The influence of habitat selection on Canada Goose *Branta canadensis* nest success on Akimiski Island, Nunavut, Canada

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Abstract

Predation avoidance is likely the foremost factor driving nest site selection among ground-nesting birds. The consequences of nest site selection were investigated on nest success for Canada Geese *Branta canadensis* breeding on Akimiski Island, Nunavut, Canada in 2010. Habitat features were measured at the scale of a nesting territory, at the nest site (*n* = 241), and at random locations for both scales. Compared with paired random locations, nests were more likely to be in woody vegetation located closer to water at the territory scale and had less lateral vegetative cover but taller vegetation nearer to the nest site. Geese did not select nesting locations in vegetation that provided maximum cover, but rather located nests in areas providing both concealment from predators and visibility for the nesting female to enable early predator detection. Assessing the effect of habitat attributes on nest success did not yield unambiguous results, with the most parsimonious model showing an increasing probability of nest success with increasing nest age alone. Although nest site selection was not random, we suggest that increasing parental investment and declining predation risk (not likely mutually exclusive) through the breeding season had more influence on Canada Goose nest success on Akimiski Island than did choice of specific habitat features or spacing of nests.

Key words: *Branta canadensis interior*, Canada Goose, habitat selection, nest success, predation.

A focus of avian ecology research involves understanding mechanisms that influence individual fitness and productivity at the population level. Nest site selection is an important determining factor for reproductive success because it influences the vulnerability of eggs and parents to predators, especially for ground nesting species (Newton 1998; Arnold *et al.* 2012; Devries *et al.* 2018). As egg predation is the leading cause of reproductive failure for most birds (Ricklefs 1969), habitat attributes of the nest site likely reflect aspects of predation risk mitigation (Martin & Roper 1988; Lima & Dill 1990; Lima 2009). Habitat features of selected nest sites may reflect elements of concealment (Greenwood *et al.* 1995; Devries *et al.* 2018), conspecific spacing (Minias 2014; McLandress 1983), thermal refuge (Piersma *et al.* 2003; Fast *et al.* 2007) and forage availability (Steele 1993; Burke & Nol 1998), with potential consequences of these choices being reduced predation risk (Martin 1993; Clark & Shutler 1999). Even though vegetation community and environmental relationships are dynamic, habitat preferences favour attributes that provide reproductive advantages (Clark & Shutler 1999).

Competition for nest sites also influences nest site selection and reproductive success (Martin 1993; Fisher & Weibe 2006). Birds breeding in seasonal environments are continuously faced with unpredictable and harsh conditions and must adjust their breeding phenology to optimise reproduction (Skinner *et al.* 1998; Gaston *et al.* 2009; Love *et al.* 2010). Optimisation involves synchronisation of breeding with seasonal phenology so that critical requirements closely match the availability of seasonal resources (Dunn 2004; Reed *et al.* 2009; Brook *et al.* 2015). In temperate zones, timing of snow melt can determine the availability of suitable breeding territories and nest sites (Petersen 1990). At higher latitudes, late snow melt relative to nest initiation timing can limit availability of breeding sites when birds are selecting them and influence reproductive strategies associated with choosing and defending a breeding territory via increased competition (*e.g.* Spaans *et al.* 1993) or the need to settle for less than optimal sites (Petersen 1990).

Canada Geese *Branta canadensis* are among the most common and wide-ranging goose species in North America, with breeding populations ranging from temperate regions to the high Arctic (Baldassarre 2014). Canada Geese tend to select nest sites that have low detection and access by terrestrial predators, thereby mitigating female incubation interruption while balancing visibility of an approaching predator (Raveling & Lumsden 1977; Lebeda & Ratti 1983; Maggiulli & Dugger 2011). Canada Geese are also among the seasonally earliest nesting species, often initiating nesting before all potential nesting sites are available (Ogilvie 1978; Kaminski & Weller 1992; Baldassarre 2014).

We evaluated nest site selection and its influence on nest success (*i.e.* at least one offspring leaving the nest) for Canada Geese when nest site availability was sufficient to allow individuals to select/avoid specific sites due to their environmental or ecological features without constraint imposed by snow cover. In 2010, spring conditions were atypical of our study area on Akimiski Island, Nunavut, Canada, since work began there in 1993 (Leafloor *et al.* 1996). Indeed, 2010 represented the earliest Canada Goose mean hatch date recorded (11 days earlier than average) over that period (Brook *et al.* 2015). When Canada Geese arrived in the study area, most of the snow had melted, meaning the only limitation to nest site selection was from conspecific competition. Accordingly, we hypothesised that nest site selection and nest success in 2010 would be primarily driven by features that increased predator avoidance. Therefore, we predicted that without a constraint on habitat availability, there would be a correlation between nest success and predation-related habitat features, such as those affecting concealment of nests and also visibility for females watching for potential predators from the nest.

Methods

Study site

Akimiski Island, Nunavut, is in James Bay, a southeasterly extension of the Hudson Bay in northeast Canada (53.18°N, 81.58°W; Fig. 1). The island is dominated by a wetland

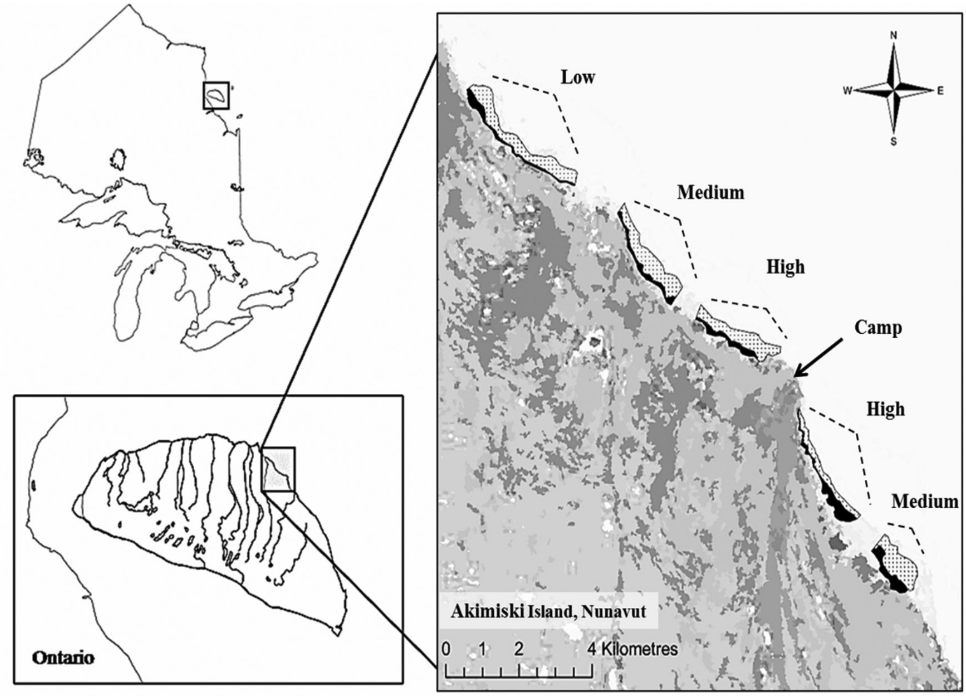

Figure 1. Location of Akimiski Island, Nunavut, in James Bay Canada, where the nesting success of Canada Geese was studied in 2010. High, Medium and Low indicate the frequency of visits to nests located in shaded (dots or black) areas. Shaded areas illustrate macro-habitat classification of Canada Goose nesting habitat, with dotted areas showing non-woody species habitat and black areas showing habitat dominated by woody species.

complex, intertidal mudflats and coastal salt marshes extending across much of the coastline, with drainage channels extending from interior freshwater fens and lakes (Martini & Glooschenko 1984). Habitat in the study area (512 ha of the coastal plain along the north shore of the island) varies from intertidal vegetation surrounded by saline mud flats to brackish and freshwater marshes and fens and willow *Salix* sp. thickets. Typically, lower intertidal marshes are dominated by Creeping Alkali Grass *Puccinellia phryganodes* progressing inland into supratidal marshes dominated by Red Fescue *Festuca rubra* and other grasses and rushes/sedges (*Juncus arcticus, J. balticus, Carex subspathacea* and *C. aquatilis*; (Blaney & Kotanen 2001; O *et al.* 2005). Inland from the supratidal zone, the vegetation is increasingly complex and dominated by various willows, Dwarf Birch *Betula glandulosa*, Tamarack *Larix laricina*, and Black and White Spruce *Picea mariana* and *P. glauca*. Akimiski Island has a humid sub-Arctic climate with temperatures ranging from –20°C to 30°C and annual precipitation averaging 650 mm (Martini & Glooschenko 1984). The predator community in this region includes both aerial egg predators (*e.g.* Common Raven *Corvus corax*, American Crow *C. brachyrhynchos* and Herring Gull *Larus argentatus*) and mammalian predators (*e.g.* Red Fox *Vulpes vulpes*, Arctic Fox *V. lagopus* and Polar Bear *Ursus maritimus*).

Nest-searching and monitoring

From 24 April to 7 June 2010, nests were found from the egg-laying stage to just before the peak of hatch by methodical searches of the study area between 08:00–18:00 h. To locate nests, observers used sightings of geese flushing, females on nests, scattered goose down near nests, or by locating unattended or destroyed nests (Leafloor *et al.* 1996, 2000). All known nesting habitats in the coastal study area were searched systematically with similar effort, leading to *c.* 80% nest detection within the study area regardless of habitat type (K. Abraham, unpubl. data). Most nests (*c.* 90%) were found during the initial search attempt while the remaining nests were discovered during our subsequent monitoring activities.

At nest sites, total clutch size was determined, and embryo age was estimated using egg flotation, with onset of laying ("nest age") calculated from the age of the embryos (Westerkov 1950; Walter & Rusch 1997). Location of both active and predated nests were recorded with a Global Positioning System (GPS) unit and active nests were marked with a 1 m tall wire stake with flagging positioned 10 m north of the nest. After each initial nest check, eggs were covered with down and nest material to restore a natural appearance and to provide thermal protection.

Effort was made to visit nests using different approach routes to ensure a thorough ground search of the study area and to minimise vegetation disturbance and other associated cues that predators could use to also find nests (Armstrong 1996). During each visit, the status of each egg was recorded and partial predation (incomplete clutch reduction; Ackerman *et al.* 2003) was assessed by noting missing eggs. Once 25% of the active nests hatched, daily nest monitoring of all remaining nests was initiated to ensure an accurate assessment of the fate of the clutches. If the egg hatching date was missed, the number of goslings leaving the nest was determined by counting intact egg membranes found at the nest site (Klett *et al.* 1986).

During nest searching and monitoring, daily visual point counts of predators were conducted at 10:00 h, 12:00 h, 14:00 h and 16:00 h (Liebezeit & Zack 2008; Gauthier 2008). Observers scanned their surroundings for both avian and mammalian predators, using binoculars to identify and count predators within the nesting area.

Habitat measurements

Habitat physical attributes were measured at nest sites and at paired random locations that were selected by choosing a random direction and distance from within a 25 m radius of the nest site following determination of nest fate (Petersen 1990). For each nest site and random point, habitat characteristics were measured at two spatial scales: micro-scale included the area within 1 m of the nest bowl or random spot, and macro-scale included the area within 25 m radius of each point. Macro-habitat (MACROHAB) was categorised based on vegetation dominance and physical characteristics either as: 1) non-woody habitat (372.7 ha) consisting primarily of Red Fescue, Alkali Grass and mudflats, or 2) woody habitat (139.3 ha) dominated by willows and Dwarf Birch. Macro-habitat zones were delineated by using GPS tracking from a helicopter, flown at 50 m above ground after all nests had hatched. Nests were assigned macro-habitat type using their locations within each zone. Micro-habitat measurements included tallest vegetation height (VEGHT; cm), vertical cover (VCOVER; %), lateral cover (LCOVER; %) and distance to nearest water (WATER; m) (Bruggink *et al.* 1994; Albrecht *et al.* 2006). Vertical vegetation cover was calculated as the proportion of concave densitometer squares obstructed by vegetation (Strickler 1959). Lateral vegetation cover (or concealment) was evaluated using a 50 cm × 50 cm chequered pattern density board, consisting of alternating 10 cm^2 orange and black squares observed from 10 m (Nudds 1977). From each cardinal direction the percent of vegetation obstructing the orange blocks was recorded in 25% categories (Lebeda & Ratti 1983; Jacobs & Dunn 2004; Magaña *et al.* 2010). Vegetation cover was evaluated in an increasing and cumulative vertical method (*i.e.* 0–10 cm, 0–20 cm, *etc.*, where 0 was the top of the nest bowl) to determine how concealment affected nest success (S_xCOVER; where x = the height [cm]). Cumulative lateral vegetation cover was evaluated to take into account the large body size of Canada Geese and the regular extension of the female's neck and head when visually scanning of the surrounding.

To assess whether nest predation was dependent on nest density, ArcGIS 10 (ESRI 2011) was used to index local nest density by calculating the distance to the nearest neighbouring nest (INTERDIST) and the distance to the nearest neighbouring nest that was predated (PREDDIST). Distances were calculated on the date of hatch for successful nests and on the last date visited for nests that failed. To control for incomplete discovery of all nests, both inter-nest distances were calculated as the mean distance to the three closest neighbours. Nests found on the inland edge of the coastal nest-search study area (*i.e.* the transition from open habitats to tree-covered habitats which were not searched, following precedent set early in the long-term study) were given the mean inter-nest distance value because the closest neighbours were only known for half of the surrounding area (coastal 180° direction).

Statistical analysis

Macro-habitat of nest sites was analysed in relation to paired random points using a Chi-squared test. The micro-habitat variables were transformed including the vertical and lateral cover percent (arcsine-square root) and distance to water ($\log_{10}$) to improve normality of errors. Micro-habitat measurements among nest sites and paired random points were analysed using paired *t*-tests (one-tailed because we predicted directional differences in micro-habitat measurements, Appendix 1). To reduce the number of lateral cover vertical strata variables for use in building nest success candidate models, we analysed these highly correlated variables individually using a logistic regression to determine the strength of their effects on nest fate.

Spatial variables (INTERDIST and PREDDIST) were calculated using the Average Nearest Neighbour Distance tool in ArcGIS 10 (ESRI 2011). The Average Nearest Neighbour (ANN) ratio

$$\mathrm{ANN} = \mathrm{D}_{\mathrm{oi}} / \mathrm{D}_{\bar{\mathrm{e}}\mathrm{i}}$$

was determined by dividing the observed mean distance between each nest and their nearest neighbour (D_{oi}) by the expected mean distance (D_{ei}) for each nest. The expected mean distance was

$$\mathrm{D}_{\bar{\mathrm{e}}} = \frac{0.5}{\sqrt{\left(\frac{n}{A}\right)}}$$

where *n* corresponds to the total number of nests and *A* is the size of the study area assuming a random distribution of nests.

We tested for correlation among variables modelled to ensure that highly correlated variables did not appear in the same models together (*i.e.* Pearson correlation where $P < 0.05$). We retained the following variables for model building: S_{30}COVER, WATER, INTERDIST, PREDDIST, and macro-habitat type. To evaluate factors affecting the daily nest survival rate, 11 habitat, spatial, and predator models were considered that represent biological hypotheses developed *a priori* (Appendix 1). We included nest age (AGE; *i.e.* the number of days since onset of laying) in all models because it is often a significant factor in explaining nesting success (Rotella *et al.* 2004) and appeared to have a relatively strong effect in our analyses. A model of observer effects was included (VISIT; binary variable representing whether a nest visit occurred). Daily nest survival probability was estimated using the nest survival model and a logit-link function in Program MARK (White & Burnham 1999; Dinsmore *et al.* 2002). Akaike Information Criterion corrected for small sample size (AIC_c) was used to rank nest success models (Burnham & Anderson 1998; Anderson *et al.* 2000). Akaike's weights (w_i) were also calculated to evaluate models relative to the candidate set and parameter estimates and their confidence intervals were used to estimate the direction and magnitude of effects. All models with $\Delta AIC_c \leq 2.0$ were considered competitive (Burnham & Anderson 2002). Models were also assessed to determine if they were informative (Arnold 2010). All statistical analyses were conducted using ArcGIS 10 (ESRI 2011), Stata 10.0 (StataCorp 2007) and Program MARK (White & Burnham 1999). For all tests where a P value is presented, we considered significance to be at $\alpha = 0.05$. Field methods were approved by Ontario Ministry of Natural Resources Animal Care Committee (protocol #10–40).

Results

Of the 241 goose nests located, we could determine conclusively the fate (*i.e.* whether or not at least one egg hatched) for 229 (95%). All nests were used in the nest site selection analysis, but only nests where the outcome of the breeding attempt was known (n = 229) were included in the survival analyses (Table 1).

Habitat selection

Nest placement differed from expected at the macro-habitat scale ($\chi_1^2 = 18.17$, $P < 0.01$). Woody habitat comprised 27% of the study area but 45.6% of the nests were

Table 1. Micro-habitat vegetation measurements for paired random points in comparison with all Canada Goose nest sites found on Akimiski Island, Nunavut, during 2010, and for nests where the fate of the clutch was determined.

	Paired Random Points		**All nests**		**Failed nests**		**Successful nests (≥ 1 egg known to have hatched)**	
Habitat variables	**mean**	**(s.e.)**	**mean**	**(s.e.)**	**mean**	**(s.e.)**	**mean**	**(s.e.)**
Sample size (*n*)	241		241		149		80	
Water distance (m)	3.09	(0.52)	2.05	(0.53)	1.07	(0.27)	2.54	(0.82)
Vegetation height (m)	0.47	(0.02)	0.54	(0.02)	0.58	(0.32)	0.53	(0.24)
Vertical cover (%)	4.65	(0.30)	3.25	(0.21)	4.77	(0.39)	4.81	(0.54)
Lateral cover (%)								
Strata 1 (40–50cm)	14.61	(1.12)	9.68	(0.87)	8.71	(0.86)	12.30	(2.07)
Strata 2 (30–40 cm)	22.55	(1.40)	15.93	(1.03)	14.92	(1.06)	18.94	(2.36)
Strata 3 (20–30cm)	34.45	(1.73)	25.69	(1.16)	25.28	(1.36)	27.36	(2.34)
Strata 4 (10–20cm)	49.23	(2.00)	37.32	(1.27)	37.29	(1.51)	37.91	(2.49)
Strata 5 (0–10cm)	69.42	(1.89)	56.86	(1.29)	58.28	(1.65)	54.79	(2.27)
Full (average 0–50cm)	38.05	(1.50)	29.10	(1.01)	28.90	(1.13)	30.26	(2.14)

in woody habitat. Lateral cover (micro-habitat) differed between macro-habitat types (woody *vs.* non-woody) at nest sites ($\chi_1^2 = 49.84$, $P < 0.01$) and at paired random points ($\chi_1^2 = 67.23$, $P < 0.01$). Nest sites in woody macro-habitat had greater nest site cover than those in non-woody macro-habitat (36.4% and 23.0%, respectively).

At the nest site (micro-habitat) scale, nests were located closer to water ($t_{482} = 3.89$, one-tailed $P < 0.01$), had taller vegetation ($t_{482} = 2.68$, one-tailed $P < 0.01$), and less lateral cover ($t_{482} = 4.83$, one-tailed $P < 0.01$) than random points (Table 1). Paired random points and nest sites differed in dominant micro-habitat vegetation type ($\chi_1^2 = 16.25$, $P < 0.001$). Fifty percent ($n = 120$) of nests had willow species as the dominant vegetation type but only 17% ($n = 41$) of the paired random points were dominated by willow. When evaluating the vegetation type providing lateral concealment, 80% ($n = 194$) of nest sites and only 54% ($n = 130$) of paired random points were concealed by willow.

Daily nest success

Vertical delineation revealed that lateral cover at the second highest stratum and above (30–40cm and > 40 cm) was marginally influential (logistic regression: Wald $\chi^2_1 = 3.09$, $P = 0.08$, n.s.), suggesting that increased concealment with elevation from the ground increased the probability of nest success. We therefore included a lateral cover variable (S_{30}COVER, as an average of the two highest strata) for building nest success candidate models.

Nine of our 11 nest success models were competitive (Table 2). The most parsimonious and informative model was the model that included only nest age ($AIC_c = 1666.59$, $w_i = 0.07$). Nest success increased with nest age ($\beta_{AGE} = 0.055$, 95% CI = 0.036–0.073) (Fig. 2). The most parsimonious model (AGE) resulted in an overall nest success estimate of 0.674 (95% CI = 0.63–0.72). All models containing habitat and spatial covariates resulted in models with uninformative variables. A model to determine if nest visits had an impact on nest success was not supported ($\Delta AIC_c = 34.69$).

Discussion

Temporal factors had an underlying effect on daily nest success; the probability of survival improved as hatch date approached. The positive effect of nest age as the most influential variable for daily nest probability of survival may reflect both changes in parental behaviour due to cumulative time investment in incubation (Sjöberg 1994) and possibly a within-season change in predator-prey community dynamics and behaviour (Johnson *et al.* 1989; Miller *et al.* 2006). Though the underlying reasons driving this observation could not be isolated, a cumulative time investment by the breeding pair might have resulted in increasing vigilance and defensive behaviour towards predators to protect their clutch as hatch date approached.

Even though there was no evidence of a link between nesting habitat and nest success in 2010, nests were not distributed randomly on available coastal habitats on Akimiski Island. This non-randomness may be adaptive and suggests that habitat features may influence nest success in years where Canada Geese are constrained in nest

Table 2. Candidate models[1] assessed to evaluate daily survival probability for Canada Goose nests found on Akimiski Island, Nunavut, Canada in 2010 (n = 132). Nest age (AGE) was included in all models.

Model	**Deviance**	**ΔAIC$_c$**	**w_i**	**K**
S(AGE + S_{30}COVER + WATER + PREDDIST)	1654.64	0.00	0.19	5
S(AGE + INTERDIST)	1658.82	0.18	0.18	3
S(AGE + WATER)	1659.57	0.92	0.11	3
S(AGE + S_{30}COVER + WATER)	1657.60	0.96	0.12	4
S(AGE + PREDDIST)	1659.85	1.20	0.11	3
S(AGE + COVER + PREDDIST)	1658.28	1.64	0.08	4
S(AGE + MACROHAB + INTERDIST)	1658.50	1.86	0.08	4
S(AGE + MACROHAB + PREDDIST)	1658.55	1.91	0.07	4
S(AGE)*	1662.59	1.95	0.07	2
S(AGE + COVER)	1661.03	2.39	0.06	3
S(AGE + MACROHAB)	1661.77	3.12	0.04	3

[1] Models ranked according to Akaike's information criterion adjusted for small sample size (AIC$_c$). The number of parameters (K), Deviance, and AIC$_c$ weights (w_i) are given for all models. Models identified with * indicate those models that were informative. The lowest AIC$_c$ value was 1664.64.

site selection. Nest predation by mammalian (Crabtree *et al.* 1989) and avian (Clark & Nudds 1991; Sugden & Beyersbergen 1986) predators decreases with greater lateral cover, particularly if the vegetation is structured, inhibiting detection and impeding access to the nest site; potentially a factor for nest success on Akimiski Island when preferred nest sites are limited.

The importance of visibility from the nest site (Miller *et al.* 2007) for Canada Geese suggests that this feature facilitates pair communication and thereby may improve coordination of nest defence strategies when faced with predators. Males are vigilant at nesting territories, readily alerting females of danger and defending offspring from predators (Owen 1980). Though nesting geese usually can defend their clutches and broods successfully against foxes (Giroux 1981; Bruggink *et al.* 1994; O'Briain *et al.* 1998), incubating females are vulnerable to mortality if ambush attacks are not detected early (Miller *et al.* 2007). In a study concurrent with ours (Miller *et al.* 2013), females observed nesting in concealing vegetation remained on nests longer in the presence of an approaching threat, suggesting that there is trade-off between individual and egg predation when selecting nest sites. This is correspondingly true for geese nesting in seasonal environments

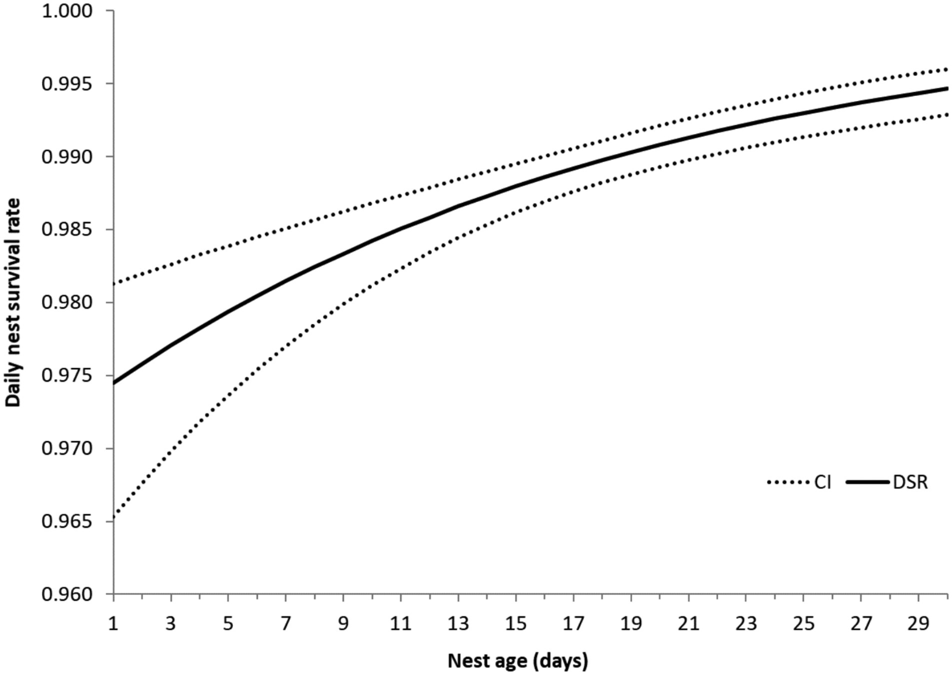

Figure 2. The estimate of daily nest survival rate (DSR) for Canada Geese on Akimiski Island, Nunavut, Canada during 2010 (*n* =132), based on the most parsimonious model including the effect of nest age. Dashed lines are the 95% confidence intervals (CI).

where predator pressure exhibits substantial inter-annual variation, being dependent on predator population growth rates (Reiter & Andersen 2011), food web relationships (Gauthier *et al.* 2004), and a sporadic influx of seasonal predators such as Polar Bears (see Stempniewicz 2006). Visibility from the nest likely is a strategy to reduce predation through early detection of predators (Götmark *et al.* 1995; Magaña *et al.* 2010; Miller *et al.* 2013) while concealment works to reduce the probability of predators locating the nest (*i.e.* an optimisation strategy; Miller *et al.* 2007).

Others have reported on the variation of the inter-annual influence of snow melt on nest site selection for goose species breeding in seasonal environments (*e.g.* Cooke & Abraham 1980; Petersen 1990) and the lack of association between nest habitat features and nest success is consistent with at least one other study of northern-breeding Canada Geese (Maggiulli & Dugger 2011). If selection of nesting sites was limited only by conspecific competition in 2010 during our study (*i.e.* not by snow cover) and all pairs selected highly suitable habitats, then other factors may have masked habitat-related effects on nest success compared to situations when nest sites are more limiting. Additional factors that could not be controlled in our models, including female experience and body condition (*e.g.* Devries *et al.* 2008), likely work in concert with habitat selection and predation risk in determining nest success. Maggiulli & Dugger (2011) suggest that the presence of alternative prey and predator abundance is more important to nest success than the island habitat features they measured. Predator-prey cycles on Akimiski Island may also have an important influence on nest success that was not captured in our 2010 study.

Despite the favourable environmental conditions that should have relaxed limitations associated with habitat availability and energy expenditure at Akimiski Island in 2010, there was a concurrent increase in predation pressure due to temporal change in the predator community. During laying and in early incubation, several Polar Bears were observed consuming goose eggs during a 13-day period within the nesting area; similar observations have rarely been made during our long-term research on Akimiski Island (K. Abraham, unpubl. data). Though the Polar Bears returned to the sea ice later in the nesting season, the overlap between nesting period and Polar Bear presence did impact early nest success. It is projected that Polar Bears will increasingly visit terrestrial environments during the goose nesting period as climatic conditions change (Rockwell *et al.* 2011), though long-term systematic studies are necessary to understand fully this potential limiting factor. It follows that, over the longer term, geese may need to adjust their habitat selection patterns to reduce the risk of nest loss to increasing bear predation, as well as other anticipated changes such as variation in plant phenology and temperature conditions.

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References

Ackerman, J.T., Eadie, J.M., Loughman, D.L., Yarris, G.S. & McLandress, M.R. 2003. The influence of partial clutch depredation on duckling production. *Journal of Wildlife Management* 67: 576– 587.

Albrecht, T., Hořák, D., Kreisinger, J., Weidinger, K., Klvaña, P. & Michot, T.C. 2006. Factors determining Pochard nest predation along a wetland gradient. *Journal of Wildlife Management* 70: 784–791.

Anderson, D.R., Burnham, K.P. & Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64: 912–923.

Armstrong, T. 1996. Effects of research activities on nest predation in Arctic-nesting geese. *Journal of Wildlife Management* 60: 265–269.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74: 1175–1178.

Arnold, T.W., Roche, E.A., Devries, J.H. & Howerter, D.W. 2012. Cost of reproduction in breeding female mallards: predation risk during incubation drives annual mortality. *Avian Conservation and Ecology* 7(1): 1.

Baldassarre, G. 2014. *Ducks, Geese and Swans of North America. Revised and Updated Edition. Volume 1*. Johns Hopkins University Press, Maryland, USA.

Blaney, C.S. & Kotanen, P.M. 2001. The vascular flora of Akimiski Island, Nunavut Territory, Canada. *Canadian Field Naturalist* 115: 88–98.

Brook, R.W., Leafloor, J.O., Abraham, K.F. & Douglas, D.C. 2015. Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada Geese. *Avian Conservation and Ecology*. 10(1): 1. http://dx.doi.org/10.5751/ACE-00708-100101.

Bruggink, J.G., Tacha, T.C., Davies, J.C. & Abraham, K.F. 1994. Nesting and brood rearing ecology of Mississippi Valley population Canada Geese. *Wildlife Monograph* 126: 1–39.

Burke, D.M. & Nol, E. 1998. Influence of food abundance, nest-site and forest fragmentation on breeding Ovenbirds. *Auk* 115: 96–104.

Burnham, K.P. & Anderson, D.R. 1998. *Model Selection and Inference: a Practical Information-Theoretic Approach, 2nd Edition*. Springer-Verlag, New York, USA.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd Edition*. Springer-Verlag, New York, USA.

Clark, R.G. & Nudds, T.D. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. *Wildlife Society Bulletin* 19: 534–543.

Clark, R.G. & Shutler, D. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80: 272–287.

Cooke, F. & Abraham, K.F. 1980. Habitat and locality selection in lesser snow geese: the role of previous experience. *Proceedings 17th International Ornithological Congress*: 998–1004.

Crabtree, R.L., Broome, L.S. & Wolfe, M.L. 1989. Effects of habitat characteristics on Gadwall nest predation and nest-site selection. *Journal of Wildlife Management* 53: 129–137.

Devries, J.H., Brook, R.W., Howerter, D.W. & Anderson M.G. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). *The Auk* 125: 618–628.

Devries, J.H., Clark, R.G., & Armstrong, L.M. 2018. Dynamics of habitat selection in birds: adaptive response to nest predation depends on multiple factors. *Oecologia* 187: 305–318.

Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.

Dunn, P. 2004. Breeding dates and reproductive performance. *Advances Ecological Research* 35: 69–87.

ESRI 2011. *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute, Redlands, California, USA.

Fast, P.L.F., Gilchrist, H.G. & Clark, R.G. 2007. Experimental evaluation of nest shelter effects on weight loss in incubating Common Eiders *Somateria mollissima*. *Journal of Avian Biology* 38: 205–213.

Fisher, R.J. & Wiebe, K.L. 2006. Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. *Oecologia* 147: 744–753.

Gaston, A.J., Gilchrist, H.G., Mallory, M.L. & Smith, P.A. 2009. Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: a case of progressive mismatching. *The Condor* 111: 111–119.

Gauthier, G. 2008. Raptor abundance. ArcticWOLVES sampling protocols v1.0. University of Laval University, Quebec, Canada.

Gauthier, G., Bety, J., Giroux, J.F. & Rochefort, L. 2004. Trophic interactions in a high Arctic Snow Goose colony. *Integrative and Comparative Biology* 44: 119–129.

Giroux, J.F. 1981. Use of artificial islands by nesting waterfowl in southern Alberta. *Journal of Wildlife Management* 45: 669–679.

Götmark, F., Blomqvist, D., Johansson, O.C. & Bergkvist, J. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? *Journal of Avian Biology* 26: 305–312.

Greenwood, R.J., Sargeant, A.B., Johnson, D.H., Cowardin, L.M. & Shaffer, T.L. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. *Wildlife Monograph* 128: 3–57.

Jacobs, K.J. & Dunn, J.P. 2004. Canada Goose nesting ecology and gosling survival at Pymatuning Wildlife Management Area, Pennsylvania. *In* T.J. Moser, K.C. Lien, K.C. VerCauteren, K.F. Abraham, D.E. Andersen, J.G. Bruggink, J.M. Coluccy, D.A. Graber, J.O. Leafloor, D.R. Luukkonen & R.E. Trost (eds.), *Proceedings of the 2003 International Canada Goose Symposium,* pp. 85–91. Madison, Wisconsin, USA.

Johnson, D.H., Sargeant, A.B. & Greenwood, R.J. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. *Canadian Journal of Zoology* 67: 291–297.

Kaminski, R.M. & Weller, M.W. 1992. Breeding habitats of Nearctic waterfowl. *In* B.D. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 568–589. University of Minnesota, Minneapolis, USA.

Klett, A.T., Duebbert, H.F. & Kruse, A.D. 1986. *Techniques for Studying Nest Success of Ducks in the Prairie Pothole Region.* U.S. Fish and Wildlife Service Resource Publication 158. USFWS, Jamestown, North Dakota, USA.

Leafloor, J.O., Abraham, K.F., Rusch, D.H., Ross, R.K. & Hill, M.R.J. 1996. Status of the southern James Bay population of Canada Geese. *In* J. Ratti (ed.), *Proceedings of the International Waterfowl symposium.* February 1996, pp. 103–108. Memphis, Tennessee, USA.

Leafloor, J.O., Hill, M.R.J., Rusch, D.H., Abraham, K.F. & Ross, R.K. 2000. Nesting ecology and gosling survival of Canada Geese on Akimiski Island, Nunavut, Canada. *In* K.M. Dickson (ed.), *Towards Conservation of the Diversity of Canada Geese (Branta canadensis),* pp.109–116. Canadian Wildlife Service Occasional Paper No. 103. CWS, Ottawa, Ontario, Canada.

Lebeda, C.S. & Ratti, J.T. 1983. Reproductive biology of Vancouver Canada Geese on Admiralty Island, Alaska. *Journal of Wildlife Management* 47: 297–306.

Liebezeit, J.R. & Zack, S. 2008. Point counts underestimate the importance of arctic foxes as avian nest predators: evidence from remote video cameras in arctic Alaskan oil fields. *Arctic* 61: 153–161.

Lima, S.L. 2009. Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. *Biological Reviews* 84: 485–513.

Lima, S.L. & Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.

Love, O.P., Gilchrist, H.G., Descamps, S., Semeniuk, C.A.D. & Bety, J. 2010. Pre-laying climatic cures can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia* 164: 277–286.

Magaña, M., Alonso, J.C., Martín, C.A., Bautista, L.M. & Martín, B. 2010. Nest-site selection by Great Bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis* 152: 77–89.

Maggiulli, N. & Dugger, B.D. 2011. Factors associated with Dusky Canada Goose (*Branta canadensis occidentalis*) nesting and nest success on artificial nest islands of the western Copper River Delta. *Waterbirds* 34: 269–279.

Martin, T.E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141: 897–913.

Martin, T.E. & Roper, J.J. 1988. Nest predation and nest site selection of a western population of the Hermit Thrush. *The Condor* 90: 51–57.

Martini, I.P. & Glooschenko, W.A. 1984. Emergent coasts of Akimiski Island, Northwestern Territories, Canada: geology, geomorphology, and vegetation. *Sedimentary Geology* 37: 229–250.

McLandress, M.R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and Lesser Snow Geese. *The Auk* 100: 335–343.

Miller, D.A., Grand, J.B., Fondell, T.F. & Anthony, R.M. 2006. Predator functional response and prey survival: direct and indirect interactions affecting marked prey population. *Journal of Animal Ecology* 75: 101–110.

Miller, D.A., Grand, J.B., Fondell, T.F. & Anthony, R.M. 2007. Optimizing nest survival and female survival: consequences of nest site selection for Canada Geese. *The Condor* 109: 769–780.

Miller, V., Abraham, K.F. & Nol, E. 2013. Factors affecting the responses of female Canada Geese to disturbance during incubation. *Journal of Field Ornithology* 84: 171–180.

Minias, P. 2014. Evolution of within-colony distribution patterns of birds in response to habitat structure. *Behavioral Ecology and Sociobiology* 68: 851–859.

Newton, I. 1998. *Population Limitations in Birds*. Academic Press, London, UK.

Nudds, T.D. 1977. Quantifying the vegetation structure of wildlife cover. *Wildlife Society Bulletin* 5: 113–117.

O, P.C., Kotanen, P.M. & Abraham, K.F. 2005. Survival and growth of the forage grass *Festuca rubra* in naturally and artificially devegetated sites in a sub-arctic coastal marsh. *Ecoscience* 12: 279–285.

O'Briain, M., Reed, A. & MacDonald, S.D. 1998. Breeding, moulting, and site fidelity of Brant (*Branta bernicla*) on Bathurst and Seymour Islands in the Canadian high Arctic. *Arctic* 51: 350–360.

Ogilvie, M.A. 1978. *Wild Geese*. Buteo Books, Vermilion, South Dakota, USA.

Owen, M. 1980. *Wild Geese of the World: Their Life History and Ecology*. B.T. Batsford Ltd., London, UK.

Petersen, M.R. 1990. Nest-site selection by Emperor Geese and Cackling Canada Geese. *Wilson Bulletin* 102: 413–426.

Piersma, T., Lindström, Å., Drent, R.H., Tulp, I., Jukema, J., Morrison, R.I.G., Reneerkens, J., Schekkerman, H. & Visser, G.H. 2003. High daily energy expenditure of incubating shorebirds on high arctic tundra: a circumpolar study. *Functional Ecology* 17: 356–362.

Raveling, D.G. & Lumsden, H.G. 1977. *Nesting Ecology of Canada Geese in the Hudson Bay Lowlands of Ontario: Evolution and Population Regulation*. Ontario Ministry of Natural Resources Fish and Wildlife Resource Report No. 98. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Reed, T.E., Warzbok, P., Wilson, A.J., Bradley, R.W., Wanless, S. & Sydeman, W.J. 2009. Timing is everything: flexile phenology and shifting selection in a colonial seabird. *Journal of Animal Ecology* 78: 376–387.

Reiter, M.E. & Andersen, D.E. 2011. Arctic foxes, lemmings and Canada Goose nest survival at Cape Churchill, Manitoba. *The Wilson Journal of Ornithology* 123: 266–276.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* 9: 1–48.

Rockwell, R.F., Gormezano, L.J. & Koons, D.N. 2011. Trophic matches and mismatches: can polar bears reduce the abundance of nesting Snow Geese in western Hudson Bay? *Oikos* 120: 696–709.

Rotella, J.J., Dinsmore, S.J. & Shaffer, T.L. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27: 186–205.

Sjöberg, G. 1994. Factors affecting nest defense in female Canada Geese *Branta canadensis*. *Ibis* 136: 129–135.

Skinner, W.R., Jefferies, R.L., Carleton, T.J., Rockwell, R.F. & Abraham, K.F. 1998. Prediction of reproductive success and failure in Lesser Snow Geese based on early season climatic variables. *Global Change Biology* 4: 3–16.

Spaans, B., Stock, M., St. Joseph, A., Bergmann, H.H. & Ebbinge, B.S. 1993. Breeding biology of dark-bellied brent geese *Branta b. bernicla* in Taimyr in 1990 in the absence of arctic foxes and under favourable weather conditions. *Polar Research* 12: 117–130.

StataCorp. 2007. *Stata Statistical Software: Release 10*. College Station, Texas, USA.

Steele, B.B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers: their relative influence on habitat choice. *The Condor* 95: 568–579.

Stempniewicz, L. 2006. Polar bear predatory behavior toward moulting Barnacle Geese and nesting Glaucous Gulls in Spitsbergen. *Arctic* 59: 247–251.

Strickler, G.S. 1959. *Use of the densitometer to estimate density of forest canopy on permanent sample plots*. USDA Forest Service Research Note No. 180. U.S. Department of Agriculture, Portland, Oregon, USA.

Sugden, L.G. & Beyersbergen, G.W. 1986. Effect of density and concealment on American Crow predation of simulated duck nest. *Journal of Wildlife Management* 50: 9–14.

Walter, S.E. & Rusch, D.H. 1997. Accuracy of egg flotation in determining age of Canada Goose nests. *Wildlife Society Bulletin* 25: 854–857.

Westerkov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14: 56–67.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from population of marked animals. *Bird Study* 46: 120–138.

Photograph: Female Canada Goose nesting on Akimiski Island, Nunavut, Canada, by Rod Brook.

Appendix 1.

Models assessed for explaining daily nest success of Canada Goose nests on Akimiski Island, Nunavut, in 2010. The covariate nest age (AGE) is included in all models.

Model Structure	**Hypothesis**
S_{30}COVER + WATER + PREDDIST	Predated neighbour spacing and concealment with visibility will affect predator detection probabilities
INTERDIST	Spacing between conspecific nests will influence risk of predation through neighbour communication and number of potential nest sites
WATER	Closer distance to water allows a trade-off of concealment and visibility of predators
S_{30}COVER + WATER	Trade-off hypothesis (Götmark *et al.* 1995) – cover and closer distance to water allows a trade-off of concealment and visibility of predators
PREDDIST	Distance to predated conspecific nests will influence predator searching and detection of additional nests
S_{30}COVER + PREDDIST	Spacing among predated neighbour and concealment will affect predator detection probability
MACROHAB + INTERDIST	Nest spacing is a product of macro-habitat ultimately influencing predator mobility and predation risk
MACROHAB + PREDDIST	Spacing of predated nests is influenced by macro-habitat type
AGE	A significant factor in explaining nesting success (Rotella *et al.* 2004)
S_{30}COVER	Concealment hypothesis (Martin 1993) – concealment is a predator avoidance strategy by the reduction of cues
MACROHAB	Habitat type will influence predator mobility