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

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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 Igloodik 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.

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

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20 Abstract

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

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

37 Predation is one of the main factors explaining nesting mortality in most bird species (Ricklefs
38 1969), and hence represents a selective force that induced the development of strategies for
39 minimizing nest predation (Smith et al. 2007b). Birds can avoid nest predation or reduce
40 predation pressure by breeding at higher latitude (McKinnon et al. 2010a), showing anti-predator
41 behaviour (e.g. Simmons 1952), and nesting in association with protective species (Haemig
42 2001, Quinn and Ueta 2008). For instance, several studies showed that predation risk increases
43 with the distance to the nest of aggressive or territorial species such as Snowy Owl (*Bubo*
44 *scandiacus*; Bêty et al. 2001), Goshawk (*Accipiter gentilis*; Mönkkönen et al. 2007), Hooded
45 Crow (*Corvus corone cornix*; Roos 2002), and Northern Lapwing (*Vanellus vanellus*; Elliot
46 1985).

47 Shorebirds, particularly the biggest species with colorful plumage and both parents contributing
48 to parental care, are known to display various behaviours to protect their nests (e.g. Drury 1961,
49 Sordahl 1981, McCaffery 1982, Larsen et al. 1996). The American Golden-Plover (*Pluvialis*
50 *dominica*, hereafter “plover”) is an example of a shorebird species using an early warning system
51 and a distractive or mobbing antipredator behaviour to protect its nest (Byrkjedal and Thompson
52 1998). Such behaviours could decrease predation risks for other species nesting nearby, as shown
53 in another arctic-nesting plover species actively defending its nest, the grey plover (*Pluvialis*
54 *squatarola*; Larsen and Grundetjern 1997). Nests of arctic-breeding birds are mainly predated by
55 arctic foxes (*Vulpes lagopus*) and avian predators such as Common Raven (*Corvus corax*),
56 Glaucous Gull (*Larus hyperboreus*), and Long-Tailed Jaeger (*Stercorarius longicaudus*) (e.g.
57 Bêty et al. 2002, Lecomte et al. 2008). Because many arctic-nesting shorebirds species are
58 currently experiencing dramatic declines across their range (Morrison et al. 2001, Gratto-Trevor

59 et al. 2011), studying the influence of these species on spatial structures in nest predation risks
60 may contribute to better understanding their importance in tundra food webs.

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

66 **Methods**

67 Study area and species

68 We conducted the study on Igloolik Island, Nunavut, Canada (69.39° N, 81.55° W; 103 km²) in
69 July 2014 (Fig. 1). There, the tundra landscape is mainly composed of raised beaches with little
70 vegetation, *dryas*-lichen slopes, and grass-sedge wet and dry meadows (Forbes et al. 1992). The
71 average annual temperature for the period of 1981-2010 was -12.9°C with the warmest month
72 (July) averaging 7.6°C (Environment Canada 2015). These temperatures and vegetation features
73 correspond to a High-Arctic climate.

74 Igloolik Island is a known breeding site for up to 33 bird species, including shorebirds,
75 waterfowls, and seabirds (Lecomte and Giroux 2015). Shorebird nest density on the Island was
76 53.5 nest.km⁻² for our study (Lecomte and Giroux, unpubl. data). The proximity to the cliffs of
77 Coxe Islands (ca 15 km away) and to a polynya (ca 1.5 km away) allow numerous cliff breeders
78 as well as offshore and pelagic species to use our study area as a foraging and resting site. The
79 following nest predators are found on the Island: arctic foxes, ermines (*Mustela erminea*),

80 Parasitic (*Stercorarius parasiticus*) and Long-Tailed Jaegers, Glaucous Gulls, and Common
81 Ravens (Ellis and Evans 1960, Forbes et al. 1992, Lecomte and Giroux, unpubl. data).

82 Experimental design

83 To evaluate the protection effect of American Golden-Plovers on their neighbouring nests, 35
84 artificial nests were disposed at different distances from seven plover nests. We used the
85 protocols used in previous studies to determine the ranges of distance from plover nests (Larsen
86 and Grundetjern 1997, Bêty et al. 2001) and the frequency of visits (Bêty et al. 2001, Nguyen et
87 al. 2006, Lecomte 2007). The artificial nests were placed 30, 50, 100, 200, and 500 m from
88 potential protectors nests (Fig. 1). They were marked in the same way as the natural nests with
89 two wooden sticks and a blue flag at 1, 5, and 10 m north from the nest. Artificial nests were
90 deployed with rubber gloves between 12:00 and 18:00 on 7 and 8 July and checked after 1, 2, 4,
91 6, 8, and 12 days of exposure. The nests were considered depredated when their egg was missing
92 or broken.

93 In addition to the linear distance (in m) to the associated plover nest, we recorded the following
94 variables: linear distance to the closest active plover nest (in m), density of active plover nests
95 within a radius of 270 m around the artificial nest (Fig. 1), habitat type (wetland or mesic
96 tundra), and vertical nest concealment. The distance to the closest active nest became different
97 from the linear distance to the associated plover nest when the latter was depredated or when
98 another plover nest was located closer to the associated plover nest due to the random allocation.
99 Nest density, nesting success, the type of nesting habitat (wetland or mesic tundra) were
100 evaluated following the Arctic Shorebird Demographic Network protocol (Brown et al. 2014)
101 within an extensive survey zone of 11.7 km². Vertical nest concealment corresponded to the

102 percent of the nest obscured when viewed through an ocular tube (PVC pipe, 4 cm diameter x 11
103 cm length) from 1m directly above the nest.

104 Lemming trapping

105 We performed live lemming trapping between June 30th and July 2nd 2014 by setting up 50
106 Sherman traps at every second intersection (20-m spacing between intersections) of a 200-m x
107 200-m grid. After the initial set-up, we visited the traps every 4-6 hours during 56 hours (total of
108 12 visits).

109 Statistical Analysis

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

120 We used a model selection approach (Burnham and Anderson 2002) to identify the combination
121 of these variables that best described variations in the predation risk of artificial nests. We
122 compared 24 biologically plausible, candidate models, including up to four of the predictors

123 described above in a single model (see Supplemental Table S1 for the full list of models). We did
124 not include predictors displaying multicollinearity ($r > 0.70$) in the same model (Dormann et al.,
125 2013). We identify the combination of predictors that best described variations in predation risk
126 using the corrected Akaike Information Criterion (AICc) for small sample size (Burnham and
127 Anderson 2002) estimated from the library AICcmodavg (Mazerolle 2015). Models with $\Delta AICc$
128 < 2 from the top model were considered competitive (Burnham and Anderson 2002). Finally, we
129 used the survfit function (library survival, Therneau 2015) to create survival probability curves
130 using the Kaplan-Meier survival estimates of Cox models.

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

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

141 Results

142 A total of 18 American Golden-Plover nests were found in our extensive search area of 11.7 km²
143 (1.5 plover nest.km⁻²). We therefore used more than a third of all available nests (seven vs. 18
144 nests) to run the experiment. We did not trap any lemming in the live-trapping grid.

145 Predation risk and density of active plover nest

146 The model that best explained variation in predation risk on artificial nests included the density
147 of active plover nests within a radius of 270 m around the artificial nest (Supplemental Table
148 S1). The Cox proportional hazard mixed-effects regression model indicated that the predation
149 risk increased by 1.4-fold (coefficient = 0.87, SE = 0.24, $P = 0.0003$, hazard ratio = 2.4; Fig. 2)
150 and 2.4-fold (coefficient = 1.22, SE = 0.37, $P = 0.001$, hazard ratio = 3.4; Fig. 2), respectively,
151 when we observed one and two active plover nests within the 270m-radius around the artificial
152 nest. The second most parsimonious model ($\Delta\text{AICc} = 1.99$) included the effect of habitat type in
153 addition to the density of active plover nest (Supplemental Table S1). However, the effect of
154 habitat type on predation risk was not significant (coefficient = 0.09, SE = 0.24, hazard ratio =
155 1.10, $P = 0.7$).

156 Predation risk and distance to the nearest active plover nest

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

162 Discussion

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

169 Spatial variations in predation risk

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

181 Because plovers actively defend their territory by displaying early warning, mobbing and
182 sometimes aggressive behaviour, we predicted that this behaviour could benefit the neighbouring

183 nests by decreasing their predation risk. Yet, low lemming abundance on Igloolik Island during
184 the summer 2014 could contribute explaining the increased predation risk observed in areas with
185 higher density of plover nests or in the vicinity of plover nests. During a year of low abundance
186 of the main prey, the presence of one or more plover nest may have rather attracted then repelled
187 predators. Hence, further studies should compare the effect of plover nests on predation risk
188 estimated through artificial nests between years of lemming abundance.

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

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

205 respectively (Larsen and Grundetjern 1997). The behaviour of the Black-bellied Plover could
206 also contribute explaining difference between the results of Larsen and Grundetjern 1997 and
207 those shown here. Indeed, the American Golden-Plover begins to perform mobbing and
208 distraction displays when the predator is within 69-100 m (Byrkjedal and Thompson 1998). In
209 response to a flying predator, while the Grey Plover attacks avian predators, the American
210 Golden-Plover crouches, leaves the nest and sometimes approaches the predators, but never
211 attacks (Byrkjedal and Thompson 1998). In particular areas of the Arctic, the American Golden-
212 Plover was reported displaying aggressive behaviour and attack avian predators, but very rarely
213 and only where predators are small (Sordahl 1981, McCaffery 1982, Paulson and Erckmann
214 1985).

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

222 Artificial nests have the advantage of providing a standardized measure of predation risks. Yet,
223 predation rates on artificial nests differ from that of real nests and, therefore, they should not be
224 used to infer predation pressure on natural nests (Moore and Robinson 2004; McKinnon et al.
225 2010b). In our study, we used artificial nests to provide a controlled measure of relative predation
226 risk at various distances from plover nests, not to infer real nest success. Success of natural nests
227 is not only determined by predation risk, but by a combination of factors such as nest defense

228 behaviour (Kis et al. 2000), parental care (Smith et al. 2007a), incubation duration (Schamel and
229 Tracy 1987), and frequency of incubation recesses (Martin et al. 2000). For instance,
230 Nuechterlein (1981) reported that Western Grebes (*Aechmophorus occidentalis*) recognized
231 alarm calls of Forster's Terns (*Sterna forsteri*) and could use this information to adjust their
232 behaviour and potentially increase their reproductive success. Dunlins (*Calidris alpina*) and
233 Short-billed Dowitchers (*Limnodromus griseus*) were reported associating with American
234 Golden-Plovers while feeding and potentially benefit from early alarm calls (Thompson and
235 Thompson 1985, Byrkjedal 1987). Artificial nests allowed us to control for such sources of
236 heterogeneity to make meaningful ecological statements concerning the influence of plover nests
237 on predation risk in arctic-nesting birds.

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

244 **Conclusion**

245 In conclusion, the artificial nests experiment conducted on Igloolik Island do not support the
246 existence of a protective effect of plover nests on nearby nests, and rather show that it might not
247 be safe to nest near a bold neighbour during years of low abundance of the main prey. Our
248 results bring new perspective on how the spatial distribution and composition of shorebird
249 communities may influence their breeding success. Understanding how the composition and

250 structure of shorebird communities generate spatial patterns in predation risks represent a key
251 step to better understand the importance of these species of conservation concern (Morrison et al.
252 2001, Gratto-Trevor et al. 2011) in tundra food webs.

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

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383 **Figure Legends**

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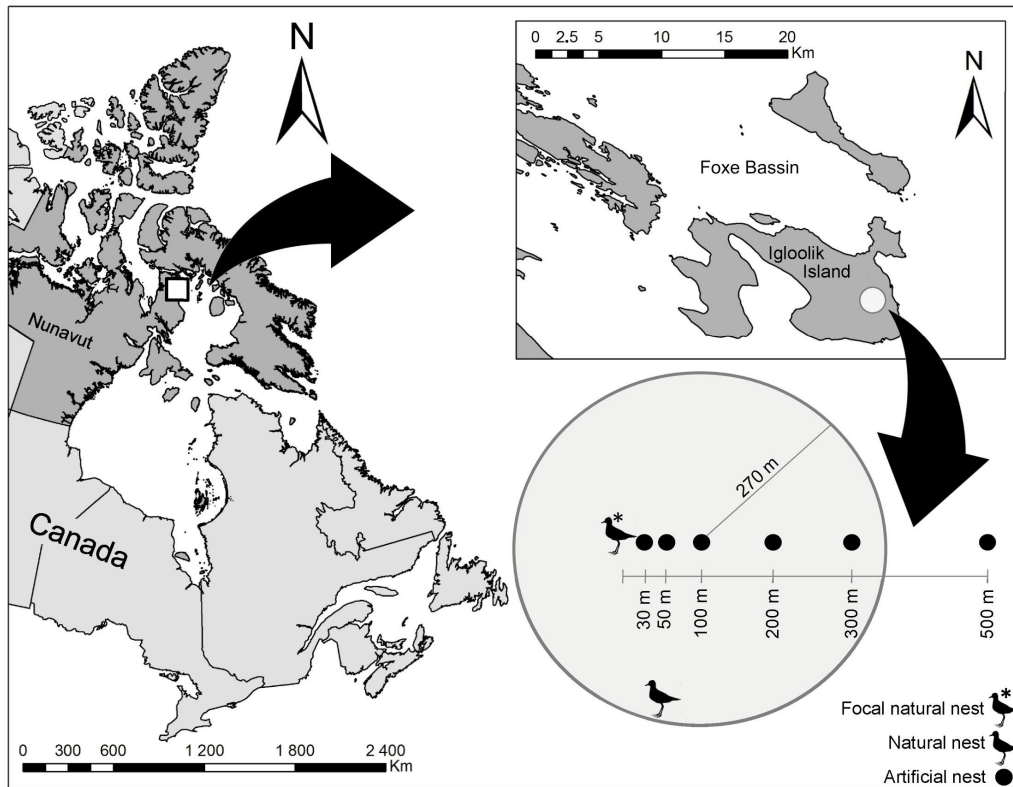
385 Fig. 1. Location of the study area on Igloolik Island (Nunavut, Canada, 69.39° N; 81.55° W).
386 Lower right side of the figure displays the experimental design of the experiment conducted in
387 July 2014 with artificial nests placed 30, 50, 100, 200 and 500 m from a focal natural plover nest.
388 Density of active plover nests within a radius of 270 m is shown for the artificial nest placed at
389 100 m from the focal natural plover nest (two active plover nests in this example).

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

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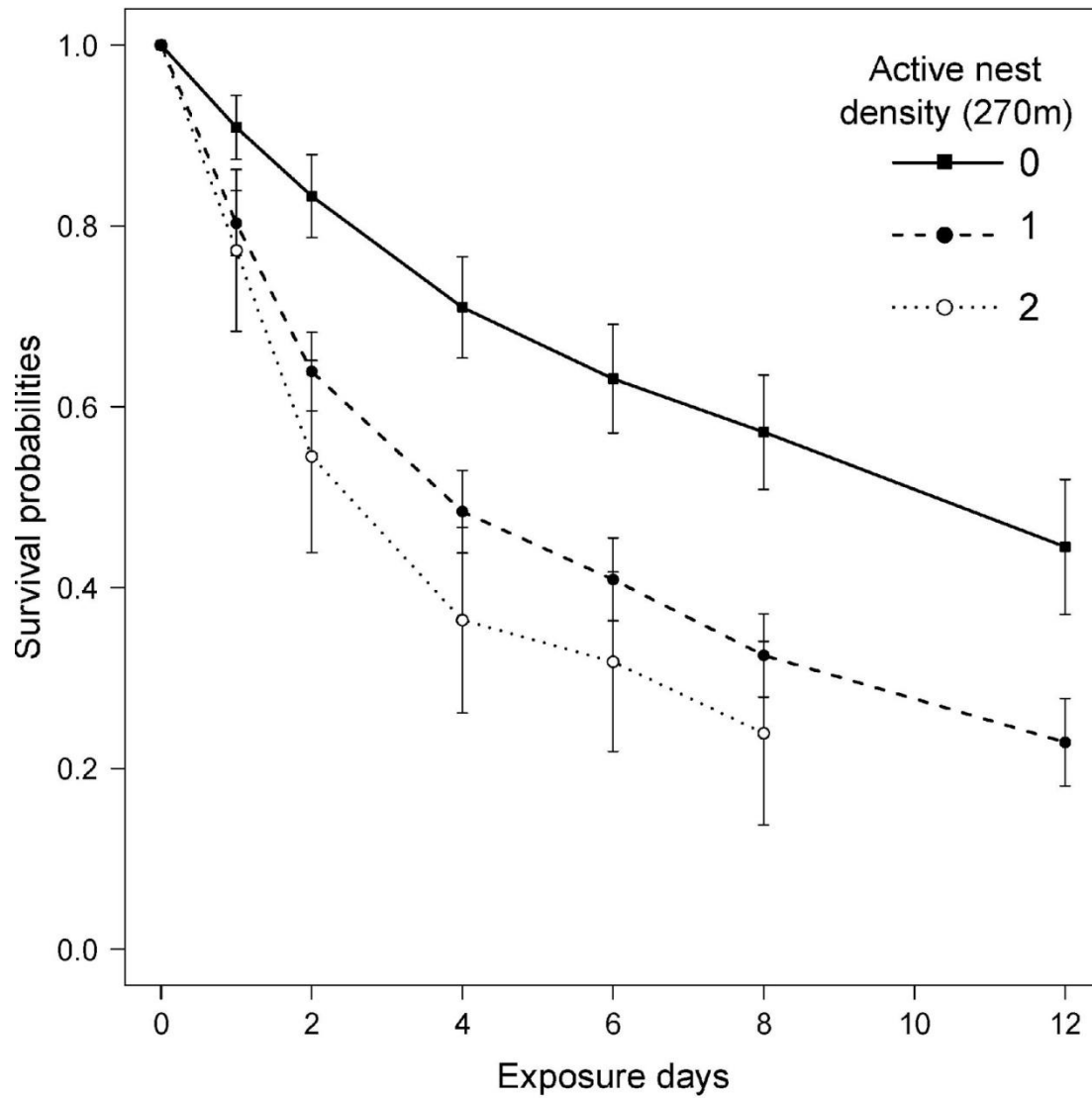
396 **Figures**

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399 **Fig. 1.**



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401 **Fig. 2.**

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405 **Supplementary Table**

406 Supplemental Table S1. Selection of models explaining variations in the risk of predation of
 407 artificial nests over 12 exposure days on Igloolik Island, (Nu, Canada) during the summer of
 408 2014 ($n=24$). We compared models including up to four of the following predictors: distance in
 409 meter to the associated plover nest (Distance), distance in meter to the closest active plover nest
 410 (Active Distance), density of active golden plover nests within a radius of 270 m around the
 411 artificial nest (Active Density), habitat type, i.e. wetland or mesic tundra (Moisture) and vertical
 412 concealment (Concealment). We also tested for quadratic effects of Distance and Active
 413 Distance. We report Akaike's information criterion corrected for small sample size (AICc),
 414 difference in AICc relative to the model with the lowest AIC (ΔAICc), as well as the AICc
 415 weight (ωAICc). Models are ranked by their AICc values and the best-fitting models ($\Delta\text{AICc} <$
 416 2) are shown in bold.

417

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
