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RESEARCH ARTICLE

Nest site characteristics, patterns of nest reuse, and reproductive output in an Arctic-nesting raptor, the Rough-legged Hawk

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ABSTRACT

Physical characteristics of nest sites are thought to influence their use by birds and the outcome of breeding attempts. The presence of preexisting nesting structures can also be an important factor influencing reuse patterns and reproductive success. We examined the relationships between nest-site physical characteristics, patterns of nest reuse, and reproductive output in Rough-legged Hawks (*Buteo lagopus*) breeding in the Canadian High Arctic. Because this species is a rodent specialist, we also examined the effect of variation in lemming density, their primary prey, on reproductive output. We monitored 109 nesting attempts over a 9 yr period and sampled physical characteristics of 87 known nesting sites in 53 territories on Bylot Island, Nunavut, Canada. The probability that a nest was used by a breeding pair increased with the distance to the nearest breeding conspecific, for nests sheltered by an overhang, and with lemming density. Hawk nests inaccessible to foxes and facing away from the north were associated with high reproductive success. Reproductive success was also positively related to summer lemming density and negatively related to rainfall. Our results suggest that nest-site physical characteristics that offer a favorable microclimate and protection from weather and predators provide the highest-quality sites. We observed a high level of reuse of preexisting nests and previously occupied territories, which is indicative of site fidelity by individuals. Hawks that bred in a newly built nest had similar clutch size and hatching date compared to those that used preexisting nests, which suggests that building a new nest entailed no short-term reproductive costs. Reproductive success was nonetheless reduced for birds breeding in new nests located in newly occupied territories compared to those nesting in previously occupied ones, which suggests that a high proportion of pairs in new territories were young birds or that some of these sites were of low quality.

Keywords: Arctic, breeding success, *Buteo lagopus*, cliff-nesting raptor, lemming abundance, nest and territory occupancy, predator accessibility, rainfall

Caractéristiques du site de nidification, patrons de réutilisation d'un nid et succès reproducteur chez un rapace nichant dans l'Arctique, la Buse pattue

RÉSUMÉ

Les caractéristiques physiques des sites de nidification peuvent influencer la probabilité qu'ils soient utilisés et l'issue des tentatives de reproduction. La présence de structures de nidification préexistantes peut également être un facteur important influençant les patrons de réutilisation de celles-ci et le succès reproducteur des oiseaux. Nous avons examiné le lien entre les caractéristiques physiques du site de nidification et la réutilisation d'un nid et d'un territoire sur le succès reproducteur de la Buse pattue (*Buteo lagopus*) nichant dans le Haut-Arctique canadien. Puisque cette espèce est considérée spécialiste des rongeurs, nous avons aussi examiné l'effet de la variation de la densité des lemmings, leur proie principale, sur le succès reproducteur. Nous avons suivi 109 tentatives de nidification sur une période de 9 ans et échantillonné les caractéristiques physiques de 87 sites de nidification au sein de 53 territoires à l'île Bylot, NU. La probabilité qu'un nid soit utilisé par un couple augmentait avec la distance du nid actif le plus proche, la présence d'un surplomb au-dessus du nid et la densité des lemmings. Les nids de buses accessibles aux renards et orientés vers le nord étaient associés à un moins bon succès reproducteur. Le succès reproducteur était aussi positivement relié à la densité estivale de lemmings et négativement relié aux précipitations. Nos résultats suggèrent que les caractéristiques physiques du site de nidification offrant un microclimat favorable et une protection contre les intempéries et les prédateurs reflètent des sites de haute qualité. Nous avons observé un haut niveau de réutilisation des nids et territoires précédemment occupés ce qui serait un indice de fidélité des individus au site de nidification. Les buses qui ont niché dans un nid nouvellement construit avaient une taille de ponte et une date d'éclosion similaires à celles ayant utilisé des nids préexistants, ce qui suggère que la construction d'un nouveau nid n'entraîne pas de coût à court terme sur la reproduction. Le succès reproducteur était néanmoins plus bas dans les territoires nouvellement occupés comparativement à ceux précédemment occupés ce qui suggère qu'une forte proportion des oiseaux établit dans les nouveaux territoires étaient jeunes et inexpérimentés ou que certains de ces sites étaient de qualité inférieure.

Mots-clés: abondance des lemmings, accessibilité aux prédateurs, Arctique, *Buteo lagopus*, occupation d'un nid et d'un territoire, pluie, rapace nichant sur des falaises, succès de reproduction

INTRODUCTION

The physical characteristics of nest sites can strongly influence the success of breeding attempts through variations in predation risk (Martin 1993, Velando and Márquez 2002, Mainwaring et al. 2014) and microclimatic conditions (Kim and Monaghan 2005, Fast et al. 2007, Robertson 2009). For instance, breeding success is generally higher for concealed nests or those located on sites inaccessible to terrestrial predators (Mallory and Forbes 2011, Haynes et al. 2014, Anderson et al. 2015). Similarly, exposure of the eggs and chicks to inclement weather such as rain can be reduced in nests that are protected by an overhang (Mearns and Newton 1988, Anctil et al. 2014), whereas nests with a southern exposure or those located at low altitude may provide a warmer environment for chicks in cold climates (White and Cade 1971, Poole and Bromley 1988a). Physical characteristics of nest sites that are positively associated with reproductive output should also be related to nest-use probability, unless high-quality sites are limited or cues used by birds to select nest sites are poor indicators of site quality (Donázar et al. 1993, Wightman and Fuller 2006, Bruggeman et al. 2016). Other environmental factors, besides nest site characteristics, that can also have a strong influence on reproductive success include food availability (Terraube et al. 2012, Therrien et al. 2014) and intraspecific and interspecific interactions (Hakkarainen and Korpimäki 1996, Sergio et al. 2003, Brambilla et al. 2006).

In species like raptors and long-legged waders, the same nest can be maintained and reused over several breeding seasons (e.g., Golden Eagle [*Aquila chrysaetos*], Kochert and Steenhof 2012; White Stork [*Ciconia ciconia*], Tobolka et al. 2013), sometimes up to a thousand years in extreme cases (Gyrfalcon [*Falco rusticolus*], Burnham et al. 2009). These nests, referred to as "ecological magnets" (Hickey 1942), constitute key resources for many species (Sergio et al. 2011, Jiménez-Franco et al. 2014a, Millsap et al. 2015), and reusing them can ultimately influence individual fitness (Tobolka et al. 2013). Indeed, nest building is considered energetically and temporally costly (Collias and Collias 1985, Mainwaring et al. 2014), and these costs can be reduced considerably if old structures are reused (Cavitt et al. 1999, Vergara et al. 2010). This can be especially important in species breeding at high latitudes where the nesting period is short. However, the strategy of nest reuse has rarely been shown to influence reproductive output in raptors, though such studies are scarce (Kochert and Steenhof 2012, Jiménez-Franco et al. 2014a, 2014b). Nests that are consistently reused may also reflect high-quality breeding territory, and the presence of preexisting nesting structures may provide important cues that could be used by individuals settling in a new breeding area (Korpimäki 1988b, Sergio et al. 2011, Millsap et al. 2015).

The Rough-legged Hawk (*Buteo lagopus*) is a medium-sized migratory raptor with a circumpolar distribution that commonly breeds on cliff edges or along steep hillsides and can occupy the same nesting structure for many years (Mindell 1983, Bechard and Swem 2002). It is mostly considered a rodent specialist, though it can use alternative prey, such as ptarmigans, ducks, and hares, when rodents are scarce (Mindell 1983, Pokrovsky et al. 2014). Hence, the abundance of small rodents can be a major factor influencing this species' annual breeding density and reproductive output (Therrien et al. 2014, Terraube et al. 2015). Predation, geomorphological processes (e.g., slope failure), chilling, and food scarcity have been documented as major causes of breeding failure in the species (Swem 1996, Potapov 1997, Pokrovsky et al. 2012). Previous studies have mainly focused on the numerical and functional responses of this predator to prey availability (Wiklund et al. 1998, Sundell et al. 2004, Hellström et al. 2014, Therrien et al. 2014, Terraube et al. 2015), and few have examined the possible influence of other environmental variables on its reproduction (Potapov 1997).

The objectives of the present study were to investigate the effects of nest-site physical characteristics and other environmental variables on (1) nest-use probability and (2) reproductive output and (3) to evaluate potential fitness benefits of using a previously occupied territory or preexisting nesting structure in Rough-legged Hawks breeding in the Canadian High Arctic. We hypothesized that nest site characteristics offering protection from inclement weather (thereby providing a favorable microclimate) and from terrestrial predators would influence nest-use probability and reproductive success. We predicted that nests sheltered by an overhang, located at low altitude, oriented toward the south, more concealed, and inaccessible to Arctic foxes (*Vulpes lagopus*) would be more likely to be occupied by Rough-legged Hawks and

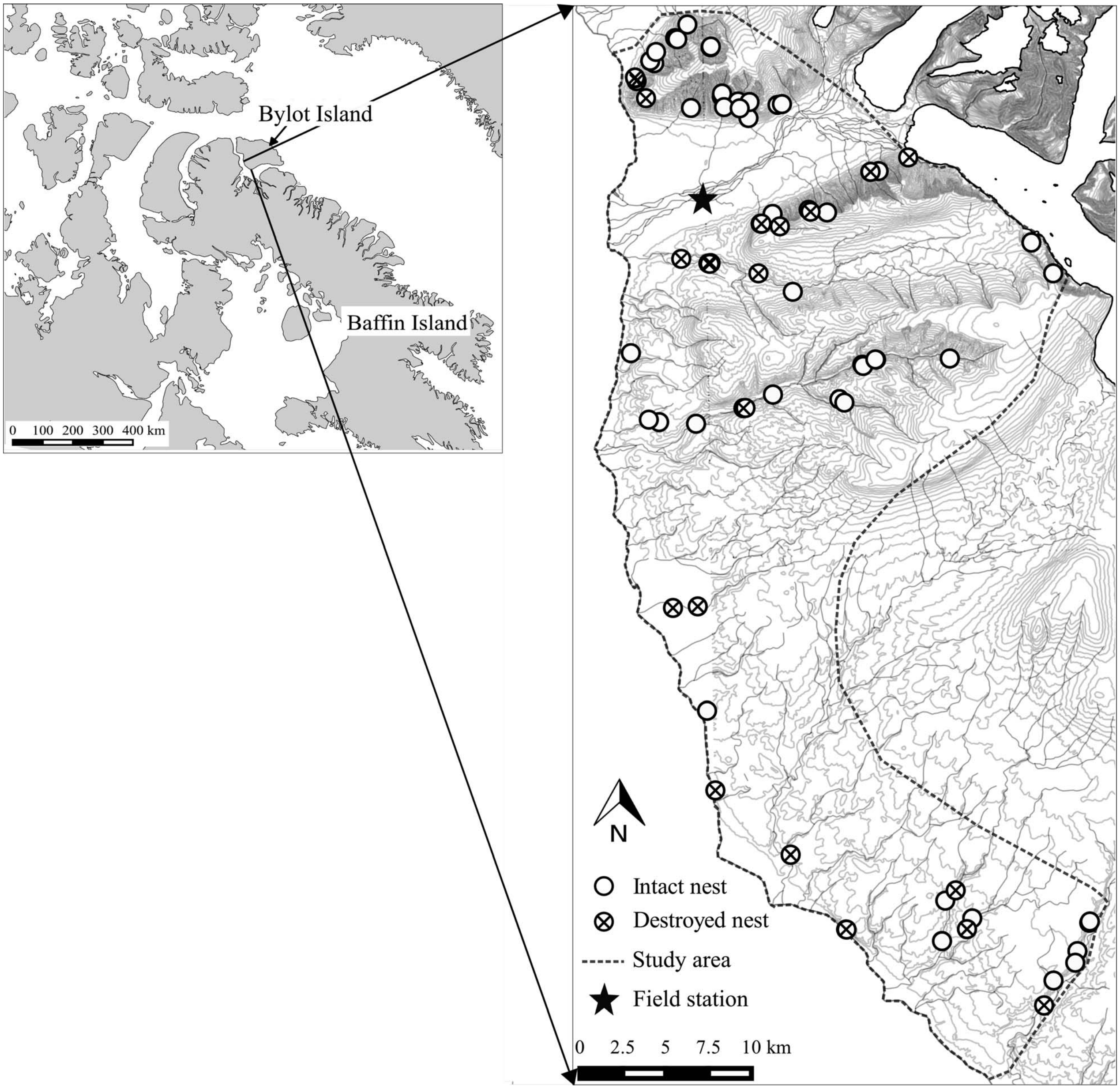

FIGURE 1. Location of the study site on Bylot Island, Nunavut, Canada, with detail of the study area on the right, including positions of all known nesting structures (intact and destroyed nests at the end of the study; $n = 87$) monitored between 2007 and 2015. Spacing between contour lines is 20 m.

associated with higher reproductive success. Previous studies have shown that rainfall (through a chilling effect on chicks) and food availability (e.g., lemming cycles) can have a strong influence on the reproductive output of Arctic raptors (e.g., Anctil et al. 2014, Therrien et al. 2014). These factors were thus considered along with nest-site physical characteristics to explain variations in reproductive success. Finally, we hypothesized that using a preexisting nest rather than a newly built one should be associated with higher reproductive success because of the potential savings in energy and time (Cavitt et al. 1999, Tobolka et al. 2013).

METHODS

Study Area and Study Species

The study area, covering ~500 km^2 of tundra, is located on the south plain of Bylot Island, Nunavut, Canada (73°N, 80°W; Figure 1). This region is characterized by rolling hills and low-elevation plateaus (100–580 m above sea level) interspersed by streams and rivers that have created frequent outcrops of exposed bedrock. The bedrock is composed of sedimentary rock (sandstone and shale) from the Lancaster Formation of the Cretaceous and Tertiary periods (Jackson and Sangster 1987). A layer of surficial deposits often covers the bedrock on low-angle slopes. Exposed bedrock along streams, ravines, and mountain slopes provides suitable breeding sites for a cliff-nesting species like the Rough-legged Hawk. Although the species can sometimes nest on flat ground (Poole and Bromley 1988a, Pokrovsky et al. 2012), nesting at our study site is restricted to cliff edges or steep hillsides. Nests are made of a relatively large amount of branches and roots (diameter range about 60–90 cm) and are generally conspicuous (Bechard and Swem 2002). Egg laying occurs in late May and early June. Incubation lasts $\geq$31 days, with nestlings hatching asynchronously in July (Bechard and Swem 2002).

Others species of raptors that nest in the study area include the Peregrine Falcon (*Falco peregrinus*) and Gyrfalcon, which are present in low abundance (6 and 1 known nesting sites, respectively), and the Snowy Owl (*Bubo scandiacus*) in lowlands, whose abundance varies considerably depending on annual lemming density (0–100 nests; Therrien et al. 2014, G. Gauthier personal observation). The 2 rodent species that are present, the brown lemming (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*), show large cyclic fluctuations of abundance (Gauthier et al. 2013). During the summer months (June–August), the average temperature is 4.5°C and the average rainfall is 91 mm (Cadieux et al. 2008). Additional details on plant communities and general landscape can be found in Gauthier et al. (2011).

Monitoring Nest Use and Reproductive Success

From 2007 to 2015, we found Rough-legged Hawk nests by conducting systematic searches on foot in all areas considered suitable for nesting individuals (i.e. along cliffs, ravines, or large rocky outcrops) and by using a helicopter to reach distant areas. These areas were defined a priori on the basis of topography and river systems within the 500 km^2 study area (Figure 1). The same areas were searched every year, although some areas within the general study area were added over the first few years of the study. Nests were found using 8–10× binoculars and were often located following alarm calls made by breeding individuals when observers entered a nesting territory. Each nest was positioned using a global positioning system (GPS) receiver (Garmin, GPSmap 60×), and several photos of the nest and surrounding environment were taken to facilitate recognition of the exact location in subsequent years.

Every year from late June to mid-July, we searched for new nests and visited all known nests to determine whether they were active. We considered a nest active when a pair of Rough-legged Hawks showed clear signs of territorial behavior (e.g., alarms calls, attacks) or when direct evidence of breeding was found (e.g., an incubating adult at the nest, presence of eggs or chicks). Systematic searches of the same areas annually allowed us to differentiate territories and nesting structures that were preexisting or new. We defined "territory" as a confined area that contained one or more nests and where no more than one pair was known to have bred at any time (Steenhof and Newton 2007). We used the minimum distance between 2 active nests in the same year (0.57 km; see below) to determine territory size in our study area. We defined a "newly occupied territory" as an area that had been visited in previous years and where a new nesting structure was detected >0.57 km from any existing nesting structure. If a new nesting structure was found <0.57 km from an existing structure, we considered it a new nest in a previously occupied territory. Alternatively, we could have used a more conservative value such as half of the minimum distance recorded between active nests (i.e. 0.3 km) to define territory size. Among the 36 nesting structures located <0.57 km from an active nest, 75% were within 0.3 km. We repeated the analyses described below with a 0.3 km threshold for territory size, but that didn't change the statistical outcome of any analyses; thus, we present only results based on the 0.57 km threshold. Obviously, we couldn't differentiate new nesting structures from preexisting ones in the first year of monitoring an area (2007 for much of the study area), and these nests were excluded from territory and nest occupancy analyses in those years.

We visited active nests at least twice between early July and mid-August to record the numbers of eggs and chicks. We estimated the age of nestlings by size and stage of feather development, using a photographic guide developed for Red-tailed Hawks (*Buteo jamaicensis*; Moritsch 1983), a species of similar size whose chicks fledge at about the same age as those of Rough-legged Hawks (Bechard and Swem 2002, Preston and Beane 2009). Repeated nest visits allowed us to determine the following components of reproductive success for active nests. First, we defined "clutch size" as the maximum number of eggs found in a nest. Second, we defined "hatching success" as the probability of hatching at least one egg. Whenever possible we recorded information on hatching date, which was often inferred from the estimated age of nestlings. Third, we defined "nesting success" as the probability of producing at least one 14-day-old chick among all active nests. Finally, we defined "brood size" as the maximum number of chicks found in a nest between the 14th and 21th days of chick rearing, excluding nests where no egg hatched. In raptors, most nestling mortality typically occurs within the first 2 wk of life (Kirkley and Gessaman

TABLE 1. Description of environmental variables used to model nest-use probability and reproductive success of Rough-legged Hawks on Bylot Island, Nunavut, Canada, 2007–2015.

Variables	Description
Nest site characteristics	
Accessibility	Accessible (1) or inaccessible (0) to Arctic fox
Orientation	North–south numerical gradient (0 [N], 0.25 [NE, NW], 0.5 [E,W], 0.75 [SE, SW], 1 [S])
Overhang	Presence (1; back wall angle $>90°$) or absence (0; back wall angle $<90°$) of an overhang above the nest
Exposure	Sum of horizontal and vertical opening (°)
Altitude	Height above sea level (m)
Food availability	
Lemming	Lemming density (n ha^{-1})
Weather	
Rain-1	Cumulative rainfall (mm) between laying and hatching dates of individual nests
Rain-2	Cumulative rainfall (mm) during the first 14 days after hatching of individual nests
Rain-3	Cumulative rainfall (mm) between laying date and 14th day of the chick-rearing period of individual nests
Intraspecific interactions	
Distance	Linear distance to the nearest active nest (km)

1990, Potapov 1997, Arroyo 2002). The numbers of chicks at 14 days and 31 days (i.e. 1–5 days before fledging in Rough-legged Hawk; Bechard and Swem 2002) were highly correlated ($r = 0.89$, $P < 0.001$, $n = 10$ nests), and total brood failure was never recorded after the 14th day of chick rearing in our study area.

Environmental Variables

Each nest was characterized according to 5 physical variables. These variables were selected on the basis of previous studies on cliff-nesting raptor species (White and Cade 1971, Wightman and Fuller 2005, 2006, Tapia et al. 2007) and are summarized in Table 1. We categorized each nest as accessible or inaccessible to the Arctic fox, the main nest predator on Bylot Island (Bêty et al. 2002, Gauthier et al. 2015). Presence of an overhang and nest orientation, exposure, and altitude were recorded because of their potential influence on the microclimatic conditions of the nest. We measured nest orientation with a compass. Because we were especially interested in the north–south component of nest orientation, a north–south numerical gradient was used for the analysis (Table 1). We recorded whether overhanging rocks provided direct cover above the nest. An overhang was considered present if the nest was partially or completely obstructed by overhead rock (back wall angle with respect to a horizontal plane $>90°$). We obtained the exposure of the nest with a compass by adding the horizontal angle of exposure (i.e. degree of opening of the nest at an angle perpendicular to main slope, from left to right) and vertical angle of exposure (i.e. angle formed by a horizontal plane at the level of the nest and the back wall above the nest). We measured the elevation above sea level using an altimeter (ADC Summit, Brunton, Louisville, Colorado, USA).

To characterize food availability, lemming density was estimated annually via capture–mark–recapture methods using live-trapping data from 2 grids (11 ha each) located near the Bylot Island field station (Figure 1; for details, see Fauteux et al. 2015). In our analyses, we used lemming density estimated in July (average of the 2 grids, both species combined) for each year. Daily rainfall (mm) was measured with a manual rain gauge at the field station. From these data, we extracted the cumulative daily rainfall for each individual reproductive event during 3 periods corresponding, respectively, to the incubation period, the brood-rearing period, and the whole nesting period (Table 1). When the hatching date was unknown for a nest, we used the mean annual hatching date to estimate cumulative rainfall for that nest.

To account for intraspecific interactions (i.e. territoriality), we used the linear distance to the nearest Rough-legged Hawk active nest measured using the package "sp" in R (Bivand et al. 2013). Interspecific interactions can also influence nest use and reproductive output in raptors (Hakkarainen and Korpimäki 1996, Sergio et al. 2004). Peregrine Falcons were present at low density (0–6 active nests yr^{-1}; 24 nests over 9 yr) and used the same habitat as the study species. We ran a preliminary analysis using the linear distance to the nearest Peregrine Falcon nest for the 3 yr with the most active Peregrine Falcon nests (4, 6, and 4 nests annually), but this variable did not affect nest use or any reproductive output variable. Therefore, this should not be considered a confounding factor in our study. Four Rough-legged Hawk nesting structures were nonetheless occupied once by Peregrine Falcons; these were considered unavailable to Rough-legged Hawks in those years and were excluded from the nest-use analysis.

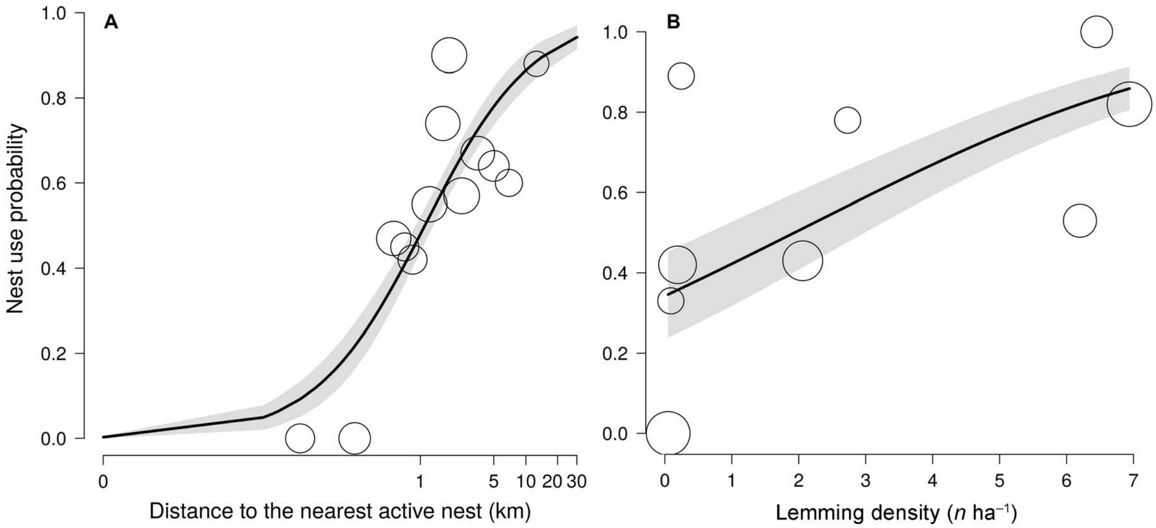

FIGURE 2. Probability that a nesting structure was used by a Rough-legged Hawk breeding pair on Bylot Island, Nunavut, Canada, 2007–2015, in relation to (**A**) the distance to the nearest active nest and (**B**) lemming density. The gray band represents ±95% CI of the regression. To illustrate observed values, each circle represents the proportion of used nest, and circle size is proportional to the number of observations: (A) $n = 202$, (B) $n = 185$. The mean response for lemming density is based on the most parsimonious models (Table 2 and Appendix Table 4) after controlling for other model effects.

Statistical Analyses

We used generalized linear mixed-effects models (GLMM) with a binomial distribution to model nest-use probability, hatching success, and nesting success, and with a Poisson distribution to model brood size. We built a set of candidate models describing multiple hypotheses to investigate the effect of environmental variables on nest use, hatching success, nesting success, and brood size. Collinearity among independent variables was checked with Pearson correlations, and we avoided including highly correlated variables ($r \geq 0.7$) simultaneously in models (i.e. these variables were tested in alternatives models). Distance was log transformed to improve the distribution of the residuals, and all continuous variables were centered ($x - \bar{x}$) to simplify calculations. Models were ranked according to Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$). When no single model had a strong support (i.e. Akaike weights <0.90), model-averaged estimates and 95% confidence intervals (CIs) were computed with multimodel inference on the most parsimonious models (i.e. $\Delta\mathrm{AIC_c} < 4$) (Burnham and Anderson 2002). Because the same nests were visited repeatedly over the years, nest ID was added as a random effect on the intercept in all models. We also used GLMM to model reproductive-success parameters according to nest and territory reuse (newly occupied territory [the reference category], new nest in a previously occupied territory, and preexisting nest in a previously occupied territory) and included nest ID and year as random effects. In this case, clutch size was modeled with a zero-truncated Poisson and hatching date with a Gaussian distribution. Relationships were considered statistically significant when the 95% CIs of the slope excluded zero. To assess the amount of variation explained by our models, we report the marginal R^2 (for fixed effects) calculated with the method proposed by Nakagawa and Schielzeth (2013) for mixed-effects models.

All analyses were performed in R Statistical Environment (R Development Core Team 2014). The packages "lme4" (for binomial, Poisson, and Gaussian distributions) and "glmmADMB" (for zero-truncated Poisson distribution) were used to estimate the parameters of GLMMs (Skaug et al. 2013, Bates et al. 2015). The package "AICcmodavg" was used for model selection and multimodel inference (Mazerolle 2015). Results are reported as means ± SE.

RESULTS

Nest-use Probability

The number of known nesting structures available at the beginning of each breeding season ranged from 11 (in 2007) to 65 (in 2015), and the number of active nests ranged from zero (in 2013) to 31 (in 2014). Over 9 yr (2007–2015), we monitored a total of 109 active Rough-legged Hawk nests, and 132 known nesting structures remained unused. The distance between an unused nest and the nearest active nest in the same year ranged from 0.001 to 14.29 km (mean = 1.70 ± 0.24 km). Nest spacing among breeding pairs ranged from 0.57 to 30.41 km (mean = 3.31 ± 0.43 km). The probability that a nesting structure was used by a breeding pair was strongly and positively related to the distance to the nearest active nest ($\beta = 1.63$, 95% CI: 0.96–2.73, $n = 202$; Figure 2A), indicating that the

TABLE 2. Model-averaged parameter estimates (with 95% confidence intervals) from the most parsimonious models ($\Delta AIC_c < 4$) explaining Rough-legged Hawk nest use and reproductive success on Bylot Island, Nunavut, Canada, 2007–2015. Estimates considered statistically significant are in bold. See Table 1 for a description of each variable.

Variables	Nest use	Hatching success	Nesting success	Brood size
Accessibility	−0.79 (−1.26, 0.78)	−2.36 (−4.78, 0.07)	**−5.10 (−10.03, −0.17)**	−0.15 (−0.48, 0.18)
Orientation	−1.18 (−2.85, 0.49)	**−2.76 (−5.35, −0.17)**	**−3.68 (−6.85, −0.52)**	−0.23 (−0.77, 0.30)
Overhang	**2.05 (0.68, 3.41)**	–	−1.34 (−4.03, 1.34)	0.12 (−0.22, 0.47)
Exposure	–	–	0.02 (−0.03, 0.07)	NA
Altitude	–	–	0.00 (−0.01, 0.01)	NA
Lemming	**0.43 (0.26, 0.60)**	**0.26 (0.02, 0.50)**	0.28 (−0.05, 0.60)	0.03 (−0.04, 0.11)
Rain-1	NA	−0.03 (−0.08, 0.01)	NA	NA
Rain-2	NA	NA	NA	−0.01 (−0.03, 0.02)
Rain-3	NA	NA	**−0.06 (−0.11, 0.00)**	NA
Distance	**2.01 (1.14, 2.87)**	NA	NA	NA

Note: Dash (–) = not retained in the most parsimonious models; NA = not included in the candidate models.

presence of an active nest limited the use of neighboring nesting structures, likely as a result of territorial behavior. Hence, nesting structures located <0.57 km from an active nest were excluded from subsequent analyses investigating the effect of nest-site physical characteristics on nest-use probability. The top-ranked model explaining nest-use probability included distance to the nearest breeding pair, lemming density, presence of an overhang, and nest orientation and explained 54% of the variation (Table 2 and Appendix Table 4). The probability that a nest was used increased with lemming density (Figure 2B) and was also higher for nests protected by an overhang (0.81 ± 0.10) compared to those unprotected by an overhang (0.37 ± 0.07). Nest-use probability also tended to decrease for nests oriented toward the north.

Reproductive Success

Average clutch size was 4.4 ± 0.1 eggs ($n = 69$ clutches), and brood size at 14 days was 4.0 ± 0.2 ($n = 38$ broods) in nests where ≥1 chick hatched (overall hatching success was 78%; $n = 77$ nests). Hatching dates ranged from June 28 to July 21 (median = July 8; $n = 43$ clutches).

Lemming density, accessibility to foxes, nest orientation, and rainfall were included in the most parsimonious model explaining either hatching or nesting success (Table 2 and Appendix Tables 5 and 6). The best model explained 42% and 77% of the variation in hatching and nesting success, respectively. Hatching success was positively related to lemming density (Figure 3), and there was a similar trend for nesting success. Nesting success was lower in nests oriented toward the north and in years with high rainfall (Figure 4), and was higher in nests inaccessible to Arctic foxes (0.99 ± 0.03) than in those accessible (0.51 ± 0.20). In 2014, the year with the largest number of active nests ($n = 31$) and the most intensive monitoring, all recorded breeding failure ($n = 4$) occurred in nests accessible to foxes, and signs of predation (fox scat and urine smell) were detected in 3 cases. Finally, none of the environmental variables explained variability in brood size at 14 days in nests that hatched successfully (Table 2 and Appendix Table 7).

Patterns of Nest and Territory Reuse

The 87 nesting structures that we found were distributed within a total of 53 territories. There were, on average, 1.6 nesting structures per territory (range: 1–4), with 31 territories (58%) comprising only 1 structure. Among the total number of nesting structures monitored, 21 (24%) were reused, 49 (56%) were used only

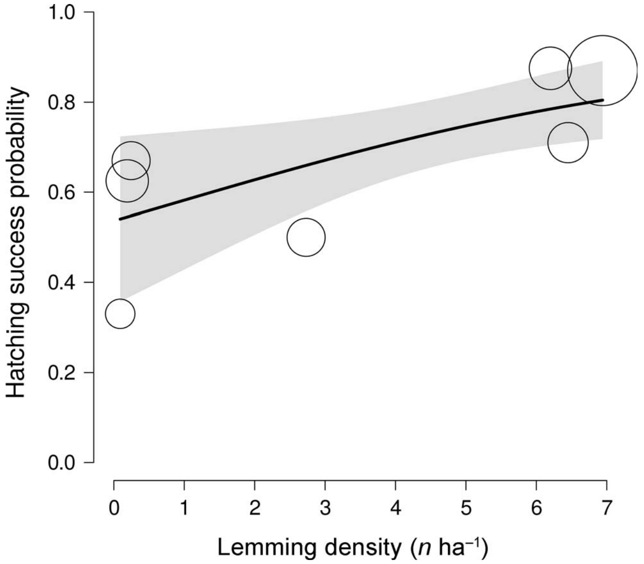

FIGURE 3. Probability of hatching success in Rough-legged Hawks on Bylot Island, Nunavut, Canada, 2007–2015, based on the most parsimonious models (Table 2 and Appendix Table 5) in relation to lemming density. The gray band represents the ±95% CI of the regression. Circles illustrate observed data, and circle size is proportional to the number of observations ($n = 68$). The mean response after controlling for other model effects is shown.

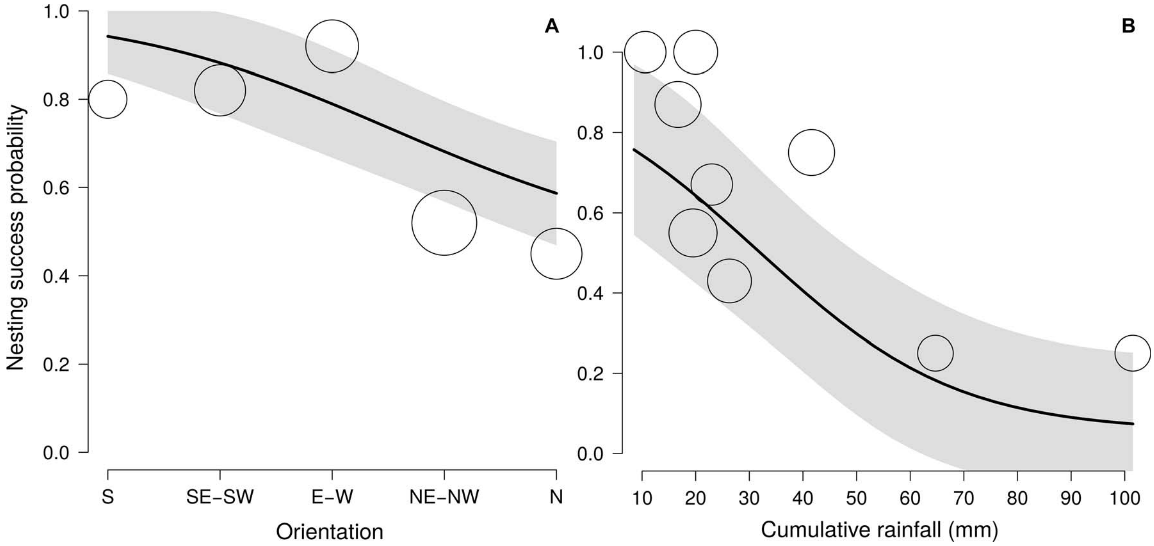

FIGURE 4. Probability of nesting success in Rough-legged Hawks on Bylot Island, Nunavut, Canada, 2007–2015, based on the most parsimonious models (Table 2 and Appendix Table 6) in relation to (**A**) nest orientation and (**B**) cumulative rainfall. The gray band represents ±95% CI of the regression. Circles illustrate observed data, and circle size is proportional to the number of observations ($n = 59$). The mean response after controlling for other model effects is shown.

once, and 17 (20%) were never used (i.e. nests that were mostly built before the study period but were never used). For nesting structures with a known history, 63% of the breeding attempts ($n = 83$) took place in preexisting structures and 80% in previously occupied territories. Finally, among the 66 breeding attempts monitored in previously occupied territories, nest reuse was more frequent than nest building (79% vs. 21%, respectively).

Hawks that bred in previously occupied territories had similar clutch size (new nest: $\beta = -0.02$, 95% CI: –0.41 to 0.36; preexisting nest: $\beta = 0.02$, 95% CI: –0.29 to 0.33), brood size (new nest: $\beta = 0.15$, 95% CI: –0.46 to 0.79; preexisting nest: $\beta = 0.38$, 95% CI: –0.13 to 0.96), and hatching dates (new nest: $\beta = -0.27$, 95% CI: –5.76 to 5.23; preexisting nest; $\beta = -2.60$, 95% CI: –7.36 to 2.17) compared to those that bred in newly occupied territories (Table 3). Hatching success and nesting success were both higher in previously occupied territories (all new nests were successful; preexisting nest: $\beta = 1.61$, 95% CI: 0.05–3.82 and $\beta = 2.09$, 95% CI: 0.33–4.24, respectively) than in newly occupied territories (Table 3).

DISCUSSION

Our results highlight the importance of several environmental factors affecting nest-use probability and reproductive output in the study species, as summarized in Figure 5. Lemming density had a strong overarching effect on Rough-legged Hawk breeding output. Accessibility to foxes, presence of an overhang, orientation of the nest, and summer rainfall also affected breeding individuals to some extent. Distance to the nearest breeding conspecific was another important factor influencing nest-use probability in our study area, which was expected because the Rough-legged Hawk is a territorial species, and a given breeding pair can have more than one nesting structure within their territory (Mindell 1983, Bechard and Swem 2002). Food availability (Korpimäki 1992, Terraube et al. 2012, Therrien et al. 2014), intraspecific nest spacing (Krüger 2004,

TABLE 3. Summary of the reproductive output of Rough-legged Hawks on Bylot Island, Nunavut, Canada, 2007–2015, according to nest and territory reuse patterns. Hatching dates are in day of the year (1 = January 1).

	Clutch size [a]	Hatching success [b]	Nesting success [b]	Brood size [a]	Hatching date [a]
New nest in a newly occupied territory	4.5 ± 0.3 (15)	0.54 (13)	0.36 (11)	3.2 ± 1.0 (5)	193 ± 3 (6)
New nest in a previously occupied territory	4.4 ± 0.3 (11)	1.00 (8)	1.00 (7)	3.7 ± 0.5 (7)	190 ± 1 (8)
Preexisting nest	4.6 ± 0.2 (28)	0.74 (31)	0.68 (28)	4.4 ± 0.3 (18)	188 ± 1 (20)

[a] Mean ± SE (*n*).
[b] Proportion of successful nests (*n*).

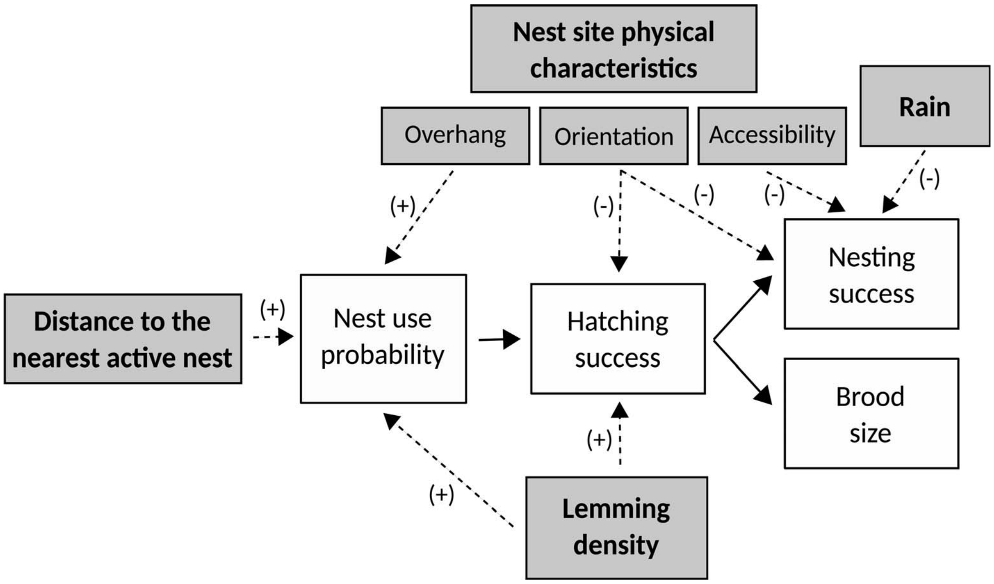

FIGURE 5. Environmental variables (gray boxes) affecting different components of Rough-legged Hawk reproduction (white boxes) on Bylot Island, Nunavut, Canada, 2007–2015. Arrows show links with various breeding parameters. Dashed arrows represent significant relationships along with their sign (+ or –) in parentheses.

Brambilla et al. 2006), weather (Bionda and Brambilla 2012, Lehikoinen et al. 2013, Anctil et al. 2014), and nest-site physical characteristics (Negro and Hiraldo 1993, Siverio et al. 2014) have previously been related to nest use and reproductive output in raptors.

In our study, Rough-legged Hawks showed a strong numerical response to the fluctuations in density of their main prey, lemmings, resulting in large variations in the number of active nests across years, as previously shown (Potapov 1997, Wiklund et al. 1998, Hellström et al. 2014, Therrien et al. 2014, Terraube et al. 2015). In the most extreme year (2013), with lemmings nearly absent, not a single Rough-legged Hawk nested in the study area. By contrast, the highest number of nests was found in the following year (2014), when lemmings bounced back. When the abundance of lemmings was low, not only did fewer Rough-legged Hawks breed, but those that did had low reproductive success, even though these were potentially the most experienced individuals (Newton and Rothery 2002, Blas et al. 2009). This shows the strong influence of lemmings in our study system. In some regions, Rough-legged Hawks can apparently breed successfully and in relatively large numbers even when small mammals are scarce, by relying on alternative prey, especially goslings, ptarmigans, and hares (Pokrovsky et al. 2014, 2015). Thus, the strong numerical response of Rough-legged Hawks on Bylot Island suggests that alternative prey are not sufficiently abundant there to support a high density of nesting Rough-legged Hawks when lemmings are scarce.

Some physical characteristics of nest sites were important predictors of nest-use probability and reproductive success. Surprisingly, only one physical variable (presence of an overhang) had a strong effect on nest use, an effect also reported in other Arctic cliff-nesting species (Poole and Bromley 1988b). The presence of an overhang is likely easy to detect visually by Rough-legged Hawks when settling for breeding and may be a simple cue to use to identify high-quality nests. Overhangs may protect nests from geomorphological hazards like rockfalls (Bechard and Swem 2002, Beardsell 2016). Overhangs may also improve nest microclimatic conditions, for instance by partially shielding the nest from strong wind or by protecting it from rainfall, which may be especially important in the cold conditions that prevail at high latitudes. Experimental studies in Arctic-breeding species have shown that nest shelters attenuate extremes in hot and cold temperatures experienced by nesting female Common Eiders (*Somateria mollissima*; Fast et al. 2007) and increase nesting success by protecting nestlings from exposure to heavy rain in Peregrine Falcons (Anctil et al. 2014). The strong negative effect of rainfall on nesting success in our study supports recent findings that nestling mortality could be induced by heavy rain in Rough-legged Hawks (Pokrovsky et al. 2012). Rainfall is increasingly regarded as a key factor influencing breeding output in several Arctic raptors (Potapov 1997, Lehikoinen et al. 2013, Anctil et al. 2014).

Nests oriented toward the north tended to be used less often, and these nests had a lower reproductive success than those oriented toward other directions, a pattern also reported in other cliff-nesting raptors (Poole and Bromley

1988a, Donázar et al. 1989, Ontiveros and Pleguezuelos 2003). A northern exposure may worsen the thermal environment of chicks in at least 2 ways. First, by decreasing exposure to the sun, it can greatly reduce the operational temperature perceived by the chicks and significantly increase their thermoregulatory costs under cold Arctic temperatures, as shown in precocial birds (Fortin et al. 2000). Second, a north-facing slope can be more exposed to cold northerly winds or storms (White and Cade 1971). Our results confirm that abiotic factors can be important determinants of breeding output in Arctic-breeding raptors. However, in years of good weather, the effects of nest-site physical characteristics, especially those affecting the microclimatic conditions of the nest, could be marginal.

The use of steep slopes by nesting raptors is likely a strategy to reduce nest predation by mammalian predators (Newton 1979). Nests accessible to mammals were less successful than inaccessible ones in Ospreys (*Pandion haliaetus*; Ames and Mersereau 1964), Prairie Falcons (*Falco mexicanus*; Ogden and Hornocker 1977), Merlins (*Falco columbarius*; Newton et al. 1978), and Ferruginous Hawks (*Buteo regalis*; Roth and Marzluff 1989). In Bald Eagles (*Haliaeetus leucocephalus*) breeding in the Aleutians, the use of accessible nests occurred only on islands lacking Arctic foxes (Sherrod et al. 1976). Swem (1996) also showed that Rough-legged Hawk nests along the Colville River in Alaska were more likely to fail when accessible to mammalian predators, which is in accordance with our results. These observations suggest that availability of high-quality nest sites inaccessible to foxes could be a limiting factor in some Arctic areas, including on Bylot Island, especially at high lemming density when a large number of pairs breed.

The effect of nest-site physical characteristics on raptor reproductive success may be modulated by environmental conditions such as prey availability. For instance, large annual fluctuations in lemming density, the preferred prey of Arctic foxes, can result in variations in annual predation pressure by foxes on alternative prey such as ground-nesting birds (Bêty et al. 2002, McKinnon et al. 2014, Gauthier et al. 2015). Hence, Rough-legged Hawk eggs or chicks in nests accessible to foxes could be exposed to higher predation risk when the abundance of lemmings is low. Therefore, the effect of lemming density on Rough-legged Hawk breeding success may partly result from top-down processes (intraguild predation) and not only through bottom-up effects (i.e. reduced food availability to breeding Rough-legged Hawks), as shown for Glaucous Gulls (*Larus hyperboreus*) on Bylot Island (Gauthier et al. 2015).

Repeated use of preexisting nesting structures suggests that such structures can be an important cue for territorial settlement and an important resource for raptors (Jiménez-Franco et al. 2014b). This result also suggests strong site fidelity of individuals, as previously reported in other raptors (Forero et al. 1999, Catlin et al. 2005, Jiménez-Franco et al. 2013), although this hypothesis could not be confirmed in our study because of the absence of marked birds. However, unlike other cliff-nesting raptors such as the Golden Eagle, whose nesting territories can include an average of 7 nests (Kochert and Steenhof 2012), Rough-legged Hawk territories had, on average, <2 nests, a majority of which contained a single nest. Factors contributing to this relatively low number of nests per territory may include a reduced life span of Rough-legged Hawks compared to other raptor species, the low availability of sites suitable for nest building, or shorter nest persistence, perhaps due to meteorological or geomorphological perturbations increasing slope instability in the Arctic (Beardsell 2016).

Birds that occupied a new territory necessarily had to build a new nest, a significant investment of time and energy, especially in the Arctic tundra, where nesting material is scarce because of the rarity of erect shrubs. Birds that built a new nest in a previously occupied territory also had to incur these costs. By contrast, reusing a preexisting nesting structure could result in significant time or energy saving that could be reallocated to reproduction, thereby allowing a larger clutch size (Vergara et al. 2010) or earlier breeding (Cavitt et al. 1999). However, we found no evidence of such short-term benefits, given that Rough-legged Hawks that built new nests had similar hatching date and clutch size compared to birds that used preexisting nesting structures. Nonetheless, it's possible that birds that don't incur the cost of building a new nest gain other benefits, such as improved body condition during chick rearing. Hatching and nesting success were, however, reduced in nests built in newly occupied territories, compared to nests built or located in previously occupied territories. This may result from an age effect if a high proportion of young and inexperienced birds, which typically have a low success rate (Nielsen and Drachmann 2003, Blas et al. 2009), occupy these new territories, or from intrinsic differences in territory quality (Korpimäki 1988a, 1988b, Newton 1989, Penteriani et al. 2003). We cannot exclude the possibility that some of the nests that were considered new may have been missed during searches of the same area in previous years, though we believe that this is unlikely, considering the strong territorial behavior of Rough-legged Hawks (Bechard and Swem 2002). However, if this occurred, it means that some nests considered new were actually preexisting, which would render our comparison between new and preexisting nests conservative.

Our results indicate that biotic factors (food availability, distance to breeding conspecifics) and abiotic factors (rainfall, nest-site physical characteristics) influence nest-use probability and reproductive success of Rough-legged Hawks in the Canadian Arctic, and that physical characteristics offering protection from weather and predators provide the highest-quality nesting sites for this cliff-nesting raptor.

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Author contributions: A.B., G.G., J.F.T., and J.B. conceived the study and collected the data. A.B. analyzed the data. A.B. wrote the paper with the assistance of G.G., J.F.T., and J.B.

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APPENDIX

APPENDIX TABLE 4. Variables, number of parameters (*K*), difference in $\mathrm{AIC_c}$ value between the current model and the preferred model ($\Delta\mathrm{AIC_c}$), Akaike weight (w_i), log-likelihood (LL), and marginal R^2 of the candidate models explaining Rough-legged Hawk nest use ($n = 185$) on Bylot Island, Nunavut, Canada, 2007–2015. Nest ID was included as a random effect in all models. See Table 1 for a description of each variable.

Variables	K	$\Delta\mathrm{AIC_c}$	w_i	LL	R^2
Distance, lemming, overhang, orientation	6	0.00	0.55	−84.90	0.54
Distance, lemming, accessibility, overhang, orientation	7	0.63	0.40	−84.13	0.55
Distance, lemming, accessibility, overhang, orientation, exposure, altitude	9	4.76	0.05	−84.00	0.55
Distance, lemming	4	12.41	0.00	−93.23	0.44
Lemming, overhang, orientation	5	32.31	0.00	−102.12	0.32
Lemming	3	33.09	0.00	−104.62	0.28
Lemming, accessibility, overhang, orientation	6	34.35	0.00	−102.07	0.32
Distance, overhang, orientation	5	35.70	0.00	−103.82	0.32
Lemming, accessibility, overhang, orientation, exposure, altitude	8	36.22	0.00	−100.83	0.34
Distance, accessibility, overhang, orientation, exposure, altitude	8	41.40	0.00	−103.43	0.33
Distance	3	47.87	0.00	−112.01	0.23
Overhang	3	76.51	0.00	−126.32	0.02
Null	2	77.98	0.00	−128.10	0.00

APPENDIX TABLE 5. Variables, number of parameters (*K*), difference in $\mathrm{AIC_c}$ value between the current model and the preferred model ($\Delta\mathrm{AIC_c}$), Akaike weight (w_i), log-likelihood (LL), and marginal R^2 of the candidate models explaining Rough-legged Hawk hatching success ($n = 68$) on Bylot Island, Nunavut, Canada, 2007–2015. Nest ID was included as a random effect in all models. See Table 1 for a description of each variable.

Variables	K	$\Delta\mathrm{AIC_c}$	w_i	LL	R^2
Lemming, accessibility, orientation	5	0.00	0.37	−28.49	0.42
Lemming, accessibility, orientation, rain-1	6	1.15	0.21	−27.86	0.48
Accessibility, orientation, rain-1	5	1.43	0.18	−29.20	0.44
Accessibility, orientation	4	4.36	0.04	−31.83	0.31
Lemming, accessibility, overhang, orientation, altitude	7	4.38	0.04	−28.22	0.43
Lemming, accessibility	4	4.48	0.04	−31.90	0.35
Lemming, accessibility, overhang, orientation, exposure	7	4.75	0.03	−28.41	0.42
Accessibility, overhang, orientation	5	5.84	0.02	−31.41	0.34
Orientation	3	6.92	0.01	−34.24	0.15
Accessibility, rain-1	4	7.21	0.01	−33.26	0.34
Accessibility, overhang, orientation, altitude	6	8.01	0.01	−31.29	0.34
Overhang, orientation, rain-1	5	8.32	0.01	−32.65	0.21
Accessibility, orientation, exposure, altitude	6	8.48	0.01	−31.52	0.33
Accessibility	3	8.95	0.00	−35.26	0.21
Overhang, orientation	4	8.99	0.00	−34.15	0.15
Lemming	3	9.85	0.00	−35.71	0.11
Null	2	13.29	0.00	−38.52	0.00

APPENDIX TABLE 6. Variables, number of parameters (K), difference in $\mathrm{AIC_c}$ value between the current model and the preferred model ($\Delta\mathrm{AIC_c}$), Akaike weight (w_i), log-likelihood (LL), and marginal R^2 of the candidate models explaining Rough-legged Hawk nesting success ($n = 59$) on Bylot Island, Nunavut, Canada, 2007–2015. Nest ID was included as a random effect in all models. See Table 1 for a description of each variable.

Variables	K	$\Delta\mathrm{AIC_c}$	w_i	LL	R^2
Lemming, accessibility, orientation, rain-3	6	0.00	0.44	−22.21	0.77
Lemming, accessibility, overhang, orientation, rain-3	7	1.57	0.20	−21.71	0.79
Lemming, accessibility, orientation, exposure, rain-3	7	2.02	0.16	−21.94	0.78
Lemming, accessibility, orientation	5	3.61	0.07	−25.26	0.57
Lemming, accessibility, overhang, orientation, altitude, rain-3	8	3.97	0.06	−21.57	0.80
Lemming, accessibility, orientation, exposure, altitude, rain-3	8	4.53	0.05	−21.85	0.78
Lemming, accessibility	4	6.92	0.01	−28.11	0.46
Lemming, orientation, rain-3	5	9.92	0.00	−28.42	0.41
Orientation, rain-3	4	10.26	0.00	−29.78	0.35
Lemming, overhang, orientation, rain-3	6	10.55	0.00	−27.49	0.46
Accessibility, orientation	4	11.16	0.00	−30.23	0.38
Lemming	3	14.72	0.00	−33.16	0.16
Rain-3	3	15.17	0.00	−33.39	0.16
Lemming, rain-3	4	15.36	0.00	−32.33	0.20
Null	2	20.12	0.00	−36.97	0.00

APPENDIX TABLE 7. Variables, number of parameters (K), difference in $\mathrm{AIC_c}$ value between the current model and the preferred model ($\Delta\mathrm{AIC_c}$), Akaike weight (w_i), log-likelihood (LL), and marginal R^2 of the candidate models explaining Rough-legged Hawk brood size ($n = 38$) on Bylot Island, Nunavut, Canada, 2007–2015. Nest ID was included as a random effect in all models. See Table 1 for a description of each variable.

Variables	K	$\Delta\mathrm{AIC_c}$	w_i	LL	R^2
Null	2	0.00	0.40	−72.36	0.00
Lemming	3	1.53	0.19	−71.94	0.03
Lemming, accessibility	4	3.16	0.08	−71.50	0.05
Accessibility, orientation	4	3.38	0.07	−71.61	0.04
Overhang, orientation	4	3.65	0.06	−71.75	0.03
Orientation, rain-2	4	3.70	0.06	−71.77	0.03
Lemming, rain-2	4	3.97	0.06	−71.90	0.03
Lemming, accessibility, orientation	5	4.96	0.03	−71.07	0.07
Lemming, accessibility, orientation, rain-2	5	5.74	0.02	−71.46	0.05
Lemming, orientation, rain-2	6	7.77	0.01	−71.06	0.07
Lemming, overhang, orientation, rain-2	6	7.96	0.01	−71.15	0.07
Lemming, accessibility, overhang, orientation, rain-2	7	10.71	0.00	−71.02	0.08