association between Rough-legged Hawks and Peregrines nests 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 ca. 0-10% of all cases of nestling mortality, while lack of food is one of the most frequent reasons of unsuccessful breeding and could be the cause of up to 90% of all nestling mortality cases (Kalyakin 1989, Potapov 1997, Pokrovsky et al. 2012). Low nest predation rate in Rough-legged Hawks also suggests that predation from Peregrines 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 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 Peregrines around their nesting site, suggesting rodents are the main factor. Alternatively, Peregrines 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 Peregrines breeding area, while Peregrines 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 Peregrines might be enhanced rodents density around the nests of Peregrines and not the Peregrines by 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 Peregrines, or whether it is forming each year starting at the moment when Peregrines arrive at their territory during spring migration. We have no firm evidence of long-term (over winter) persistence of high rodent densities near Peregrine nests. However, we could suggest this persistence due to the details of our results of the trapping sessions around the Peregrine nests and control locations. The density of small rodents was indeed higher close to the nests of Peregrines than at 500 m from the nest in all cases except two (Appendix Figures 2 and 3). These two cases (one in Yamal and one in Nenetsky)

occurred on nests, which had changed their locations relative to the previous year. By chance, control plots in these two cases were placed close to the location where the nest was situated in the previous year. These observations could mean that Peregrines 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 behaviour of Peregrines (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 Peregrines themselves when they establish a nest in the association. In Yamal and in Nenetsky during all the years we observed seven nest associations with a very close distance between the nests (from 357 to 567 meters). Such an association could be formed only if Rough-legged Hawks established first on the nesting site. Peregrines 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 Peregrines, 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 result suggest three conditions for Rough-legged Hawks to form nest association: 1) hawks should come earlier than Peregrines 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 Peregrines.

Peregrines can facilitate a local high density of rodents around their nests only if they nest in suitable habitat. Nests of Peregrines in Nenetsky were situated on sandy cliffs in two 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 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 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 the Kolguev Island. The postulated underlying mechanisms for the nest association formation implies that appearance of the Peregrine in the 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 Peregrines. The difference between nests in and out of nest association was ca. 0.5 fledgling and the variation in these groups was very high. We could not conclude that nesting in association with Peregrines could give Rough-legged Hawks an important gain in reproductive output. At the same time, that allows them to nest in the years with a low rodent density. In the systems with higher rodent cycles amplitude, formation of high density around the Peregrine nests could be even more pronounced. As well as local patches of the high density of rodents 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 as well. 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 in particular, raptors, can adapt to the unstable tundra environment and compensate for resource depletion.

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APPENDIX (Tables and Figures)

Appendix Table 1. The number of the buzzards' nests associated with peregrines nest for different cut off distances.

Distance (m)	Nenetsky	Yamal	Total
750	5	6	11
1000	8	8	16
1500	11	17	28

Appendix Table 2. The number of the buzzards' nests associated with peregrines nest 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 1000 m			
in nest association	8	5	13
out of nest association	14	25	39
for 1500 m			
in nest association	11	10	21
out of nest association	11	20	31

Appendix Table 3. Results of the AICc for six 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, 1000, and 1500 meters – “Association750”, “Association1000”, and “Association1500”), region (Nenetsky or Yamal – “Region”), the average small rodent trapping index for the whole summer (log transformed – “Rodents”), and the habitat where the buzzards nest was located (in the river valley or in the open tundra – “Location”). * – interaction between variables.

Model	K	AICc	Δ AICc	Wt	Σ Wt	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 4. 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 nest/control) and region (Nenetsky or Yamal) are fixed effects. Effect sizes are on the log scale.

Explanatory variable and interactions	Estimate	Std. Error	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 5. Buzzards and peregrines nest association occurrence (calculated for 750 m cut off distance) relative to the region and the rodent abundance. ‘Intercept: Yamal’ – the intercept for the trend line for Yamal. ‘Rodents’ – the slope for Yamal, ‘Nenetsky’ – the difference between two intercepts (for Yamal and Nenetsky). ‘Nenetsky/Yamal’ – difference between two slopes: for Nenetsky and for Yamal. Effect sizes are on the log scale.

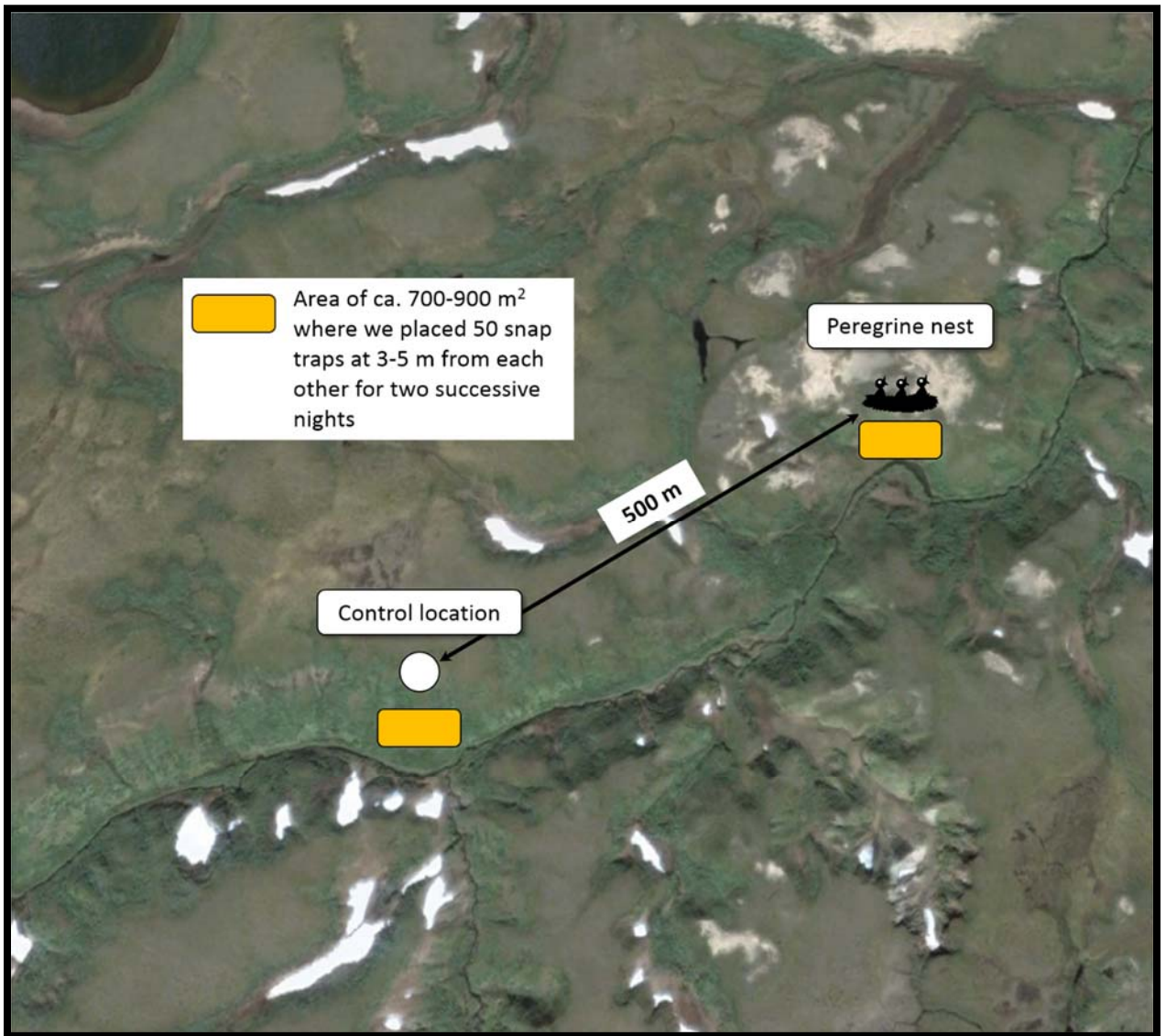
Explanatory variable and interactions	Estimate	Std. Error	z value	p-value
Intercept: Yamal	2.29	1.76	1.31	
Rodents	-2.62	1.18	-2.21	0.027
Nenetsky	-5.25	2.39	-2.20	0.028
Nenetsky/Yamal	3.21	1.41	2.28	0.023

Appendix Table 6. Buzzards and peregrines nest association occurrence (calculated for 1500 m cut off distance) relative to the region and the rodent abundance. ‘Intercept: Yamal’ – the intercept for the trend line for Yamal. ‘Rodents’ – the slope for Yamal, ‘Nenetsky’ – the difference between two intercepts (for Yamal and Nenetsky). ‘Nenetsky/Yamal’ – difference between two slopes: for Nenetsky and for Yamal. Effect sizes are on the log scale.

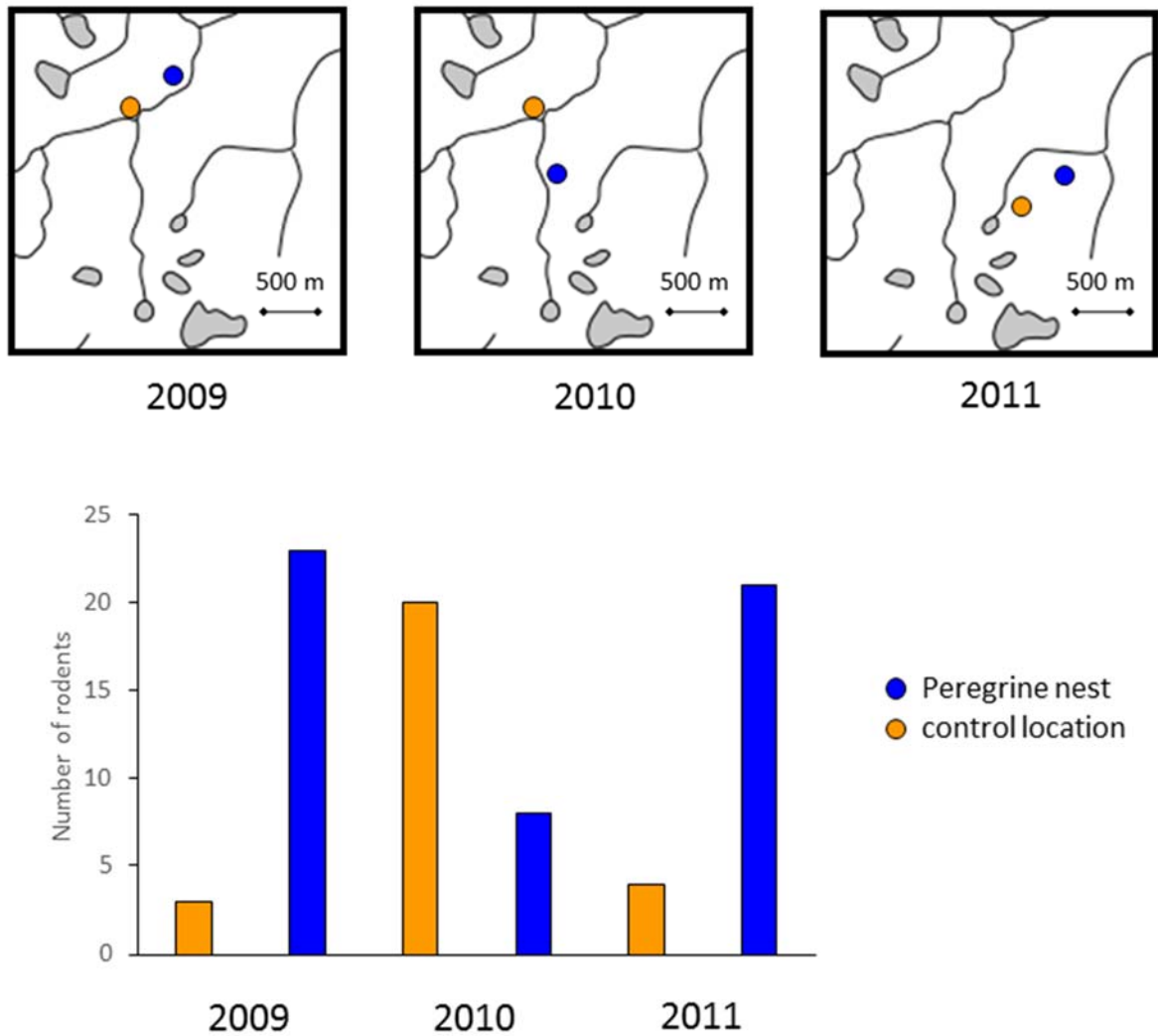
Explanatory variable and interactions	Estimate	Std. Error	z value	p-value
Intercept: Yamal	2.57	1.37	1.88	
Rodents	-1.69	0.77	-2.20	0.028
Nenetsky	-4.13	1.77	-2.33	0.020
Nenetsky/Yamal	2.09	0.95	2.19	0.029

Appendix Table 7. Breeding success of buzzards depending on association with peregrines (“in” or “out”; 1500 m cut off distance). Explanatory variables: ‘Intercept:out’ – breeding success in the nests out of associations, ‘Assocaiation.in’ – breeding success in the nests in associations. Estimates are on the log scale. See also Figure 5.

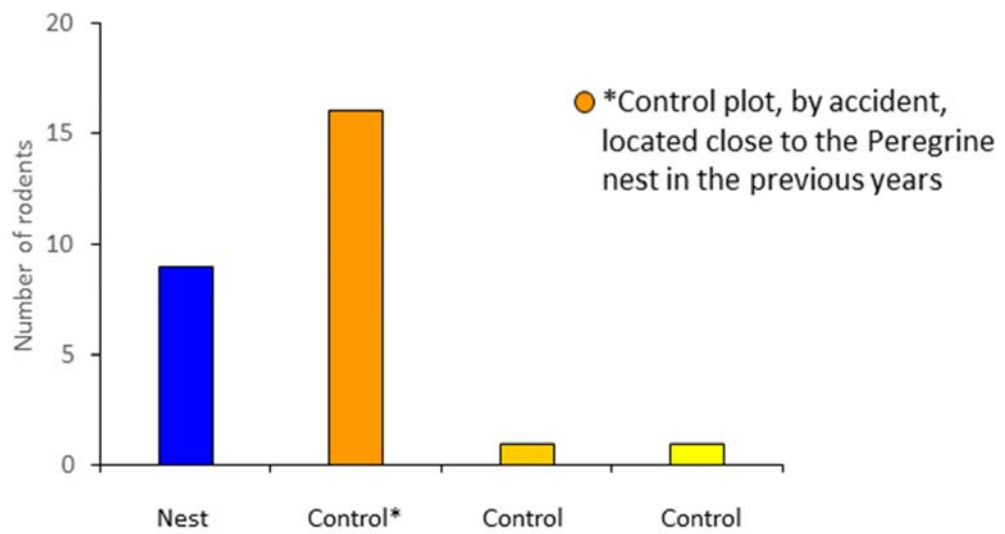
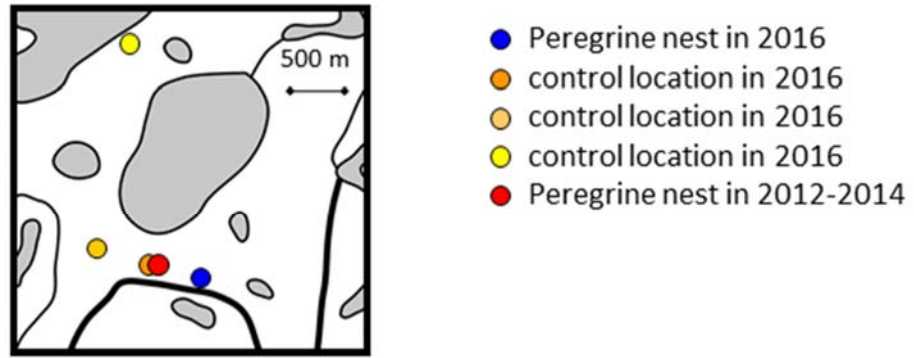
Explanatory variable	Estimate	Std. Error	z value	p-value
Intercept:out	-0.176	0.196	-0.897	
Assocaiation.in	0.597	0.264	2.262	0.0237



Appendix Figure 1. Example of Peregrine nest and associated control location and area where we placed 50 snap traps at 3-5 m from each other for two successive nights.



Appendix Figure 2. The density of rodents around one of the Peregrine nests and associated control locations in Nenetsky, where during one of the year (2010) the control plot, by accident, was located close to the nest of Peregrines in the previous years.



Appendix Figure 3. The density of rodents around one of the Peregrine nests and associated control locations in Yamal where one of the control plots, by accident, was located close to the nest of Peregrines in the previous years.