

ARTICLE

Vulnerability to geomorphological hazards of an Arctic cliff-nesting raptor, the rough-legged hawk¹

Andréanne Beardsell, Gilles Gauthier, Daniel Fortier, Jean-François Therrien, and Joël Bêty

Abstract: Increase in temperature and precipitation associated with climate change may enhance the risk of destruction by geomorphological processes of nests or dens used by Arctic wildlife. We assessed nest vulnerability to mass movements and identified environmental factors associated with the persistence of nesting structures of rough-legged hawks (*Buteo lagopus*), a species that typically nests on steep slopes or cliffs. The study was conducted on Bylot Island (Nunavut) where 82 permanent hawk nesting structures, built mainly on sedimentary rocks, were monitored from 2007 to 2015. More than a quarter of known nests were destroyed during the course of the study and among those still intact, more than half were associated with a moderate to high risk of being destroyed. Nest survival analysis suggested a relatively short persistence of rough-legged hawk nesting structures on Bylot Island compared to other Arctic cliff-nesting species. Nest destruction probability increased for nests built on unconsolidated sediments, with heavy rainfall and temperature during the summer. The anticipated increase in precipitation and temperature due to climate change is likely to augment the exposure of hawk nests to mass movements, which could ultimately reduce the availability of suitable sites for the reproduction of this Arctic-nesting raptor.

Key words: nest destruction, mass movements, nest persistence, rainfall, Buteo lagopus.

Résumé: La hausse des températures et des précipitations due aux changements climatiques peuvent augmenter le risque de destruction par des processus géomorphologiques des nids ou tanières d'espèces fauniques arctique. Nous avons évalué la vulnérabilité des nids aux mouvements de masse et identifié les facteurs environnementaux associés à la persistance des nids de buse pattue (Buteo lagopus), une espèce qui niche typiquement sur les versants escarpés et les falaises. L'étude s'est déroulée à l'île Bylot (Nunavut) où 82 nids permanents, construits principalement sur des roches sédimentaires, ont été suivis entre 2007 et 2015. Plus du quart des nids connus ont été détruits pendant l'étude et parmi ceux encore intacts, la majorité étaient à risque modéré et élevé de destruction. Une analyse de survie a suggéré que la persistance des nids de buses est relativement courte comparativement à d'autres espèces nichant sur les falaises en Arctique. La probabilité de destruction était élevée pour les nids construits sur des sédiments non consolidés et positivement associée aux fortes précipitations et à la température. La hausse anticipée des précipitations et des températures due aux changements climatiques est susceptible

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d'augmenter la vulnérabilité des nids aux mouvements de masse ce qui pourrait ultimement réduire la disponibilité de sites appropriés pour la reproduction de ce rapace.

Mots-clés: destruction des nids, mouvements de masse, persistance des nids, précipitations, Buteo lagopus.

Introduction

Future weather patterns are predicted to be strongly modified in the light of climate change and this has the potential to affect natural landscapes (IPCC 2013). A better understanding of the mechanisms by which weather patterns can affect landscapes is essential for assessing the vulnerability of wildlife populations to such changes. Indeed, although weather can directly impact species by affecting their breeding success (e.g., Anctil et al. 2014; Fisher et al. 2015), its impacts can also be indirect through habitat modifications (e.g., McCarty 2001; Laidre et al. 2008). In the Arctic, the rapid pace of warming and the deepening of the active layer have strong potential to cause perturbations to the geomorphology of the tundra and be a source of hazards due to permafrost degradation (Harris et al. 2001; Harris 2005; Rowland et al. 2010; AMAP 2012).

Mass movements are especially prevalent in the Arctic (French 2007). A deepening of the active layer or increase in summer temperature and rainfall events as a result of ongoing climate warming is likely to augment the frequency and amplitude of mass movements such as active layer detachment failures, retrogressive thaw slumps, or rockfalls (Lewkowicz and Harris 2005; Lantuit and Pollard 2008; French and Slaymaker 2012). These processes can result in the destruction or alteration of critical sites for wildlife species such as permanent structures used for reproduction (i.e., dens or nests: Potapov 1997; Gallant et al. 2014). In birds, long-lasting structures are important for reproduction, especially in raptor species (e.g., Sergio et al. 2011; Millsap et al. 2015). Raptor densities can be limited by the availability of suitable nesting habitat for building such structures (Newton 1979; Wightman and Fuller 2005; Jiménez-Franco et al. 2014a). Thus, it is important to better understand how local geomorphology and weather variables influence their persistence. Physical characteristics such as slope aspect, material type, vegetation cover, and ground ice content are the main factors related to the occurrence of mass movements (McRoberts and Morgenstern 1974; Rapp 1986; French 2007) and hence, these factors could affect the persistence of nesting structure.

In this study, we assessed nest vulnerability to mass movements and identified environmental factors associated with the persistence of nesting structures in Arctic-nesting rough-legged hawks (Buteo lagopus), a species that typically nests on cliff edges or hoodoos or along steep hillsides (Bechard and Swem 2002; Beardsell et al. 2016). Nesting structures used by rough-legged hawks are exposed to mass movements and nest destruction has been previously reported as a cause of nesting failure in this species (Swem 1996; Potapov 1997). Our specific objectives were to (1) determine the main causes of nest destruction, (2) assess whether geomorphological characteristics and weather variables influence nest persistence, and (3) examine whether vulnerability to mass movements affects nest use and reproductive success of rough-legged hawks in the Canadian High Arctic. We expected that nest persistence would be related to local geomorphological characteristics, such as material type, slope gradient, and slope vegetation cover, because these characteristics are related to slope stability at high latitudes (French 2007; Gruber and Haeberli 2007). We predicted that nesting structures located on unconsolidated material, steep, and unvegetated slopes should be more vulnerable to mass movements. The frequency and magnitude of mass movements are often related to air temperatures and rainfall events (Lewkowicz 1992; Can et al. 2005; Gruber and Haeberli 2007; Lantuit and Pollard 2008; Allen et al. 2009). We therefore also hypothesized that these weather variables should be related to nest persistence. We predicted that high precipitation and air temperatures should increase mass movements and negatively affect nest persistence through their influence on slope stability.

Finally, we hypothesized that nest use probability and reproductive success should be related to nest vulnerability to mass movements. We expected that less vulnerable nests should be more likely to be used and should be associated with a higher reproductive success.

Methods

Study area

The study area, covering about 500 km² of tundra, is located on the southern plain of Bylot Island (Nunavut, Canada; 73°N, 80°W). This region is characterized by rolling hills and low-elevation plateaus (ranging from 100 to 580 m above sea level) crossed by numerous streams and rivers associated with frequent outcrops of exposed bedrock (Fig. 1). The bedrock of the area consists of Cretaceous and Tertiary sedimentary rock (sandstone and shale) of the Lancaster formation (Jackson and Sangster 1987; Klassen 1993). Exposed bedrock eroded by water and wind along streams, ravines, and mountain slopes provides suitable breeding sites for a cliff-nesting species like the rough-legged hawk. Additional details on plant communities and general landscape can be found in Gauthier et al. (2011a).

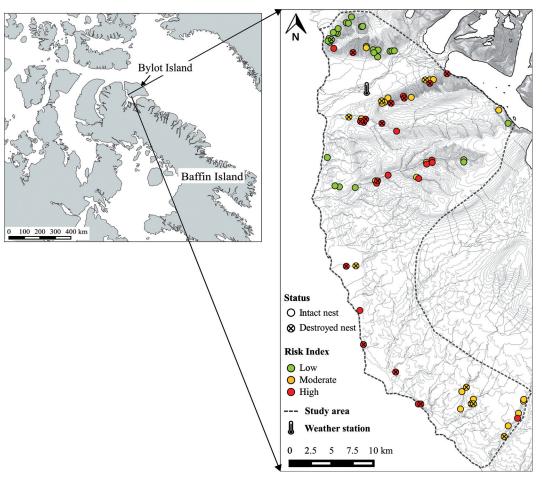
Nest searching and monitoring

From 2007 to 2015, rough-legged hawk nests were found by conducting systematic searches on foot in all areas considered suitable for nesting hawks, i.e., along cliffs, streams, ravines, or large rocky outcrops. Nests (diameter range ~60–90 cm) are made of a relatively large amount of branches and are generally conspicuous. Nests were found using 8–10× binoculars and were often located following alarm calls made by breeding hawks when the observer entered a nesting territory. We positioned each nest using a global positioning system receiver and several photographs of the nest and surrounding environment were taken to facilitate recognition of the exact location in subsequent years, in particular if a nest had collapsed or disappeared (see Beardsell et al. (2016) for details).

The status of nests was categorized as being intact or destroyed upon each visit. We considered a nest intact when it was used by a bird or unused but unaltered since the last visit. We considered it destroyed when the nest had fallen or had been dislocated due to the collapse of material supporting it, when it had been fully or partly (>50%) buried by falling material, or when it had totally disappeared. Using photographs and field observations, we classified the most likely cause of nest destruction into one of three categories: rockfall, slope failure, and tipping over. Rockfall is a rapid mass movement of rock debris, due to either the free fall of blocks breaking away from a cliff or rock wall or by blocks rolling down a steep slope or cliff (Rapp 1986). Slope failure involves the rapid displacement of unconsolidated and loose material on a steep slope. When the local geomorphological environment remained unchanged before and after the disappearance of a nest, the nest was classified as having tipped over at its site.

Every year from late June to mid-July, we searched for new nests and visited all known nests to determine if they were still present and being used. We considered a nest used when a pair of hawks showed clear signs of territorial behavior (e.g., alarms calls, approaches) or when direct evidence of breeding was found (e.g., an incubating adult at the nest, the presence of eggs or young). We visited occupied nests at least twice between early July and mid-August to determine nesting success and brood size. Even though nesting success of raptors is often estimated at 80% fledging age (Steenhof and Newton 2007), we defined it as the probability of producing at least one young of 14 days of age because this is a good proxy of nesting success near fledging in our study species (Beardsell et al. 2016). Brood size was defined as the number of young found in a nest between the 14th and the 21th day of nestling development, excluding nests where no egg hatched. We estimated age of nestlings by the size of young and stage of feather development using

Fig. 1. Location of the study site on the southern plain of Bylot Island, Nunavut, Canada. The study area is shown on the right, including location of the weather station and location, status (i.e., destroyed during the study period or intact at the end), and risk index (probability of being destroyed according to our analysis; low: ≤0.25, moderate: 0.26–0.49, high: \geq 0.5) of all rough-legged hawk nesting structures (n = 82) monitored between 2007 and 2015. Spacing between contour lines is 20 m.



a photographic guide developed for red-tailed hawks (*Buteo jamaicensis*) (Moritsch 1983), a similar-sized species for which young fledge at about the same age as rough-legged hawks (Bechard and Swem 2002; Preston and Beane 2009).

Geomorphological characteristics and weather variables

Because geomorphological characteristics can be different downslope and upslope of a nest, we measured three geomorphological characteristics separately below and above each nest. We characterized each nesting structure according to material type, slope (degree of inclination), and vegetation cover. Material type was classified as follows: consolidated and weakly altered rock, consolidated and altered rock, poorly consolidated rock, and unconsolidated sediments (Fig. A1) (Appendix) based on field geological observations and surficial geology maps (Miall et al. 1980; Jackson and Sangster 1987; Klassen 1993). In our study area, consolidated and weakly altered rock corresponds to sedimentary rocks (mainly sandstone) with few apparent cracks and joints, whereas consolidated and altered rock corresponds to rocks showing numerous cracks, open joints, and clear signs of rock weathering. Poorly consolidated refers to weakly cemented sedimentary rocks, essentially

shale, that underwent a weak diagenesis and that can be destroyed by hand. Unconsolidated material refers mainly to surficial deposits, essentially poorly sorted coarse-grained sediments such as gravel and sand and occasionally silt. Vegetation cover on the slope was visually classified as absent (<5%) or present (5%–100%). Finally, the degree of inclination of the local slope was measured using a clinometer (four measures were taken and the average value was used for analysis; 0° = flat terrain). Daily rainfall (mm) was measured manually with a rain gauge from June to August. An automated weather station located at

20 m above sea level recorded air temperature at 2 m all year round on an hourly basis

Data analysis

(Fig. 1) (see CEN (2014) for details).

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We used Kaplan–Meier estimates to quantify survival rates of nests (Kaplan and Meier 1958). This method allows the inclusion of right-censored data, i.e., the inclusion of nesting structures whose exact time of destruction was unknown if they persisted until the end of the study. Nest persistence was calculated in relation to the age of a nest, i.e., from the year a nest was first found until the year it was destroyed or until the last visit. This may not always represent the true age of a nest because some nests were already present at the start of the study. When the exact date of nest loss was unknown, the median date between two visits was used.

We used logistic regression to model nest destruction probability in relation to geomorphological characteristics. This method has been previously used for assessing susceptibility to geomorphological hazards such as landslides (e.g., Lee 2005; Akgun 2012). We built a set of candidate models describing multiple working hypotheses. Models were ranked based on second-order Akaike's information criterion (AICc). To assess the amount of variation explained by our models, we report the R^2 calculated with the method proposed by Nakagawa and Schielzeth (2013). The dependent variable was whether a nest was intact (0) or destroyed (1) at the end of the study and separate analyses were done using geomorphological variables recorded above and below the nest. When no single model had a strong support (i.e., Akaike weights <0.90), we applied multimodel inference to obtain modelaveraged estimates and unconditional 95% confidence intervals for variables retained in the most parsimonious models (i.e., $\Delta AICc < 4$) (Burnham and Anderson 2002). From these estimates, we obtained a predicted probability of nest destruction according to geomorphological characteristics. We defined a probability of occurrence of a mass movement (hereafter referred to as "risk index") for each nest, which was simply the highest value between the predicted probability of nest destruction from slope characteristics below and above the nest.

We used mixed logistic regression to model nest destruction probability according to summer rainfall and temperature. Because the same nests were visited repeatedly over the years, nest ID was modeled as a random effect. Summer was defined from 8 June to 17 August (duration of our presence at the site). Although summer precipitation is generally low in the Arctic, it can be nevertheless an important triggering factor of mass movements by increasing pore-water pressure and tensile stress in unconsolidated material or by melting ice in surficial cracks and rock joints, which can reduce the tensile strength of rock material (Murton et al. 2006; Gruber and Haeberli 2007; Vedie et al. 2011). At our study site, the average daily rainfall (including only days with >0 mm of rain) is 3.0 mm (SD = 4.1 mm, maximum daily rainfall 31 mm, n = 213 rainy days over the period 2007–2015). Because we expected that episodes of high rainfall should be more important than average values (Rapp 1986; Rebetez et al. 1997), we used the number of days with heavy rain (defined as \geq 7 mm per day, i.e., mean + 1 SD, which represents 10% of all rainy events) between consecutive nest visits during the summer (or during a previous summer). To evaluate the

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sensitivity of our conclusion to this threshold value, we repeated the analyses using lower values, i.e., number of days with ≥ 3 or ≥ 5 mm of rain. For temperature, we used the cumulative thawing degree-days, defined as the sum of the daily mean temperature above 0 °C between consecutive nest visits during the summer (or during a previous summer). Cumulative thawing degree-days was used because it is closely related to active-layer thickness, which is a key parameter for the occurrence of mass movements (French 2007). We used separate models because summer rainfall and temperature were highly correlated (r = -0.9) and these variables were log-transformed to improve the distribution of the residuals.

We used generalized linear mixed-effects models with a binomial distribution to analyze nest use probability and nesting success in relation to the risk index, whereas we analyzed brood size with a Poisson distribution. As the rough-legged hawk is a territorial species, nests located <0.57 km from a occupied nest (the shortest distance ever recorded between two occupied nests on our study area) were excluded for investigating the effect of the risk index on nest use probability (Beardsell et al. 2016). Also, because not a single hawk nested in the study area in 2013 due to the near total absence of lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) that year (Beardsell et al. 2016), we excluded the year 2013 from the analysis. To account for variation in nest use probability and reproductive success over time and because the same nests were used repeatedly, year and nest ID were included as random effects in those models.

Relationships were considered statistically significant when the 95% confidence intervals of the slope excluded 0. All analyses were performed in the R Statistical Environment (R Core Team 2015). We used the package "survival" for survival analyses (Therneau 2015). We used the package "lme4" to estimate the parameters of all GLMMs with the Laplace approximation (Bates et al. 2015). We used the package "AICcmodavg" for model selection and multimodel inference (Mazerolle 2015).

Results

Causes of nest destruction

From summers 2007 to 2015, 28% of all known hawk nesting structures (23/82) were destroyed. Overall, 87% of all nest destructions were caused by slope failure (74%) (Fig. A2) and rockfalls (13%) (Fig. A2). Finally, three (13%) nest destruction events were likely caused directly by extreme weather conditions such as strong winds, since the nesting structures had tipped over and the geomorphological environment remained unchanged before and after the event.

Factors influencing nest persistence

Survival rate of nesting structures after 8 years of monitoring was estimated at 0.56 (Fig. 2a). Factors affecting the likelihood of nest destruction were very similar when considering either geomorphological characteristics below (Table 1) or above (Table A1) the nest. Material type was always included in the most parsimonious models explaining the likelihood of nest destruction. Nests built on unconsolidated sediments were the least persistent as their risk of loss was 12.6 times greater than those built on consolidated and weakly altered rock. Nests built on consolidated and altered or poorly consolidated rock were respectively 6.3 and 5.8 times more likely of being destroyed than nests built on consolidated and weakly altered rock (Fig. 3). The survival of nests built on consolidated and weakly altered rock was 0.77 after 8 years but only 0.29 for those built on unconsolidated sediments (Fig. 2b). The probability of nest destruction also tended to be lower when vegetation cover above the nest was present (Table A1).

We calculated the destruction risk of nests based on the model-averaged estimates of variables retained in the previous analysis (Tables 1 and A1). This allowed us to characterize

Fig. 2. Kaplan–Meier survival curves of all rough-legged hawk nesting structures (a) in relation to their age (\pm 95% CI) and (b) according to material type below the nest. Each tick mark represents the time a nest was censored (i.e., the last time that an undestroyed nest was visited). Sample size on Fig. 2a ranged from 78 at age 0 to 16 at 8 years. Initial sample size is shown for each category on Fig. 2b.

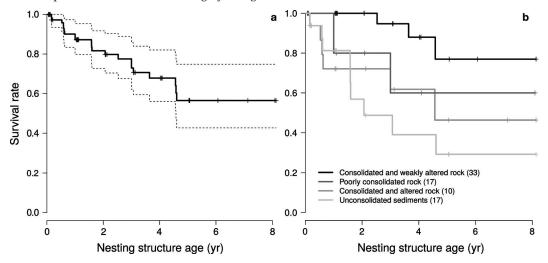


Table 1. (A) Model selection among candidate models explaining destruction of rough-legged hawk nests in relation to geomorphological characteristics of the slope below the nest (n = 82); number of parameters (k), ΔAICc values, AICc weights (w), log-likelihood values (LL), and R^2 are presented for each model. (b) Model-averaged parameter estimates (on a logit scale) from the most parsimonious models (ΔAICc < 4) and their 95% confidence intervals (CI).

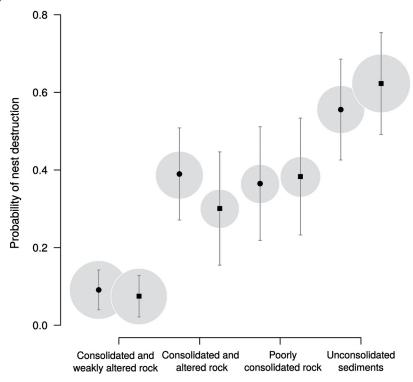
(A) Variables in the model ^a	k	ΔΑΙСc	wi	LL	R^2				
Material	4	0.00	0.37	-42.91	0.23				
Material, vegetation	5	0.43	0.30	-41.99	0.25				
Material, slope	5	2.22	0.12	-42.89	0.23				
Material, vegetation, slope	6	2.75	0.09	-41.99	0.25				
Slope	2	4.39	0.04	-47.29	0.07				
Material, vegetation, slope, vegetation × slope	7	5.12	0.03	-41.98	0.25				
Vegetation, slope	3	5.35	0.03	-46.69	0.09				
Null	1	6.85	0.01	-49.57	0.00				
(B) Parameters	β	95% CI							
Intercept	-2.34		-4.14, -0.54						
Slope	0.00		-0.03, 0.03						
Vegetation	-1.15		-2.92, 0.61						
Unconsolidated sediments	2.53		0.87, 4.18						
Poorly consolidated rock	1.75		-0.01, 3.51						
Consolidated and altered rock	1.85		0.31, 3.40						

[&]quot;Material: consolidated and weakly altered rock (reference level), consolidated and altered rock, poorly consolidated rock, and unconsolidated sediments. Vegetation: <5% (reference level) and 5%–100%. Slope: aspect (°).

all known nests as being at a low (i.e., probability \leq 0.25), moderate (0.26–0.49), or high (\geq 0.5) risk of destruction (Fig. 1). Among 58 nests still intact in summer 2015, 46% were at low, 33% at moderate, and 21% at high risk of being destroyed by mass movement processes.

The probability that a nest was destroyed was positively associated with the number of days with heavy rain (\geq 7 mm) recorded since the last visit (β = 3.33, 95% CI = 2.01, 5.11, n = 361, R^2 = 0.22) (Fig. 4a). Similar results were found with thresholds of 3 mm (β = 3.28,

Fig. 3. Probability of destruction of rough-legged hawk nesting structures in relation to material type below (circles) and above (squares) the nest based on model-averaged estimates (Tables 1 and A1) after controlling for vegetation (fixed at <5%, the most common occurrence in our study) and slope (mean). Error bars represent 95% confidence intervals and circle size is proportional to the number of observations (smallest circle, n = 10; largest circle, n = 33).



95% CI = 1.87, 5.87) and 5 mm (β = 3.04, 95% CI = 1.82, 4.74). The probability of nest destruction was also positively associated with cumulative thawing degree-days since the last visit (β = 3.00, 95% CI = 1.60, 5.97, n = 361, R^2 = 0.27) and increased sharply during very warm summers (Fig. 4*b*).

Nest vulnerability, nest use, and reproductive success

Nest use probability by hawks decreased with an increase in the risk of destruction by mass movement processes (β = -2.98, 95% CI = -6.12, -0.39, n = 162) (Fig. 5). Mass movements directly caused nest destruction and hence a partial or complete breeding failure in only two cases (one in 2008 and one in 2014). We documented in detail a nest destruction that occurred in summer 2014 due to a slope failure following high precipitation events, which resulted in the death of young. However, the vulnerability of the nest did not explain variation in hawk nesting success (β = -1.81, 95% CI = -5.19, 1.19, n = 59) and brood size (β = -0.23, 95% CI = -0.98, 0.52, n = 38).

Discussion

Although the geomorphology of Arctic landscape is considered particularly sensitive to climate warming, little is known about the mechanisms linking geomorphological processes to the reproduction of Arctic wildlife. Mass movements have been suspected to influence Arctic cliff-nesting species (Cade 1960; White and Cade 1971; Poole and Bromley 1988b). Studies in Russia and in the western Canadian Arctic reported the destruction of raptor

Fig. 4. Probability of destruction of rough-legged hawk nests in relation to (a) the number of days with heavy rain (\geq 7 mm) and (b) cumulative thawing degree-days since the last nest visit. Dashed lines are the 95% confidence interval of the regression. To illustrate observed values, each circle represents the proportion of destroyed nests (circle size is proportional to the number of observations: smallest circle, n = 4; largest circle, n = 184).

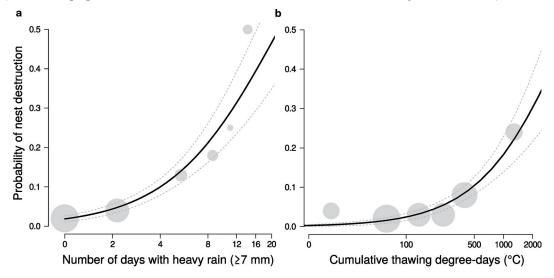
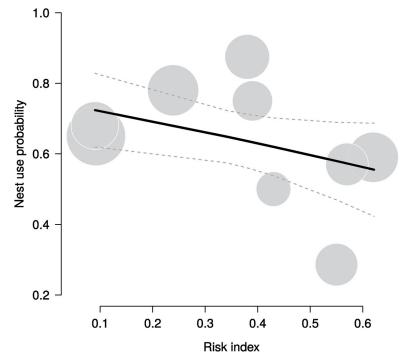


Fig. 5. Probability that a nest was used by a rough-legged hawk breeding pair in relation to its probability of destruction by a mass movement (risk index). Dashed lines are the 95% confidence interval of the regression. To illustrate observed values, each circle represents the proportion of used nest grouped by similar risk index (circle size is proportional to the number of observations: smallest circle, n = 8: largest circle, n = 34).



nests by such processes (White and Cade 1971; Swem 1996; Potapov 1997; Gauthier et al. 2011b), but the frequency of these events and the factors affecting the vulnerability of those nests to geomorphological hazards remained largely unknown. Our study showed that

mass movements were the main cause of destruction of rough-legged hawk nesting structures and hence strongly affected their lifespan on Bylot Island. A high proportion of nesting structures were destroyed or exposed to a moderate or high risk of being destroyed. In addition, we found a strong influence of material type and summer precipitation and temperature on the risk of nest destruction. Hawks tended to avoid breeding in nesting structures more vulnerable to mass movements, although such movements were rarely the direct cause of breeding failure. Overall, our study provides a new perspective by integrating ecology and geomorphology to better understand nest persistence of an Arctic top predator.

Our nest survival analysis suggests a shorter persistence of rough-legged hawk nesting structures on Bylot Island compared to other species such as forest raptors (median nest lifespan of 12 years) (Jiménez-Franco et al. 2014a) or gyrfalcons (*Falco rusticolus*), for which nests may remain for hundreds of years (Burnham et al. 2009). Permanent nesting structures are key resources for raptors (Jiménez-Franco et al. 2014b; Millsap et al. 2015) and the availability of alternative nests may be critical when a nest sustains damage close to the laying period, forcing a pair to change its nesting site (Newton 1979; Kochert and Steenhof 2012; Millsap et al. 2015). Destruction of a nest would likely have a greater impact in a territory containing only one nest than in a territory harbouring several nests (Kochert and Steenhof 2012). Unlike other cliff-nesting raptors such as golden eagles (*Aquila chrysaetos*), where most breeding territories have five or more nests (Kochert and Steenhof 2012), or bearded vultures (*Gypaetus barbatus*), where territories can have >10 nests (Margalida and García 1999), most (58%) (Beardsell et al. 2016) rough-legged hawk territories contained only one nesting structure on Bylot Island.

Compared to other Arctic cliff-nesting raptors and ravens, rough-legged hawks demonstrate more flexibility in their use of nesting sites and can build their nest in a wide range of habitat such as bluffs, steep hillside, and rocky outcrops (White and Cade 1971; Bechard and Swem 2002). In contrast, gyrfalcons and common ravens (*Corvus corax*) mainly use nesting sites sheltered by overhang providing protection from falling rock (White and Cade 1971; Poole and Bromley 1988a). Thus, the exposed nest placement characteristics of rough-legged hawks make them more susceptible to nest destruction by mass movement processes such as rockfalls compared to other Arctic cliff-nesting raptors.

Our results showed the strong influence of material type on the risk of nest destruction. Mass movements are especially frequent on slopes underlain by unconsolidated sediments (French 2007; Daanen et al. 2012), which can explain why nests built on such substrate had the highest probability of being destroyed. The bedrock of our study area is constituted of sedimentary rock (Jackson and Sangster 1987; Klassen 1993), which is more likely to contain ground ice and to be more susceptible to frost heave and shattering than crystalline rock, especially where slopes have a steep inclination (Hodgson and Nixon 1998; Dredge et al. 1999; Murton et al. 2006). Thus, the influence of material type on nest persistence may vary among sites in the Arctic depending on general lithology and types of surficial deposits underlying steep slopes used by rough-legged hawks. For example, hawk nests along the west coast of Hudson Bay are mainly found on crystalline rock (Laporte 1975; Court 1986), which is more stable than sedimentary rocks. In contrast, raptor nests on Herschel Island, which are mostly built on muddy or sandy cliffs, also suffer from a high loss rate (Gauthier et al. 2011b), likely due to coastal erosion and retrogressive thaw slump activity in this case (Lantuit and Pollard 2008). High loss rate (25%) was also reported along Colville River in Alaska where nests are built mainly on unconsolidated sediments (Swem 1996). There was also some indication in our study that destruction risk increased when vegetation cover was absent, presumably because vegetation helps in stabilizing the ground, both during precipitation events and as the slope's active layer thaws downward. A multisite analysis

would help understanding the effects of local lithology and geomorphology on variations in rough-legged hawk nest lifespan.

Mass movements such as slope failure and rockfalls are also known to be influenced by climatic factors (Gruber and Haeberli 2007; Daanen et al. 2012; French and Slaymaker 2012) and our results showed that heavy rain and very warm summers increased the risk of destruction of rough-legged hawk nesting structures. Heavy rain can trigger mass movements in several ways, for instance by reducing tensile strength due to the added weight of water in ground material and ground ice thawing (Church et al. 1979; Rapp 1986; Font et al. 2006). Also, physical properties of sedimentary rocks such as their high porosity and permeability make them especially sensitive to precipitation through weathering processes (French et al. 1986; Hodgson and Nixon 1998). Given the high thermal conductivity of rocks, warmer temperature will result in a deepening of the active layer on rock faces, which will melt ice in rock joints and increase the temperature of cleft ice deeper in the rock wall. This situation will reduce the tensile strength of the rock faces, which will likely increase block falls. Anticipated increases in summer precipitation and temperature in northern areas as a result of ongoing climate warming (IPCC 2013) are likely to intensify the frequency and magnitude of mass movements in the Arctic (Lewkowicz and Harris 2005; Lantuit and Pollard 2008; Daanen et al. 2012), which will expose hawk nesting structures to higher risks of destruction. The chilling effect of rainfall on young nestlings is known to be a key factor directly influencing reproductive success in Arctic raptors (Potapov 1997; Anctil et al. 2014; Beardsell et al. 2016). Our results show that rainfall can also indirectly affect their reproduction through habitat modifications.

We found that nest destruction by mass movements is a relatively minor source of breeding failure of rough-legged hawks in our study area. Potapov (1997) reported that 4% of breeding failure was due to nest destruction in Kolyma Lowlands (Northern Siberia), which further supports this conclusion. However, Swem (1996) found that 25% of breeding failure of rough-legged hawk in Alaska was related to mass movements, especially slope failure, a surprisingly high value. These differences may be related to variations in local geomorphology between sites. In our study, it is also possible that nest destruction was underestimated because most nests were monitored only until halfway through the brood rearing period. Nests could be more likely to be destroyed late in the nesting season because mass movements are more frequent in late summer with the accumulation of thawing degree-days and penetration of the thawing front in the slope's active layer (Mackay 1981; Lewkowicz 1992; French 2007).

To our knowledge, this study is the first to assess quantitatively the links between geomorphological processes and nest persistence in a cliff-nesting species. Availability of suitable nesting sites is often limited for raptor species (Newton 1979; Restani 1991; Kennedy et al. 2014) and hence, changes in nest persistence could affect their population. Further investigations would be required to evaluate to what extent a reduction in nesting structure persistence due to increased slope instability will affect the abundance and distribution of Arctic-nesting rough-legged hawks.

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Appendix

Fig. A1. Material type classification: (a) unconsolidated sediments (diamicton essentially comprising silty sand and gravel, some cobbles, mixed with organic matter), (b) poorly consolidated rock (sandstone), (c) consolidated and weakly altered rock, and (d) consolidated and altered rock. Diameter of nests is about 60–90 cm.

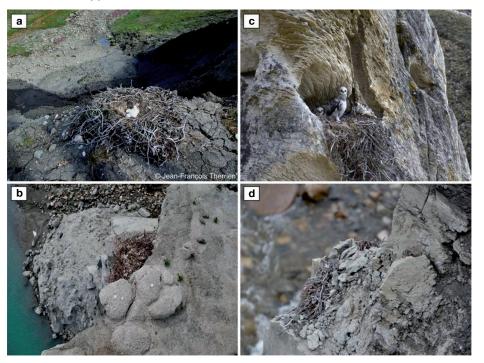


Fig. A2. Photographs documenting the destruction of two rough-legged hawk nesting structures (white circles, diameter of nests is about 60–90 cm). (a) Destruction of a nesting structure built on consolidated and altered rock and caused by a rockfall that occurred in 2013 between (a1) 14 June and (a2) 30 July. Note the unstable debriscovered apron over the nesting structure on Fig. a1 and fallen debris that accumulated close to the nest on Fig. a2. (b) Destruction of a nesting structure built on unconsolidated sediments and caused by a slope failure in diamicton that occurred between (b1) July 2014 and (b2) June 2015. Note the tensile cracks in the surficial deposit near the edge of the cliff.

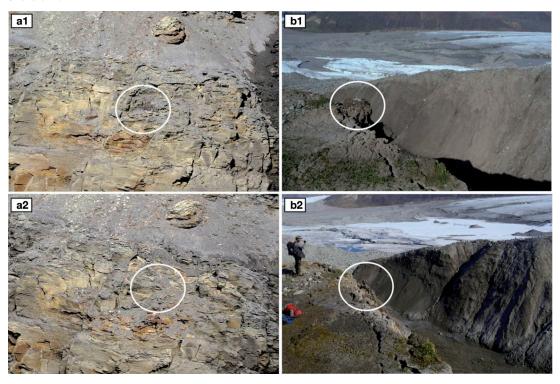


Table A1. (A) Model selection among candidate models explaining destruction of rough-legged hawk nests in relation to geomorphological characteristics of the slope above the nest (n = 78); number of parameters (k), Δ AICc values, AICc weights (wi), log-likelihood values (LL), and R^2 are presented for each model. (B) Model-averaged parameter estimates (on a logit scale) from the most parsimonious models (Δ AICc < 4) and their 95% confidence intervals (CI).

(A) Variables in the model ^a	k	ΔAICc	wi	LL	R^2		
Material, vegetation	5	0.00	0.46	-39.11	0.30		
Material	4	1.98	0.17	-41.24	0.26		
Material, vegetation, slope	6	2.34	0.14	-39.10	0.30		
Material, slope	5	4.17	0.06	-41.20	0.26		
Slope	2	4.46	0.05	-44.68	0.13		
Vegetation, slope	3	4.67	0.04	-43.70	0.16		
Material, vegetation, slope, vegetation × slope	7	4.75	0.04	-39.10	0.30		
Vegetation, slope, vegetation × slope	4	6.70	0.02	-43.60	0.17		
Null	1	9.29	0.00	-48.14	0.00		
(B) Parameters	β		95% CI				
Intercept	-2.53	-4.46, -0.61					
Slope	0.00	-0.03, 0.03					
Vegetation	-1.50	-3.00, 0.00					
Unconsolidated sediments	3.02	1.07, 4.97					
Poorly consolidated rock	2.04		0.04, 4.03				
Consolidated and altered rock	1.67		-0.40, 3.74				

[&]quot;Material: consolidated and weakly altered rock (reference level), consolidated and altered rock, poorly consolidated rock, and unconsolidated sediments. Vegetation: <5% (reference level) and 5%–100%. Slope: aspect (°).