Giroux M, Trottier-Paquet M, Bêty J, Lamarre V, Lecomte N. 2016. Is it safe to nest near conspicuous neighbours? Spatial patterns in predation risk associated with the density of American Golden-Plover nests. PeerJ 4:e2193 https://doi.org/10.7717/peerj.2193

Is it safe to nest near bold neighbours? Spatial patterns in predation risk associated with the density of American Golden-Plover nest

Marie-Andrée Giroux, Myriam Trottier-Paquet, Joël Bêty, Vincent Lamarre, Nicolas Lecomte

Predation is one of the main factors explaining nesting mortality in most bird species. Birds can avoid nest predation or reduce predation pressure by breeding at higher latitude, showing anti-predator behaviour, and nesting in association with protective species. Plovers actively defend their territory by displaying early warning and aggressive/mobbing behaviour, potentially benefiting the neighbouring nests by decreasing their predation risk. To test for the existence of such a protective effect, we studied the influence of proximity to plover nests on predation risk of artificial nests on Igloolik Island (Nunavut, Canada) in July 2014. We predicted that the predation risk of artificial nests increases and decreases with the distance to and the density of plover nests, respectively. We monitored 18 plover nests and set 35 artificial nests at 30, 50, 100, 200 and 500 m from seven of those plover nests. Surprisingly, we showed that predation risk of artificial nests increases with the density of active plover nests. We also found a significant negative effect of the distance to the nearest active protector nest on predation risk of artificial nests. Understanding how the composition and structure of shorebird communities generate spatial patterns in predation risks represent a key step to better understand the importance of these species of conservation concern in tundra food webs.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1929v1 | CC-BY 4.0 Open Access | rec: 5 Apr 2016, publ: 5 Apr 2016

Marie-Andrée Giroux
Université du Québec à Rimouski
Département de biologie
300, Allée des Ursulines
Rimouski, QC
Canada G5L 3A1

Is it safe to nest near bold neighbours? Spatial patterns in predation risk associated with the density of American Golden-Plover nests

Marie-Andrée Giroux[1,2,3,4,5], Myriam Trottier-Paquet[1,3,4], Joël Bêty[2,3], Vincent Lamarre[1,3] and Nicolas Lecomte[1,3,4]

[1] *Canada Research Chair in Polar and Boreal Ecology, Université de Moncton, Moncton, NB, Canada*

[2] *Canada Research Chair on Northern Biodiversity, Université du Québec à Rimouski, Rimouski, QC, Canada*

[3] *Centre d'Études Nordiques & Département de Biologie, Université du Québec à Rimouski, Rimouski, QC, Canada*

[4] *Quebec Center for Biodiversity Science, Université du Québec à Rimouski, Rimouski, QC, Canada*

Abstract

Predation is one of the main factors explaining nesting mortality in most bird species. Birds can avoid nest predation or reduce predation pressure by breeding at higher latitude, showing anti-predator behaviour, and nesting in association with protective species. Plovers actively defend their territory by displaying early warning and aggressive/mobbing behaviour, potentially benefiting the neighbouring nests by decreasing their predation risk. To test for the existence of such a protective effect, we studied the influence of proximity to plover nests on predation risk of artificial nests on Igloolik Island (Nunavut, Canada) in July 2014. We predicted that the predation risk of artificial nests increases and decreases with the distance to and the density of plover nests, respectively. We monitored 18 plover nests and set 35 artificial nests at 30, 50, 100, 200 and 500 m from seven of those plover nests. Surprisingly, we showed that predation risk of artificial nests increases with the density of active plover nests. We also found a significant negative effect of the distance to the nearest active protector nest on predation risk of artificial nests. Understanding how the composition and structure of shorebird communities generate spatial patterns in predation risks represent a key step to better understand the importance of these species of conservation concern in tundra food webs.

Keywords: Arctic, community, nest protection, predation, shorebirds, territory

Predation is one of the main factors explaining nesting mortality in most bird species (Ricklefs 1969), and hence represents a selective force that induced the development of strategies for minimizing nest predation (Smith et al. 2007b). Birds can avoid nest predation or reduce predation pressure by breeding at higher latitude (McKinnon et al. 2010a), showing anti-predator behaviour (e.g. Simmons 1952), and nesting in association with protective species (Haemig 2001, Quinn and Ueta 2008). For instance, several studies showed that predation risk increases with the distance to the nest of aggressive or territorial species such as Snowy Owl (*Bubo scandiacus*; Bêty et al. 2001), Goshawk (*Accipiter gentilis*; Mönkkönen et al. 2007), Hooded Crow (*Corvus corone cornix*; Roos 2002), and Northern Lapwing (*Vanellus vanellus*; Elliot 1985).

Shorebirds, particularly the biggest species with colorful plumage and both parents contributing to parental care, are known to display various behaviours to protect their nests (e.g. Drury 1961, Sordahl 1981, McCaffery 1982, Larsen et al. 1996). The American Golden-Plover (*Pluvialis dominica*, hereafter "plover") is an example of a shorebird species using an early warning system and a distractive or mobbing antipredator behaviour to protect its nest (Byrkjedal and Thompson 1998). Such behaviours could decrease predation risks for other species nesting nearby, as shown in another arctic-nesting plover species actively defending its nest, the grey plover (*Pluvialis squatarola*; Larsen and Grundetjern 1997). Nests of arctic-breeding birds are mainly predated by arctic foxes (*Vulpes lagopus*) and avian predators such as Common Raven (*Corvus corax*), Glaucous Gull (*Larus hyperboreus*), and Long-Tailed Jaeger (*Stercorarius longicaudus*) (e.g. Bêty et al. 2002, Lecomte et al. 2008). Because many arctic-nesting shorebirds species are currently experiencing dramatic declines across their range (Morrison et al. 2001, Gratto-Trevor et al. 2011), studying the influence of these species on spatial structures in nest predation risks may contribute to better understanding their importance in tundra food webs.

The main purpose of the study is to test the hypothesis that the American Golden-Plover can generate spatial structure in predation risks within tundra ecosystems. We predict that nest predation risks decrease with 1) the proximity to a plover nest and 2) the density of plover nests. To test the existence of such a protective effect, we conducted an experimental study with artificial nests in a High-Arctic breeding site.

Methods

Study area and species

We conducted the study on Igloolik Island, Nunavut, Canada (69.39° N, 81.55° W; 103 km^2) in July 2014 (Fig. 1). There, the tundra landscape is mainly composed of raised beaches with little vegetation, *dryas*-lichen slopes, and grass-sedge wet and dry meadows (Forbes et al. 1992). The average annual temperature for the period of 1981-2010 was -12.9°C with the warmest month (July) averaging 7.6°C (Environment Canada 2015). These temperatures and vegetation features correspond to a High-Arctic climate.

Igloolik Island is a known breeding site for up to 33 bird species, including shorebirds, waterfowls, and seabirds (Lecomte and Giroux 2015). Shorebird nest density on the Island was 53.5 $nest.km^{-2}$ for our study (Lecomte and Giroux, unpubl. data). The proximity to the cliffs of Coxe Islands (ca 15 km away) and to a polynya (ca 1.5 km away) allow numerous cliff breeders as well as offshore and pelagic species to use our study area as a foraging and resting site. The following nest predators are found on the Island: arctic foxes, ermines (*Mustela erminea*), Parasitic (*Stercorarius parasiticus*) and Long-Tailed Jaegers, Glaucous Gulls, and Common Ravens (Ellis and Evans 1960, Forbes et al. 1992, Lecomte and Giroux, unpubl. data).

Experimental design

To evaluate the protection effect of American Golden-Plovers on their neighbouring nests, 35 artificial nests were disposed at different distances from seven plover nests. We used the protocols used in previous studies to determine the ranges of distance from plover nests (Larsen and Grundetjern 1997, Bêty et al. 2001) and the frequency of visits (Bêty et al. 2001, Nguyen et al. 2006, Lecomte 2007). The artificial nests were placed 30, 50, 100, 200, and 500 m from potential protectors nests (Fig. 1). They were marked in the same way as the natural nests with two wooden sticks and a blue flag at 1, 5, and 10 m north from the nest. Artificial nests were deployed with rubber gloves between 12:00 and 18:00 on 7 and 8 July and checked after 1, 2, 4, 6, 8, and 12 days of exposure. The nests were considered depredated when their egg was missing or broken.

In addition to the linear distance (in m) to the associated plover nest, we recorded the following variables: linear distance to the closest active plover nest (in m), density of active plover nests within a radius of 270 m around the artificial nest (Fig. 1), habitat type (wetland or mesic tundra), and vertical nest concealment. The distance to the closest active nest became different from the linear distance to the associated plover nest when the latter was depredated or when another plover nest was located closer to the associated plover nest due to the random allocation. Nest density, nesting success, the type of nesting habitat (wetland or mesic tundra) were evaluated following the Arctic Shorebird Demographic Network protocol (Brown et al. 2014) within an extensive survey zone of 11.7 km^2. Vertical nest concealment corresponded to the percent of the nest obscured when viewed through an ocular tube (PVC pipe, 4 cm diameter x 11 cm length) from 1m directly above the nest.

Lemming trapping

We performed live lemming trapping between June 30th and July 2nd 2014 by setting up 50 Sherman traps at every second intersection (20-m spacing between intersections) of a 200-m x 200-m grid. After the initial set-up, we visited the traps every 4-6 hours during 56 hours (total of 12 visits).

Statistical Analysis

We modeled the variations in predation risk on artificial nests (response variable) using mixed-effect Cox proportional hazard regression models (library coxme; Therneau 2012) including the following predictor variables: distance to the associated plover nest (linear and quadratic terms), distance to the closest active plover nest (linear and quadratic terms), density of active plover nests within a radius of 270 m around the artificial nest, habitat type, and vertical concealment. We included the artificial and natural nest identity as random terms. Mixed-effect Cox proportional hazard regression models estimates the relationship between Kaplan-Meier survival estimates and the response variables. The exponent of the parameter estimate for each response variable provides the estimate of the hazard ratio, which corresponds to the hazard risk (or predation risk in our study) relative to a baseline measure of risk.

We used a model selection approach (Burnham and Anderson 2002) to identify the combination of these variables that best described variations in the predation risk of artificial nests. We compared 24 biologically plausible, candidate models, including up to four of the predictors described above in a single model (see Supplemental Table S1 for the full list of models). We did not include predictors displaying multicollinearity (r > 0.70) in the same model (Dormann et al., 2013). We identify the combination of predictors that best described variations in predation risk using the corrected Akaike Information Criterion (AICc) for small sample size (Burnham and Anderson 2002) estimated from the library AICcmodavg (Mazerolle 2015). Models with ΔAICc < 2 from the top model were considered competitive (Burnham and Anderson 2002). Finally, we used the survfit function (library survival, Therneau 2015) to create survival probability curves using the Kaplan-Meier survival estimates of Cox models.

We tested the assumption of the Cox models that the hazard function does not change over time for each covariate by regressing the Schoenfield residuals across time (Hess, 1995). A significant non-zero slope indicates a violation of the assumption. We confirmed that the assumption was respected for each predictor variable through visual inspection of the regression of the Schoenfield residuals against time confirmed, and also for each model (cox.zph function, library survival; Therneau 2015). We performed all statistical analyses in R 3.2.3 (R Development Core Team 2015).

The experiment and field protocols were approved by the Université de Moncton Animal Care Committee (permit # 14-05), by the Department of Environment – Government of Nunavut (permit # WL-2014-039), and by the Canadian Wildlife Service (permits #NUN-SCI-14-04).

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1929v1 | CC-BY 4.0 Open Access | rec: 5 Apr 2016, publ: 5 Apr 2016

Results

A total of 18 American Golden-Plover nests were found in our extensive search area of 11.7 km^2 (1.5 plover nest.km^{-2}). We therefore used more than a third of all available nests (seven vs. 18 nests) to run the experiment. We did not trap any lemming in the live-trapping grid.

Predation risk and density of active plover nest

The model that best explained variation in predation risk on artificial nests included the density of active plover nests within a radius of 270 m around the artificial nest (Supplemental Table S1). The Cox proportional hazard mixed-effects regression model indicated that the predation risk increased by 1.4-fold (coefficient = 0.87, SE = 0.24, *P* = 0.0003, hazard ratio = 2.4; Fig. 2) and 2.4-fold (coefficient = 1.22, SE = 0.37, *P* = 0.001, hazard ratio = 3.4; Fig. 2), respectively, when we observed one and two active plover nests within the 270m-radius around the artificial nest. The second most parsimonious model (ΔAICc = 1.99) included the effect of habitat type in addition to the density of active plover nest (Supplemental Table S1). However, the effect of habitat type on predation risk was not significant (coefficient = 0.09, SE = 0.24, hazard ratio = 1.10, *P* = 0.7).

Predation risk and distance to the nearest active plover nest

To confirm the direction of the results obtained through the best fitting model shown above, we also report the results of the model including the distance to the nearest active plover nest, although this model had a ΔAICc>2 (ΔAICc = 2.36; Supplemental Table S1). This model showed that predation risk of artificial nests decreased by 20% for each additional 100 m further away from an active plover nest (coeff = -0.21, SE = 0.06, *P* = 0.0003, hazard ratio = 0.81).

Discussion

We showed that, during a year of low lemming abundance, predation risk on artificial nests increases with the density of active plover nests and decreases with the distance to the nearest active plover nest. Contrary to our predictions, these results do not support the existence of a protective effect of plover nests on nearby nests. As discussed below, various factors can explain those unexpected results, such as the disadvantages of nesting near bold neighbours, especially during years of low lemming abundance.

Spatial variations in predation risk

Several studies showed that predation risk increases with the distance to the nest of an aggressive or territorial species (Bêty et al. 2001, Mönkkönen et al. 2007, Roos 2002, Larsen and Grundetjern 1997, Elliot 1985). Yet, some studies have shown that there are some disadvantages to nesting around a bold species (Paulson and Erckmann 1985), especially during years of higher nest predation rates. For instance, nesting near an aggressive species like the Sabine's Gull (*Xema sabini*) increased nest survival of Red Phalaropes (*Phalaropus fulicarius*) but only in years when nest predation rates was generally low due to high lemming abundance; when lemming abundance decreased, nest predation rates generally increased, and nesting near Sabine's Gulls induced negative effects on phalarope nest survival (Smith et al. 2007b). These results suggests that conspicuous behaviour may attract shared predators in years when the abundance of the main prey is low.

Because plovers actively defend their territory by displaying early warning, mobbing and sometimes aggressive behaviour, we predicted that this behaviour could benefit the neighbouring nests by decreasing their predation risk. Yet, low lemming abundance on Igloolik Island during the summer 2014 could contribute explaining the increased predation risk observed in areas with higher density of plover nests or in the vicinity of plover nests. During a year of low abundance of the main prey, the presence of one or more plover nest may have rather attracted then repelled predators. Hence, further studies should compare the effect of plover nests on predation risk estimated through artificial nests between years of lemming abundance.

Predation risk on artificial nests increased with two predictor variables that indexed the presence of plovers, namely the density of plover nests and the proximity to an active plover nest. The model best explaining variations in predation risk included the density of plover nests only, but we also observed an effect of the proximity to an active plover nest in a concurrent model that was not retained in the model selection process. The effect of density matches the results of previous studies that showed an increase in predation rates of artificial nests with their densities (Göransson et al. 1975). Yet, the effect of distance is not congruent with a previous study showing either a decrease or no variation in predation risk with the distance from Grey Plover nests or from Pacific Golden Plover nests (Larsen and Grundetjern 1997). Although this study has been performed with natural rather than artificial nests, and that predation rates on natural nests cannot be inferred using artificial nests (McKinnon et al. 2010b), the Larsen and Grundetjern (1997) study still provide an interesting point of comparison to better interpret our results.

The difference in the behaviour of both species likely explained the difference in the effect of plover species observed by Larsen and Grundetjern (1997). Grey Plovers and Pacific Golden Plover attacked 50% and 10% of predators entering a 200m radius surrounding their nests,

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1929v1 | CC-BY 4.0 Open Access | rec: 5 Apr 2016, publ: 5 Apr 2016

respectively (Larsen and Grundetjern 1997). The behaviour of the Black-bellied Plover could also contribute explaining difference between the results of Larsen and Grundetjern 1997 and those shown here. Indeed, the American Golden-Plover begins to perform mobbing and distraction displays when the predator is within 69-100 m (Byrkjedal and Thompson 1998). In response to a flying predator, while the Grey Plover attacks avian predators, the American Golden-Plover crouches, leaves the nest and sometimes approaches the predators, but never attacks (Byrkjedal and Thompson 1998). In particular areas of the Arctic, the American Golden-Plover was reported displaying aggressive behaviour and attack avian predators, but very rarely and only where predators are small (Sordahl 1981, McCaffery 1982, Paulson and Erckmann 1985).

Consistent with the results of Smith et al. (2007a), we found no habitat effect in driving the survival of the artificial nests. Powell (2001) reported that habitat characteristics were not a good predictor for the nest survival of snowy plover. Some studies provide evidence of a spatial heterogeneity in predator activity (Schmidt et al. 2006). For instance, Lecomte et al. (2008) reported a higher predation risk in the mesic tundra compared to arctic wetlands because of their physical structure slowing down fox attacks. We could not find such an influence of the habitat in the current study.

Artificial nests have the advantage of providing a standardized measure of predation risks. Yet, predation rates on artificial nests differ from that of real nests and, therefore, they should not be used to infer predation pressure on natural nests (Moore and Robinson 2004; McKinnon et al. 2010b). In our study, we used artifical nests to provide a controlled measure of relative predation risk at various distances from plover nests, not to infer real nest success. Success of natural nests is not only determined by predation risk, but by a combination of factors such as nest defense behaviour (Kis et al. 2000), parental care (Smith et al. 2007a), incubation duration (Schamel and Tracy 1987), and frequency of incubation recesses (Martin et al. 2000). For instance, Nuechterlein (1981) reported that Western Grebes (Aechmophorus occidentalis) recognized alarm calls of Forster's Terns (Sterna forsteri) and could use this information to adjust their behaviour and potentially increase their reproductive success. Dunlins (Calidris alpina) and Short-billed Dowitchers (Limnodromus griseus) were reported associating with American Golden-Plovers while feeding and potentially benefit from early alarm calls (Thompson and Thompson 1985, Byrkjedal 1987). Artificial nests allowed us to control for such sources of heterogeneity to make meaningful ecological statements concerning the influence of plover nests on predation risk in arctic-nesting birds.

Physical differences between articificial and natural nests may also result in different predation rates and attraction of predators (Thompson and Burhans 2004, Burke et al. 2004). Such bias is reduced when setting up shorebird artificial nests in tundra ecosystems. Indeed, arctic-nesting shorebirds lay their eggs in small depressions excavated in the tundra, and their eggs remained uncovered by structural material. Mimicing a real nest simply required to place quail eggs upon a depression with a small marker hidden underneath.

Conclusion

In conclusion, the artificial nests experiment conducted on Igloolik Island do not support the existence of a protective effect of plover nests on nearby nests, and rather show that it might not be safe to nest near a bold neighbour during years of low abundance of the main prey. Our results bring new perspective on how the spatial distribution and composition of shorebird communities may influence their breeding success. Understanding how the composition and structure of shorebird communities generate spatial patterns in predation risks represent a key step to better understand the importance of these species of conservation concern (Morrison et al. 2001, Gratto-Trevor et al. 2011) in tundra food webs.

Acknowledgments

We thank M.-C. Frenette, Amanda Taqtaq, and Mike Qrunuk for their valuable assistance in the field as well as the Government of Nunavut for its logistical support. This study was supported by (alphabetical order): Canada Foundation for Innovation; Canada Research Chairs; Environment Canada; Government of Nunavut; Indian and Northern Affairs Canada; Igloolik Hunters and Trappers Organization; Natural Sciences and Engineering Research Council of Canada; Polar Continental Shelf Project (PCSP); Université de Moncton. The experiment and field protocols were approved by the Université de Moncton Animal Care Committee (permit # 14-05), by the Department of Environment – Government of Nunavut (permit # WL-2014-039), and by the Canadian Wildlife Service (permits #NUN-SCI-14-04).

Literature Cited

Bêty, J., G. Gauthier, E. Korpimäki, And J.-F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. Journal of Animal Ecology 71: 88-98.

Bêty, J., G. Gauthier, J.-F. Giroux, And E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93: 388–400.

Burke, D. M., Elliott, K. E. N., Moore, L., Dunford, W., E. Nol, J. Phillips, S. Holmes, and K. Freemark. 2004. Patterns of nest predation on artificial and natural nests in forests. Conservation Biology 18: 381-388.

Burnham, K. P., And D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York.

Brown, S. C., H. R. Gates, J. R. Liebezeit, P. A. Smith, B. L. Hill, And R. B. Lanctot. 2014. Arctic Shorebird Demographics Network Breeding Camp Protocol, Version 5. Unpublished paper by U.S. Fish and Wildlife Service and Manomet Center for Conservation Sciences.

Byrkjedal, I. 1987. Short-billed dowitchers associate closely with lesser golden plovers. Wilson Bulletin 99: 494–495.

Byrkjedal, I., And D. Thompson. 1998. Tundra Plovers: The Eurasian, Pacific, and American Golden Plovers and Grey Plover. T & AD Poyser, London.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36: 027-046.

Drury, W. H. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. The Auk 78: 176–219.

Elliot, R. D. 1985. The exclusion of avian predators from aggregations of nesting lapwings (*Vanellus vanellus*). Animal Behaviour 33: 308–314.

Ellis, D. V, And J. Evans. 1960. Comments on the distribution and migration of birds in Foxe Basin, Northwest Territories. The Canadian Field Naturalist 74: 59–70.

Environment Canada [online]. 2015. Canadian Climate Normals 1981-2010 Station Data. <http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=1756&autofwd=1> (25 March 2015).

Forbes, G., K. Robertson, C. Ogilvie, And L. Seddon. 1992. Breeding densities, biogeography, and nest depredation of birds on Igloolik Island, NWT. Arctic 45: 295–303.

Göransson, G., J. Karlsson, S. G. Nilsson, And S. Ulfstrand. 1975. Predation on Birds ’ Nests in Relation to Antipredator Aggression and Nest Density: An Experimental Study. Oikos 26: 117–120.

Gratto-Trevor, C. L., R. I. G. Morrison, B. Collins, J. Rausch, M. Drever, And V. H. Johnston. 2011. Trends in Canadian shorebirds. Canadian Biodiversity: Ecosystem Status and Trends 2010, Technical Thematic Report No. 13. Canadian Councils of Resource Ministers. Ottawa, ON.

Haemig, P. D. 2001. Symbiotic nesting of birds with formidable animals: a review with applications to biodiversity conservation. Biodiversity and Conservation 10: 527–540.

Hess, K. R. 1995. Graphical methods for assessing violations of the proportional hazards assumption in cox regression. Statistics in Medicine 14: 1707-1723.

Kis, J., Liker, A., Szekely, T. 2000. Nest defence by lapwings: observations on natural behaviour and an experiment. Ardea 88: 155-163.

Larsen, T., And S. Grundetjern. 1997. Optimal choice of neighbour: predator protection among tundra birds. Journal of Avian Biology 28: 303–308.

Larsen, T., T. A. Sordahl, And I. Byrkjedal. 1996. Factors related to aggressive nest protection behaviour: a comparative study of Holarctic waders. Biological Journal of the Linnean Society 58: 409–439.

Lecomte, N. 2007. Risque de prédation, hétérogénéité de l'habitat et fidélité au site de reproduction: le cas de la Grande Oie des neiges dans le Haut-Arctique. Ph.D. dissertation. Université Laval, Québec, PQ.

Lecomte, N., V. Careau, G. Gauthier, And J.-F. Giroux. 2008. Predator behaviour and predation risk in the heterogeneous Arctic environment. Journal of Animal Ecology 77: 439–447.

Lecomte, N., And M.-A. Giroux. 2015. New avian breeding records for Igloolik, Nunavut. Canadian Field Naturalist 129:194-196.

Martin, T. E., Scott, J., And C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society B 267:2287-2293.

Mazerolle, M. J. 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3. <http://CRAN.R-project.org/package=AICcmodavg> (19 January 2016).

McCaffrey, B. J. 1982. Geographic variation in predator-mobbing behaviour - a hypothesis. Wader Study Group Bulletin 35: 30-30.

McKinnon, L., P. A. Smith, E. Nol, J.-L. Martin, F. I. Doyle, K. F. Abraham, H. G. Gilchrist, R. I. G. Morrison and J. Bêty. 2010a. Suitability of artificial nests. Science 328: 46-47.

McKinnon, L., P. A. Smith, E. Nol, J. L. Martin, F. I. Doyle, K. F. Abraham, H. G. Gilchrist, R. I. G. Morrison and J. Bêty. 2010b. Lower Predation Risk for Migratory Birds at High Latitudes. Science 327: 326-327.

Mönkkönon, M., M. Husby, R. Tornberg, P. Helle, And R. L. Thomson. 2007. Predation as a landscape effect: The trading off by prey species between predation risks and protection benefits. Journal of Animal Ecology 76: 619–629.

Moore, R. P., And W. D. Robinson. 2004. Artificial bird nests, external validity, and bias in ecological field studies. Ecology 85: 1562-1567

Morrison, R. I. G., Aubry, Y., Butler, R.W., Beyersbergen, G.W., Downes, C., Donaldson, G.M., Gratto-Trevor, C.L., Hicklin, P.W., Johnston, V.H. and Ross, R.K. 2001. Declines in North American shorebird populations. Wader Study Group Bulletin 94: 34-38.

Nguyen, L. P., K. F. Abraham, And E. Nol. 2006. Influence of arctic terns on survival of artificial and natural Semipalmated Plover Nests. Waterbirds 29: 100–104.

Nuechterlein, G. L. 1981. "Information parasitism" in mixed colonies of western grebes and Forster terns. Animal Behaviour 29: 985–989.

Paulson, D. R., And W. J. Erckmann. 1985. Buff-breasted sandpipers nesting in association with black-bellied plovers. The Condor 87: 429–430.

Powell, A. N. 2001. Habitat Characteristics and Nest Success of Snowy Plovers Associated with California Least Tern Colonies. The Condor 103: 785-792.

Quinn, J. L., And M. Ueta. 2008. Protective nesting associations in birds. Ibis 150: 146–167.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (19 January 2016).

Ricklefs, R. E. 1969. An Analysis of Nesting Mortality in Birds. Smithsonian Contributions to Zoology 9: 1–48.

Roos, S. 2002. Functional response, seasonal decline and landscape differences in nest predation risk. Oecologia 133: 608–615.

Schamel D., And D.M. Tracy. 1987. Latitudinal trends in breeding red phalaropes. Journal of Field Ornithology 58:126–134

Schmidt, K. A., R. S. Ostfeld, And K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. Oecologia 148: 22–29.

Simmons, K. E. L. 1952. The Nature of the Predator-Reactions of Breeding Birds. Behaviour 4: 161–171.

Smith, P. A., H. G. Gilchrist and J. N. M. Smith, 2007a. Effects of Nest Habitat, Food, and Parental Behavior on Shorebird Nest Success. The Condor 109: 15-31.

Smith, P. A., H. G. Gilchrist, J. N. M. Smith, E. Nol and D. B. Lank. 2007b. Annual variation in the benefits of a nesting association between red phalaropes (*Phalaropus fulicarius*) and Sabine's gulls (*Xema sabini*). The Auk 124: 276-290.

Sordahl, T. A. 1981. Predator-mobbing behaviour in the shorebirds of North America. Wader Study Group Bulletin 31: 41–44.

Therneau, T. 2012. coxme: Mixed Effects Cox Models. R package version 2.2-5. <http://CRAN.R-project.org/package=coxme> (15 January 2016).

Therneau, T. 2015. A Package for Survival Analysis in S. R package version 2.38-3. <http://CRAN.R-project.org/package=survival> (15 January 2016).

Thompson, F. R, And D. E.. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. Conservation Biology 18: 373-380.

Thompson, D. B. A., And M. L. P. Thompson. 1985. Early warning and mixed species association: the Plover's Page revisited. Ibis 127: 559–562.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1929v1 | CC-BY 4.0 Open Access | rec: 5 Apr 2016, publ: 5 Apr 2016

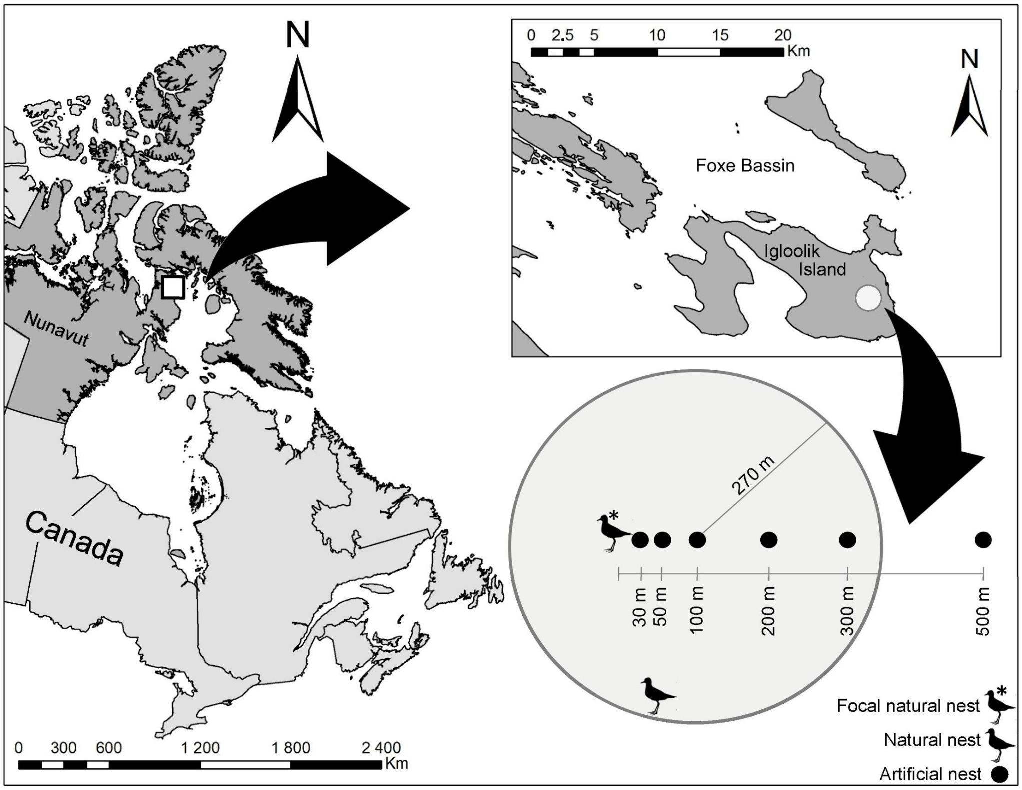
Figure Legends

Fig. 1. Location of the study area on Igloolik Island (Nunavut, Canada, 69.39° N; 81.55° W). Lower right side of the figure displays the experimental design of the experiment conducted in July 2014 with artificial nests placed 30, 50, 100, 200 and 500 m from a focal natural plover nest. Density of active plover nests within a radius of 270 m is shown for the artificial nest placed at 100 m from the focal natural plover nest (two active plover nests in this example).

Fig. 2. Kaplan-Meier survival probabilities over 12 exposure days for artificial nests with varying active plover nest density (zero, one or two active nest(s) with a radius of 270 m around the artificial nest) on Igloolik Island (Nunavut, Canada) during the summer of 2014. Each data point on the curve represents the Kaplan-Meier survival estimate at time t (± SE), which provides the probability that a nest will survive past time t.

396 **Figures**

397



398

399 **Fig. 1.**

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1929v1 | CC-BY 4.0 Open Access | rec: 5 Apr 2016, publ: 5 Apr 2016

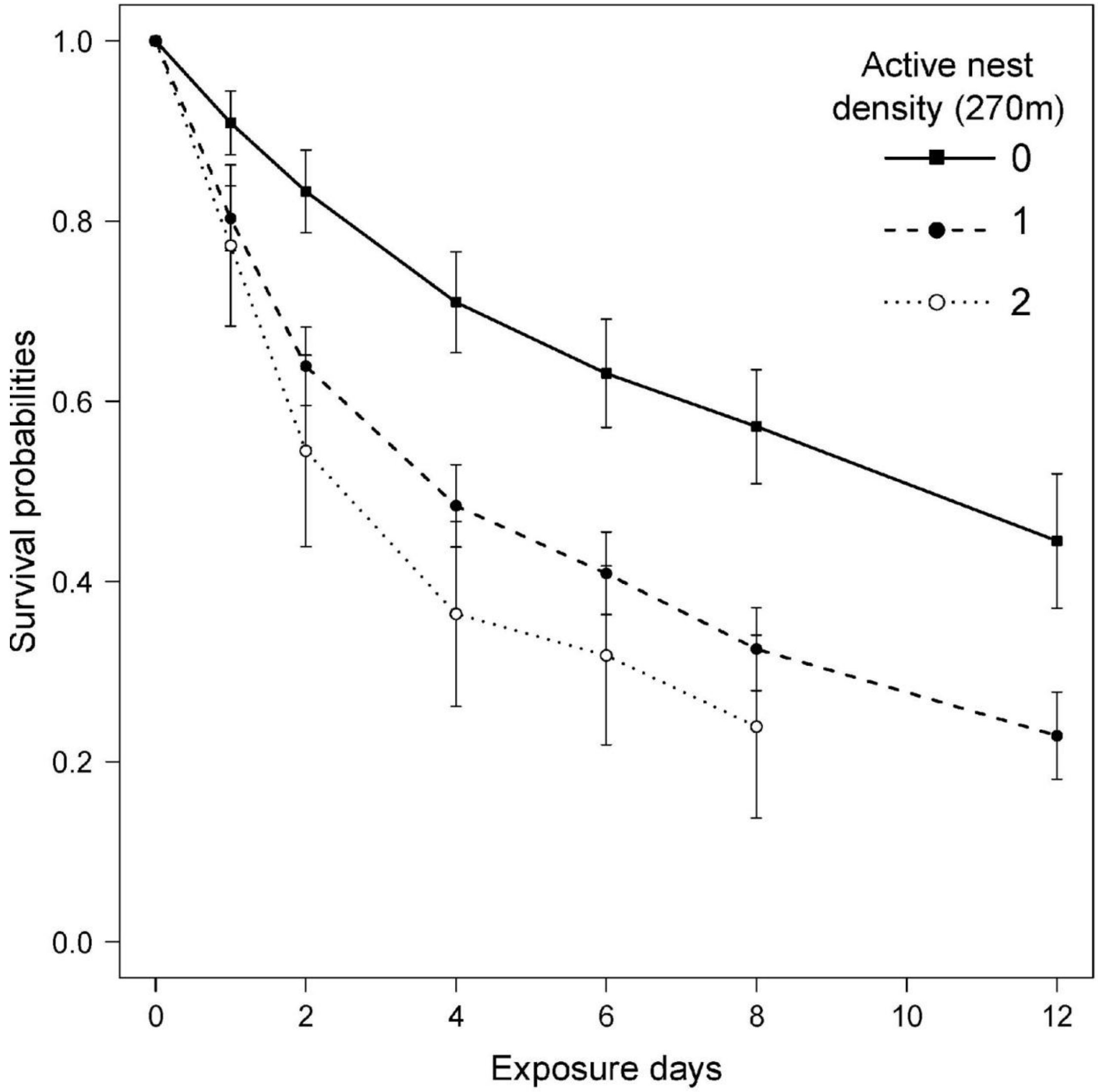

Active nest density (270m)
0
1
2
Survival probabilities
Exposure days
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12

Fig. 2.

Supplementary Table

Supplemental Table S1. Selection of models explaining variations in the risk of predation of artificial nests over 12 exposure days on Igloolik Island, (Nu, Canada) during the summer of 2014 (*n*=24). We compared models including up to four of the following predictors: distance in meter to the associated plover nest (Distance), distance in meter to the closest active plover nest (Active Distance), density of active golden plover nests within a radius of 270 m around the artificial nest (Active Density), habitat type, i.e. wetland or mesic tundra (Moisture) and vertical concealment (Concealment). We also tested for quadratic effects of Distance and Active Distance. We report Akaike's information criterion corrected for small sample size (AICc), difference in AICc relative to the model with the lowest AIC (ΔAICc), as well as the AICc weight (ωAICc). Models are ranked by their AICc values and the best-fitting models (ΔAICc < 2) are shown in bold.

Model	AICc	ΔAICc	ωAICc
Active Density	**1237.0**	**0.00**	**0.36**
Active Density + Moisture	**1239.0**	**1.99**	**0.13**
Active Density + Concealment	1239.0	2.04	0.13
Active Distance	1239.3	2.36	0.11
Active Distance + Active Distance^2	1240.3	3.38	0.07

Active Density + Concealment + Moisture	1241.1	4.10	0.05
Active Distance + Concealment	1241.2	4.27	0.04
Active Distance + Moisture	1241.4	4.42	0.04
Active Distance + Active Distance^2 + Concealment	1242.4	5.40	0.02
Active Distance + Active Distance^2 + Moisture	1242.4	5.47	0.02
Active Distance + Concealment + Moisture	1243.3	6.37	0.01
Active Distance + Active Distance^2 + Concealment + Moisture	1244.5	7.52	0.01
Distance + Moisture	1246.3	9.38	0.00
Distance	1247.8	10.84	0.00
Null	1248.1	11.17	0.00
Distance + Distance^2 + Moisture	1248.2	11.25	0.00
Distance + Concealment + Moisture	1248.4	11.46	0.00
Moisture	1248.5	11.49	0.00
Distance + Concealment	1249.2	12.20	0.00
Concealment	1249.7	12.76	0.00
Distance + Distance^2	1249.8	12.85	0.00

Distance + Distance^2 + Concealment + Moisture	1250.3	13.34	0.00
Concealment + Moisture	1250.5	13.57	0.00
Distance + Distance^2 + Concealment	1251.2	13.57	0.00

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1929v1 | CC-BY 4.0 Open Access | rec: 5 Apr 2016, publ: 5 Apr 2016