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Écologie de la nidification de la buse pattue dans le Haut-Arctique et vulnérabilité des nids aux risques géomorphologiques

Mémoire

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Écologie de la nidification de la buse pattue dans le Haut-Arctique et vulnérabilité des nids aux risques géomorphologiques

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Sous la direction de:

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Résumé

Les caractéristiques physiques d'un site de nidification peuvent influencer la probabilité qu'il soit utilisé et l'issue des tentatives de nidification. La buse pattue (*Buteo lagopus*) construit un imposant nid, qui peut être réutilisé plusieurs années, en bordure des falaises et des versants en Arctique. Ces habitats escarpés sont perturbés par des mouvements de masse pouvant entraîner la destruction de sites critiques pour la reproduction des buses. Nous avons d'abord examiné l'effet de plusieurs variables environnementales et de la réutilisation d'un nid sur la reproduction de la buse pattue. Ensuite, nous avons évalué la vulnérabilité des nids aux mouvements de masse et identifié les facteurs environnementaux associés à la persistance des nids. L'étude s'est déroulée à l'île Bylot (Nunavut) de 2007 à 2015. 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 accessibles aux renards et orientés vers le nord étaient associés à un moins bon succès reproducteur. Celui-ci 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 prédateurs reflètent des sites de haute qualité. Le succès reproducteur était similaire entre les nouveaux nids et ceux préexistants, suggérant que la construction d'un nid n'entraîne pas de coût sur la reproduction à court terme. Parmi les 82 nids connus, près du tiers ont été détruits par des mouvements de masse et parmi ceux encore intacts, la majorité sont à risque modéré et haut de l'être. La probabilité de destruction était élevée pour les nids construits sur des sédiments non consolidés et positivement associée aux fortes précipitations. La hausse anticipée des précipitations due aux changements climatiques est susceptible 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.

Abstract

The physical characteristics of a nest site are thought to influence both its use by birds and the outcome of breeding attempts. The rough-legged hawk (*Buteo lagopus*) built a massive nest, which can be reused several years, along cliffs and slopes in the Arctic. These steep habitats are exposed to mass movements which may result in the destruction of critical sites for hawks. We examined the relationships between several environmental variables, patterns of nest reuse and reproductive output in rough-legged hawks. We also assessed nest vulnerability to mass movements and identified environmental factors associated with the persistence of nesting structures. The study was conducted on Bylot Island (Nunavut) from 2007 to 2015. Nest use probability increased with the nearest distance to breeding conspecific, with lemming density and for sheltered nest. Hawk nests inaccessible to foxes and facing away from the north were associated with a 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 offering a favorable microclimate and protection from weather and predators provide the highest-quality site. Hawks that bred in a newly-built nest had similar success compared to those that used pre-existing nests, suggesting that building a new nest entailed no short term reproductive costs. Among 82 known nests, nearly a third were destroyed during the study and among those still intact, more than half are exposed to a moderate to high risk of being destroyed. The probability of nest destruction was high for nests built on unconsolidated sediments and positively associated with heavy rainfall. The anticipated increase in precipitation due to climate change is likely to increase the exposure of nest to mass movements which could ultimately reduce the availability of suitable sites for the reproduction of this raptor.

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Avant-propos

Ce mémoire comprend une introduction générale suivie par 2 chapitres rédigés en anglais sous la forme d'articles scientifiques et se termine par une conclusion générale. Bien que je sois l'auteure principale de ces chapitres, Gilles Gauthier (directeur), Joël Bêty et Jean-François Therrien ont contribué à l'élaboration des objectifs, aux activités de terrain, aux analyses et à la rédaction des deux chapitres. Daniel Fortier (codirecteur) a participé à tous les aspects du second chapitre.

Introduction

Succès reproducteur des oiseaux nichant en Arctique

Lors de la période de nidification, de nombreuses composantes biotiques et abiotiques sont susceptibles d'influencer le succès reproducteur des oiseaux telles que les conditions climatiques (e.g., Skagen et al., 2012), la disponibilité de la nourriture (e.g., Terraube et al., 2012), les caractéristiques physiques du nid (e.g., Chiavacci et al., 2014; Bruggeman et al., 2015), les interactions intra et interspécifiques (e.g., Krüger, 2004; Brambilla et al., 2006) et la disponibilité de sites appropriés (e.g., Newton, 1979; Korpimäki, 1988*b*). Les oiseaux qui se reproduisent dans le milieu arctique sont soumis à des conditions particulières comparativement aux espèces qui nichent aux plus basses latitudes, telles qu'une fenêtre temporelle réduite pour se reproduire et des conditions climatiques rigoureuses, pouvant avoir des incidences sur la reproduction.

Les conditions climatiques peuvent directement influencer le succès reproducteur des oiseaux notamment en modifiant les coûts liés au déplacement des individus ou à la thermorégulation (Krüger, 2004; Bionda and Brambilla, 2012; Lehikoinen et al., 2009). Par exemple, il a été expérimentalement démontré chez le faucon pèlerin (*Falco peregrinus*) que les jeunes faucons protégés des fortes précipitations par un abri survivaient mieux que les jeunes non-protégés. L'exposition directe aux précipitations était responsable de plus du tiers des cas de mortalité des jeunes de cette population (Anctil et al., 2014). Les précipitations sont considérées comme un facteur déterminant influençant la reproduction de plusieurs oiseaux nichant en Arctique (e.g., Potapov, 1997; Lehikoinen et al., 2013; Anctil et al., 2014).

Le rôle crucial que jouent les petits mammifères au sein des écosystèmes nordiques est reconnu depuis longtemps, particulièrement comme consommateurs primaires et comme source de nourriture majeure pour une multitude de prédateurs spécialistes et généralistes (Korpimäki and Krebs, 1996; Gauthier et al., 2011*a*). L'abondance et le succès reproducteur de nombreux prédateurs tels le harfang des neiges (*Bubo scandiacus*), les labbes (*Stercorarius pomarinus* et *Stercorarius parasiticus*) et la buse pattue (*Buteo lagopus*) sont souvent fortement associés à l'abondance des lemmings (Gilg et al., 2003; Therrien et al., 2014*a*).

De plus, les fluctuations d'abondance des lemmings peuvent avoir un effet indirect sur la reproduction de plusieurs espèces d'oiseaux à travers une variation annuelle de la pression de prédation (Bêty et al., 2002). Par exemple, la pression de prédation exercée par le renard arctique (*Vulpes lagopus*), un prédateur commun aux oiseaux et aux lemmings, sur les oeufs d'un prédateur généraliste, le goéland bourgmestre (*Larus hyperboreus*), était plus marquée lors des années de faible abondance de lemmings et sur les nids accessibles par voie terrestre, sur le bord des étangs et des lacs (Gauthier et al., 2015). L'effet de la disponibilité de la nourriture peut ainsi influencer directement ou indirectement la reproduction et ce par divers mécanismes.

Les caractéristiques physiques d'un nid peuvent influencer la probabilité qu'il soit utilisé et le succès reproducteur à travers des variations du risque de prédation (Gilchrist and Gaston, 1997; Haynes et al., 2014) et des conditions microclimatiques du nid (Kim and Monaghan, 2005; Fast et al., 2007). Plusieurs études ont documenté que la végétation près du nid (e.g., eider à duvet, *Somateria mollissima*, Kim and Monaghan, 2005), la présence d'un surplomb au-dessus du nid (e.g., faucon gerfaut (*Falco rusticolus*) et corbeau (*Corvus corax*), Poole and Bromley, 1988*a*), l'inaccessibilité au contenu du nid par les prédateurs (e.g., mouette de Sabine, *Xema sabini*, Mallory et al., 2012) et une orientation du nid vers le sud (e.g., faucon pèlerin, aigle royal (*Aquila chrysaetos*) et buse pattue, White and Cade, 1971; Poole and Bromley, 1988*a*) étaient des caractéristiques associées positivement à l'utilisation d'un nid ou au succès reproducteur. Par exemple, chez le plongeon du pacifique (*Gavia pacifica*) et à bec blanc (*Gavia adamsii*), les individus nichant sur des îles ont un meilleur succès reproducteur par une réduction du risque de prédation par voie terrestre (Haynes et al., 2014). L'utilisation de nids encaissés chez le fulmar boréal (*Fulmarus glacialis*) était associée avec une meilleure protection contre les prédateurs aviaires mais également à un microclimat plus froid occasionnant des coûts élevés liés à la thermorégulation (Mallory and Forbes, 2011). Ce dernier exemple illustre bien les compromis parfois nécessaires dans les caractéristiques physiques du site de nidification, notamment entre le risque de prédation et les conditions microclimatiques du nid.

Lorsqu'une espèce aviaire utilise un habitat restreint à certaines zones géographiques (e.g., falaises) ou encore très spécifique (e.g., cavités, plates-formes) pour se reproduire, les nids sont souvent espacés irrégulièrement et ne sont pas répartis uniformément dans le paysage (Ontiveros, 1999; Sullivan et al., 2003; Wightman and Fuller, 2006). Chez les rapaces qui utilisent les habitats escarpés pour nicher en Arctique, la répartition et le nombre de nids

semblent être limités par les interactions intra- et inter-spécifiques et aussi de façon plus importante, par la disponibilité de sites appropriés à leurs besoins (White and Cade, 1971; Newton, 1979; Wightman and Fuller, 2005). Bien que les mécanismes exacts expliquant la répartition de ces oiseaux sont peu connus, ces facteurs semblent être des acteurs importants expliquant l'utilisation d'un site de nidification et le succès reproducteur.

Rôles écologiques des structures existantes pour la reproduction

Chez les rapaces (Falconiformes, Accipitriformes) et les grands échassiers (Ciconiiformes), les mêmes structures peuvent être réutilisées plusieurs années (e.g., Vergara et al., 2006; Margalida et al., 2007), parfois plus de mille ans dans des cas extrêmes (Burnham et al., 2009). La présence et la réutilisation de ces nids, considérés comme des "aimants écologiques" (Hickey, 1942), peuvent avoir plusieurs rôles écologiques pouvant affecter le succès reproducteur des individus (Tobolka et al., 2013). Par exemple, chez l'aigle royal, la présence de structures existantes a été utilisée comme un indice de qualité du territoire lors de l'établissement des oiseaux (Millsap et al., 2015). Également, les nids réutilisés au fil des ans peuvent être le reflet d'un territoire de haute qualité ou d'individus plus expérimentés qui réutilisent les mêmes nids, comme il a été bien démontré chez la cigogne blanche (*Ciconia ciconia* ; Vergara et al., 2007; Janiszewski et al., 2013). La réutilisation d'un nid peut aussi se traduire par une réduction de temps et d'énergie pouvant être alors allouée à la reproduction, ce qui peut résulter en une plus grande taille de couvée (Redmont et al., 2007) ou en une reproduction plus hâtive (Cavitt et al., 1999; Vergara et al., 2010; Tobolka et al., 2013). Cette économie de temps peut être particulièrement importante chez les espèces qui se reproduisent dans les hautes latitudes, où la période propice à la reproduction est restreinte. Enfin, bien que des liens directs entre la stratégie de la réutilisation d'un nid et le succès reproducteur aient été documentés chez les grands échassiers, peu de liens ont été documentés chez les rapaces bien que de telles études soient rares (Kochert and Steenhof, 2012; Jiménez-Franco et al., 2014*b*,*a*).

Persistance des nids et géomorphologie

La persistance des structures de reproduction (e.g., cavités, coupoles) est influencée par différents facteurs tels que les événements météorologiques extrêmes (Watts and Byrd, 2007; Penteriani et al., 2002; Martínez et al., 2013), les caractéristiques physiques de l'habitat (Edworthy et al., 2012) et les activités anthropiques (Catlin and Rosenberg, 2006; Edworthy and Martin, 2013). Par exemple, la persistance des cavités, qui sont des structures clés pour la reproduction de plusieurs espèces, est associée au stade de décomposition de l'arbre (Edworthy et al., 2012) et au type d'exploitation forestière (Edworthy and Martin, 2013). Plusieurs études se sont également intéressées aux liens entre une réduction de la persistance des structures et différents paramètres de la reproduction (Penteriani et al., 2002; Martínez et al., 2013). Par exemple, suite à l'ouragan Isabel, 127 nids de pygargue à tête blanche (*Haliaeetus leucocephalus*) dans la région de la baie de Chesapeake ont été détruits par les vents forts, affectant négativement la reproduction lors de l'événement mais également l'année suivante (Watts and Byrd, 2007). Une réduction de la disponibilité des habitats propices à la construction des structures et la perte de celles-ci à travers une réduction de leur persistance, peuvent avoir des impacts sur la distribution, la densité et le succès reproducteur de plusieurs espèces (Newton, 1979; Cockle et al., 2010).

Les habitats escarpés en Arctique sont régulièrement perturbés par des mouvements de masse tels que des chutes de blocs, des coulées de débris et des ruptures de pente qui sont susceptibles d'influencer la persistance des structures de reproduction construites dans ces habitats. Bien que les mouvements de masse ne soient pas propres aux régions froides, certains voient leurs effets amplifiés en contexte périglaciaire (French, 2007). Le terme périglaciaire fait référence à une gamme assez étendue de conditions environementales caractérisées par une alternance des cycles de gel-dégel et par la présence d'un sol continuellement gelé, le pergélisol (French, 2007). Les environnements périglaciaires sont considérés comme des milieux morphologiquement sensibles et donc particulièrement susceptibles d'être affectés par les changements climatiques (French and Slaymaker, 2012).

Le réchauffement climatique est accru aux hautes latitudes par rapport au reste du biome terrestre, un phénomène appelé l'amplification arctique (Bekryaev et al., 2010; Pithan and Mauritsen, 2014). L'augmentation des températures annuelles de l'Arctique est plus de quatre fois supérieure à la moyenne mondiale (IPCC, 2013). Selon les modèles climatiques du Groupe

intergouvernemental d'experts sur le climat (GIEC ; IPCC, 2013), l'Arctique connaîtra aussi une hausse considérable des précipitations allant de 15 à 25% selon les saisons. L'équilibre de l'environnement arctique repose sur des conditions biogéophysiques particulières, qui dépendent toutes de la présence d'une imposante cryosphère (AMAP, 2012), laquelle inclue le pergélisol, caractéristique universelle définissant les paysages arctiques. Le dégel du pergélisol causé par le réchauffement climatique est susceptible de modifier la structure physique des habitats utilisés par la faune arctique (Smith et al., 2010; AMAP, 2012). Certaines structures importantes pour la reproduction, telles que des nids ou des tanières, peuvent être exposées à des mouvements de masse et sont susceptibles d'être détruites par ceux-ci.

Le déclenchement des mouvements de versants est étroitement associé aux événements de fortes précipitations et aux hautes températures (Lewkowicz, 1992; Can et al., 2005; Gruber and Haeberli, 2007; Lantuit and Pollard, 2008; Allen et al., 2009). Les effets des changements climatiques sont ainsi susceptibles d'augmenter la fréquence d'occurrence et l'amplitude d'une grande variété de mouvements de masse (Lewkowicz and Harris, 2005; Gruber and Haeberli, 2007; Chiarle et al., 2011; French and Slaymaker, 2012). Par exemple, Lewkowicz and Harris (2005) ont reporté que la fréquence des détachements de couche active sur la péninsule Fosheim (île d'Ellesmere) a plus que doublé entre 1975 et 2000 et la cause de cette augmentation serait liée à une augmentation des températures. Enfin, plusieurs auteurs ont mentionné que la fréquence et l'amplitude des mouvements de masse semblent avoir augmenté dans les dernières décennies (Lewkowicz, 1992; Rebetez et al., 1997; Lewkowicz and Harris, 2005; Lantuit and Pollard, 2008; Daanen et al., 2012; French and Slaymaker, 2012).

En plus des conditions climatiques, les caractéristiques physiques du versant telles que la pente, le type de matériel, le couvert végétal et le contenu en glace du matériel sont des facteurs qui peuvent influencer la probabilité d'occurrence d'un mouvement de masse (McRoberts and Morgenstern, 1974; Rapp, 1986; French, 2007). Par exemple, sur la péninsule Fosheim sur île Ellesmere, les détachements de couche active sont communs dans les régions où les sédiments sont riches en glace et peu consolidés (Harris and Lewkowicz, 2000). Également, l'alternance des cycles de gel-dégel, caractéristique des environnements périglaciaires, est un paramètre favorisant l'altération et le fractionnement des roches (French, 2007). Sous l'effet du gel, les roches subissent de fortes contraintes causées par la variation de la pression interstitielle qui est causée par la présence d'eau entre les pores (Murton et al., 2000). Ainsi, plus la teneur en eau et glace de la roche est élevée, ce qui varie selon le type de matériel, plus les roches sont mécaniquement sollicitées et donc fragilisées (Murton et al., 2006). En-

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fin, une combinaison de facteurs climatiques et physiques modifie et façonne les versants périglaciaires.

La buse pattue : prédateur de l'écosystème nordique

La buse pattue est une espèce migratrice ayant une vaste répartition circumpolaire. Elle se reproduit en région arctique et subarctique, majoritairement entre les latitudes 61° et 76°N (Bechard and Swem, 2002). Cette espèce longévive niche en bordure des falaises, sur les affleurements rocheux ou sur les versants escarpés de la toundra. L'arrivée sur les sites de reproduction a lieu à la fin mai, début juin, et précède de quelques jours la date de ponte. La taille de ponte est généralement de 3 à 6 oeufs, la période d'incubation est de 28-31 jours et les jeunes quittent le nid 41 jours suite à l'éclosion (Newton, 1979). Le nid, constitué d'un amoncellement de branches et de racines, peut être réutilisé pendant plusieurs années (Mindell, 1983). Mindell (1983) et Brodeur et al. (1994) ont observé que la majorité des sites actifs comportent un ou plusieurs nids inactifs au sein d'un même territoire, suggérant l'utilisation de nids alternatifs. Ce comportement est répandu chez plusieurs espèces de rapaces (e.g., Margalida et al., 2007; Ontiveros et al., 2008; Millsap et al., 2015).

Il est communément assumé que les buses (genre *Buteo*) sont fidèles à leur site de reproduction (Newton, 1979). Il existe toutefois peu d'évidences d'un tel comportement basées sur des oiseaux marqués. Quelques études ont documenté la fidélité au territoire de reproduction à l'aide d'oiseaux marqués chez au moins quatre espèces de buses : la buse des Galápagos (*Buteo galapagoensis* ; De Vries, 1975), la petite buse (*B. platypterus* ; Matray, 1974), la buse rouilleuse (*B. regalis* ; Schmutz and Schmutz, 1981) et la buse à queue rousse (*B. jamaicensis* ; Janes, 1984). Ce comportement n'a toutefois jamais été confirmé à l'aide d'oiseaux marqués chez la buse pattue (Bechard and Swem, 2002).

Ce prédateur est situé au sommet du réseau trophique de la toundra arctique (Gauthier et al., 2011*a*). Il est considéré comme un spécialiste des petits mammifères mais peut s'alimenter d'oisillons, de lagopèdes et de lièvres lorsque les petits mammifères sont rares ou absents (Pokrovsky et al., 2014). Il a été démontré que les fluctuations d'abondance des lemmings sont un facteur important influençant la densité des nids et le succès de nidification (Sundell et al., 2004; Therrien et al., 2014*a*; Terraube et al., 2015). Enfin, plusieurs études ont porté

sur les réponses numériques et fonctionnelles de ce prédateur (Wiklund et al., 1998; Sundell et al., 2004; Hellström et al., 2014; Therrien et al., 2014*a*; Terraube et al., 2015) mais peu se sont intéressées à l'influence possible de d'autres variables environnementales sur la reproduction des buses (Potapov, 1997).

Les principales causes d'échec de la reproduction chez ce rapace seraient liées à la prédation, à l'abondance de nourriture, aux mauvaises conditions météorologiques et à la destruction du nid (Potapov, 1997; Pokrovsky et al., 2012). Potapov (1997) et Swem (1996) ont observé respectivement que 4 et 25% des échecs de la reproduction étaient associés à la destruction du nid. De telles observations ont également été rapportées dans l'ouest de l'Arctique canadien (Gauthier et al., 2011*b*).

Objectifs de l'étude

Les habitats escarpés utilisés par la buse pattue pour nicher peuvent conférer des bénéfices, comme une réduction du risque de prédation par le renard ou un microclimat favorable. Toutefois, ces habitats exposent les nids de ce rapace à des processus géomorphologiques. Ces processus, susceptibles d'être amplifiés par les changements climatiques, peuvent entraîner la destruction ou l'altération de sites critiques pour la reproduction de cet oiseau.

Le premier chapitre de ce mémoire aborde les liens entre les caractéristiques physiques du site de nidification et différents paramètres de la reproduction de la buse pattue nichant dans le Haut-Arctique. Puisque cette espèce est territoriale, l'effet de la distance du nid actif le plus près a été considéré sur la probabilité qu'un nid soit utilisé de même que les variations annuelles d'abondance de nourriture qui peuvent être importantes dans la toundra (Therrien et al., 2014*a*). Sachant que la disponibilité de la nourriture et les précipitations peuvent avoir une forte influence sur le succès reproducteur des rapaces en Arctique (Anctil et al., 2014; Therrien et al., 2014*a*), ces variables ont été considérées en plus des caractéristiques physiques pour expliquer les variations du succès reproducteur. Nous nous attendions à ce que les caractéristiques physiques associées au risque de prédation et au microclimat du nid influencent l'utilisation d'un nid et le succès reproducteur. Nous avons aussi évalué les bénéfices potentiels de la réutilisation d'un nid et d'un territoire sur le succès reproducteur des buses. Sachant qu'il y a potentiellement des coûts en temps et en énergie associés à la

construction d'un nid, nous avons émis l'hypothèse que la réutilisation d'un nid influence le succès reproducteur. Finalement, la réutilisation d'un territoire est susceptible de refléter sa qualité ou l'expérience des individus, et ceci pourrait avoir une influence positive sur le succès reproducteur.

Le deuxième chapitre de ce mémoire vise d'une part à évaluer la vulnérabilité des sites de nidification des buses aux risques géomorphologiques et d'autre part à identifier les facteurs climatiques et géomorphologiques qui sont associés à la persistance ou à la disparition des nids au fil des ans. Considérant que le type de matériel, l'angle de la pente et le couvert végétal sont des caractéristiques géomorphologiques associées à la stabilité des pentes aux hautes latitudes (McRoberts and Morgenstern, 1974; Rapp, 1986; French, 2007), nous nous attendions à ce que ces caractéristiques influencent la persistance des nids. De plus, comme les hautes températures et les événements de fortes précipitations sont associés à l'occurrence des risques géomorphologiques (Rebetez et al., 1997; Lewkowicz and Harris, 2005; French and Slaymaker, 2012), nous avons émis l'hypothèse que la persistance des nids est influencée par ces variables climatiques. Finalement, comme les risques géomorphologiques peuvent engendrer la destruction du nid (Swem, 1996; Potapov, 1997), nous nous attendions à ce que cet effet se reflète sur la probabilité qu'un nid soit utilisé et sur le succès reproducteur.

Chapitre 1

Nest site characteristics, patterns of nest reuse and reproductive output in an arctic nesting raptor, the rough-legged hawk

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Résumé

Nous avons examiné l'effet de plusieurs variables environnementales et de la réutilisation d'un nid sur le succès reproducteur de la buse pattue (*Buteo lagopus*) nichant dans le Haut-Arctique. Nous avons suivi 109 tentatives de nidification sur une période de 9 ans et échantillonné les caractéristiques physiques de 87 sites de nidification 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. Finalement, 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.

Abstract

We examined the relationships between several environmental variables, patterns of nest reuse and reproductive output in rough-legged hawks (*Buteo lagopus*) breeding in the High Arctic. We monitored 109 nesting attempts over a 9-yr period and sampled physical characteristics of 87 known nesting sites on Bylot Island, NU. Nest use probability increased with the nearest distance to breeding conspecific, with lemming density and for sheltered nest. Hawk nests inaccessible to foxes and facing away from the north were associated with a 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 offering a favorable microclimate and protection from weather and predators provide the highest-quality site. Finally, hawks that bred in a newly-built nest had similar clutch size and hatching date compared to those that used pre-existing nests, suggesting that building a new nest entailed no short term reproductive costs.

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 for 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 protected by an overhang (Mearns and Newton, 1988; Anctil et al., 2014) whereas nests with a southern exposure or located at low altitude may provide a warmer environments for chicks in cold climates (White and Cade, 1971; Poole and Bromley, 1988a). Physical characteristics of nest sites 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 site are poor indicators of site quality (Donázar et al., 1993; Wightman and Fuller, 2006; Bruggeman et al., 2015). Besides nest site characteristics, food availability (Terraube et al., 2012; Therrien et al., 2014a) or intra and interspecific interactions (Hakkarainen and Korpimäki, 1996; Sergio et al., 2003; Brambilla et al., 2006) are other environmental factors that can also have a strong influence on reproductive success.

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., 2014b; Millsap et al., 2015) and reusing those nests can ultimately influence individual fitness (Tobolka et al., 2013). Indeed, nest building is considered energetically and temporally costly (Collias and Collias, 1984; 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,b). Nests that are consistently reused may also reflect high quality breeding territory and the presence of pre-existing nesting structures may provide important cues that could be used by individuals settling in a new breeding area

(Korpimäki, 1988*b*; Sergio et al., 2011; Millsap et al., 2015).

The rough-legged hawk (*Buteo lagopus*) is a medium-size migratory raptor with a circumpolar distribution. This species 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). The rough-legged hawk is mostly considered a rodent specialist although alternative prey, such as ptarmigans, ducks and hares, can also be used when rodents are scarce (Mindell, 1983; Pokrovsky et al., 2014). Hence, abundance of small rodents can be a major factor influencing hawk annual breeding density and reproductive output (Therrien et al., 2014*a*; 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 this 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; Therrien et al., 2014*a*; Hellström et al., 2014; Terraube et al., 2015) and few of them have examined the possible influence of others environmental variables on their reproduction (Potapov, 1997).

The objectives of this study were to: 1) investigate the effects of nest site physical characteristics and other environmental variables on nest use probability and 2) reproductive output, and 3) evaluate potential fitness benefits of using a previously occupied territory or pre-existing 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 that are sheltered by an overhang, located at low altitude, oriented toward the south, more concealed and inaccessible to arctic foxes (*Vulpes lagopus*), should be more likely to be occupied by hawks and associated with higher reproductive success. Previous studies have shown that rainfall, through a chilling effect on chicks, and food availability (lemming cycles) can have a strong influence on the reproductive output of arctic raptors (e.g., Anctil et al., 2014; Therrien et al., 2014*a*). These factors were thus considered along with nest site physical characteristics to explain variations in reproductive success. Finally, we hypothesized that using a pre-existing nest rather than a newly built one should be associated with a higher reproductive success because of the potential energy and time-saving (Cavitt et al., 1999; Tobolka et al., 2013).

Methods

Study area and study species

The study area, covering ∼500 km² of tundra, is located on the south plain of Bylot Island (Nunavut, Canada; 73°N, 80°W; Figure 1.1). This region is characterized by rolling hills and low elevation plateaus (ranging from 100 to 580 meters above sea level) interspersed by streams and rivers that created frequent outcrops of exposed bedrock. The bedrock is constituted 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 provide suitable breeding sites for a cliff-nesting species like the rough-legged hawk. Although the species can sometimes nest on flat grounds (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: ∼60-90 cm) and are generally conspicuous (Bechard and Swem, 2002). Egg laying starts from late May to early June, incubation lasts at least 31 d and nestlings hatch asynchronously in July (Bechard and Swem, 2002).

Others species of raptors nesting 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 (from 0 to 100 nests; Therrien et al., 2014a, G. Gauthier, unpubl. obs.). Two species of rodents are present (brown lemming, *Lemmus trimucronatus* and collared lemming, *Dicrostonyx groenlandicus*) and show large cyclic fluctuations of abundance (Gauthier et al., 2013). During the summer months (i.e. June to August), the average temperature is 4.5°C and the average rainfall is 91 mm (Cadieux et al., 2008).

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 hawks (i.e. along cliffs, ravines or large rocky outcrops) and by using a helicopter to reach distant areas. These areas were defined a

priori based on the topography and river systems within the 500 km^2 study area (Figure 1.1). 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 8-10x binoculars and were often located following alarm calls made by breeding hawks when observers entered a nesting territory. Each nest was positioned using a global positioning system (GPS) receiver 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 if they were active. We considered a nest active when a pair of hawks showed clear signs of territorial behavior (e.g., alarms calls, attacks) or when direct evidence of breeding were found (e.g., an incubating adult at the nest, the presence of eggs or chicks). Systematic searches of the same areas annually allowed us to differentiate territories and nesting structures that were pre-existing or new. A territory was defined as a confined area that contained one or more nests and where no more than one pair is known to have bred at any time (Tapia et al., 2007). We used the minimum distance between two active nests in the same year (0.57 km, see results) to determine the minimum territory size of hawks 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 that it was a new nest in a previously occupied territory. Obviously, we could not differentiate new nesting structures from pre-existing ones in the first year of monitoring of an area (2007 for much of the study area) and these nests were excluded from territory/nest occupancy analysis in those years.

We visited active nests at least twice between early July and mid-August to record the number of eggs and chicks. We estimated age of nestlings by size and stage of feather development using a photographic guide developed for red-tailed hawks (*Buteo jamaicensis*; Moritsch, 1983), a similar-size species for which chicks fledged at about the same age as 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 based on the estimated age of nestlings. Third, we defined *nesting success* as the probability of producing at least one

chick of 14 d of age among all active nests. Finally, we defined *brood size* as the maximum number of chicks found in a nest between the 14th and the 21th day of chick rearing, excluding nests where no egg hatched. In raptors, most nestling mortality typically occurs within the first two weeks of life (Kirkley and Gessaman, 1990; Potapov, 1997; Arroyo, 2002). The number of chicks at 14 d and 31 d (i.e. 1-5 days before fledging in rough-legged hawk; Bechard and Swem, 2002) was 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 hawk nest was characterized according to five physical variables. These variables were selected based on 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 1.1. 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). Nest orientation, the presence of an overhang, nest exposure and altitude were recorded because of their potential influence on the microclimatic conditions of the nest. We measured nest orientation with a compass. As we were especially interested in the north-south component of nest orientation, a north-south numerical gradient was used for the analysis (Table 1.1). We recorded if overhanging rocks provided direct cover over 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.

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 (see Fauteux et al., 2015 for details; Figure 1.1). In our analyses, we used lemming density estimated in July (average of the 2 grids, both species combined) for each year. For weather, 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 three periods corresponding respectively to the incubation period, the brood-rearing period and the whole nesting period (Table 1.1). 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 on maps. 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 (from 0 to 6 active nests per year; 24 nests over 9 years) and used the same habitat than hawks. We ran preliminary analysis using the linear distance to the nearest falcon nest for the 3 years with the most active falcon nests (4, 6 and 4 nests annually) but this variable did not affect nest use or any reproductive output variable of hawks. Therefore, this should not be considered as a confounding factor in our study. Four hawk nesting structures were nonetheless occupied once by peregrine falcons; these were considered unavailable to hawks in those years and were excluded from the nest use analysis.

Statistical analyses

We used generalized linear mixed-effects models (GLMM) with a binomial distribution to model nest use probability, hatching 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 ($r \geqslant 0.7$) 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 (AICc). When no single model had a strong support (i.e. Akaike weights < 0.90), model averaged estimates and 95% confidence intervals were computed with multi-model inference on the most parsimonious models (i.e. ΔAICc < 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, new nest in a previously occupied territory and pre-existing nest in a previously occupied territory; newly occupied territory was the reference category) 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% confidence intervals of the slope excluded 0. 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 Core Team, 2014). The package 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). All means are reported with standard errors.

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 0 in 2013 to 31 in 2014. Over 9 years (2007-2015), we monitored a total of 109 active 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 (β = 1.63, 95% CI = 0.96, 2.73, n = 202; Figure 1.2), indicating that the presence of an active nest limited the use of neighboring nesting structures, likely due to territorial behavior. Hence, nesting structures located at <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 1.2 and A.1). The probability that a nest was used increased with lemming density (Figure 1.2) and was also higher for nests protected by an overhang (0.81 ± 0.10) compared to those unprotected (0.37 ± 0.07). Nest use probability also tended to decrease for nests oriented toward the north.

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Reproductive success

Average clutch size was 4.4 ± 0.1 eggs (*n* = 69 clutches) and brood size at 14 d was 4.0 ± 0.2 (*n* = 38 broods) in nests where at least 1 chick hatched (overall hatching success was 78%, *n* = 77 nests). Hatching dates ranged from 28 June to 21 July (median = 8 July; *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 1.2, A.2 and A.3). The best model explained respectively 42% and 77% of the variation in hatching and nesting success. Hatching success of hawks was positively related to lemming density (Figure 1.3) 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 1.4). Nesting success probability was also higher in nest 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 nest accessible to foxes and signs of predation (fox scats and urine smell) were detected in 3 cases. Finally, none of the environmental variables explained variability in brood size at 14 d in nests that hatched successfully (Table 1.2 and A.4).

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 one structure. Among the total number of nesting structures monitored, 21 (24%) were reused, 49 (56%) were used only once and 17 (20%) were never used (i.e. nests that were mostly built before the study period but they were never used). For nesting structures with a known history, 63% of the breeding attempts (*n* = 83) took place in pre-existing 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: β = -0.02, 95% CI = -0.41, 0.36; pre-existing nest: β = 0.02, 95% CI = -0.29, 0.33), brood size (new nest: β = 0.15, 95% CI = -0.46, 0.79; pre-existing nest: β = 0.38, 95% CI = -0.13,

0.96) and hatching dates (new nest: β = -0.27, 95% CI = -5.76, 5.23; pre-existing nest; β = -2.60, 95% CI = -7.36, 2.17) compared to those that bred in newly occupied territories (Table 1.3). Hatching and nesting success were both higher in previously occupied territories (all new nests were successful; pre-existing nest: β = 1.61, 95% CI = 0.05, 3.82 and β = 2.09, 95% CI = 0.33, 4.24, respectively) compared to newly occupied territories (Table 1.3).

Discussion

Our results highlight the importance of several environmental factors affecting rough-legged hawk nest use probability and reproductive output as summarized in Figure 1.5. Lemming density had a strong overarching effect on hawk breeding output. Accessibility to foxes, presence of an overhang, orientation of the nest and summer rainfall also affected breeding hawks 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 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., 2014a), intraspecific nest spacing (Krüger, 2004; 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, 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., 2014a; Terraube et al., 2015). In the most extreme year (2013), not a single hawk nested in the study area due to the near absence of lemmings that year whereas the highest number of nests was found in the following year when lemmings bounced back. Not only fewer individuals bred when the abundance of lemmings was low but even among those that bred, which were potentially more experienced individuals (Newton and Rothery, 2002; Blas et al., 2009), reproductive success was reduced. 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 hawks on Bylot Island suggests that alternative prey are not sufficiently abundant to support a high density of nesting 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, 1988a). The presence of an overhang is likely easy to detect visually by 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; Chapter 2). Overhang may also improve nest microclimate conditions, for instance by partially shielding the nest from strong wind or by protecting it from rainfall, which may be especially important under the cold conditions prevailing at high latitudes. Experimental studies in arctic breeding species showed that nest shelters attenuate extremes in hot and cold temperatures experienced by nesting females in common eiders (*Somateria mollissima*; Fast et al., 2007) or 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 showing 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 orientations, 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 at least in two 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 the 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 effect 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 occured only on islands lacking arctic foxes (Sherrod et al., 1977). 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, 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 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 hawks), as shown for glaucous gulls (*Larus hyperboreus*) on Bylot Island (Gauthier et al., 2015).

Repeated use of pre-existing 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 due to the absence of marked birds. However, unlike other cliff-nesting raptors such as the golden eagle, for which nesting territory can include an average of 7 nests (Kochert and Steenhof, 2012), rough-legged hawks territories had on average <2 nests with a majority of them containing a single nest. Factors contributing to this relatively low number of nests per territory may include a reduced lifespan 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 geo-

morphological perturbations increasing slope instability in the Arctic (Chapter 2).

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 due to the rarity of erect shrubs. Birds that built a new nest in a previously occupied territory also had to incur these costs. In contrast, reusing a pre-existing nesting structure could result in significant time or energy saving that could be reallocated to reproduction, thereby allowing a higher clutch size (Vergara et al., 2010) or earlier breeding (Cavitt et al., 1999). However, we found no evidence of such short term benefits as hawks that built new nests had similar hatching date and clutch size compared to birds that used pre-existing nesting structures. Nonetheless, it is still possible that birds that do not 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 (Nielsen and Drachmann, 2003; Blas et al., 2009), occupy these new territories or from intrinsic differences in territory quality (Korpimäki, 1988b,a; Newton, 1989; Penteriani et al., 2003). We cannot exclude the possibility that some of the nests 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 pre-existing, which would render our comparison between new and pre-existing nests conservative.

According to our findings, nest use probability and reproductive success of rough-legged hawk in the Canadian Arctic are influenced by both biotic (i.e. food availability, distance to breeding conspecific) and abiotic factors (i.e. rainfall, nest site physical characteristics). Our results show that physical characteristics offering protection from weather and predators provide the highest quality nesting sites for this cliff-nesting raptor.

Acknowledgments

Table 1.1 – Description of environmental variables used to model nest use probability and reproductive success of rough-legged hawks.

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	Degree 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 14 th day of the chick-rearing period of individual nests
Intraspecific interactions	
Distance	Linear distance to the nearest active nest (km)

Table 1.2 – Model-averaged parameter estimates (with 95% confidence intervals) from the most parsimonious models (ΔAICc <4) explaining rough-legged hawk nest use and reproductive success. Estimates considered statistically significant are marked in bold. See Table 1.1 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

- : Not retained in the most parsimonious models.
NA: Not included in the candidate models.

Table 1.3 – Summary of reproductive output of rough-legged hawk on Bylot Island, NU, from 2007 to 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*)	192.5 ± 2.8 (*6*)
New nest in a previously occupied territory	4.4 ± 0.3 (*11*)	1.00 (*8*)	1.00 (*7*)	3.7 ± 0.5 (*7*)	189.5 ± 1.0 (*8*)
Pre-existing nest	4.6 ± 0.2 (*28*)	0.74 (*31*)	0.68 (*28*)	4.4 ± 0.3 (*18*)	188.0 ± 1.2 (*20*)

[a] Mean ± SE (*n*).
[b] Proportion of successful nests (*n*).
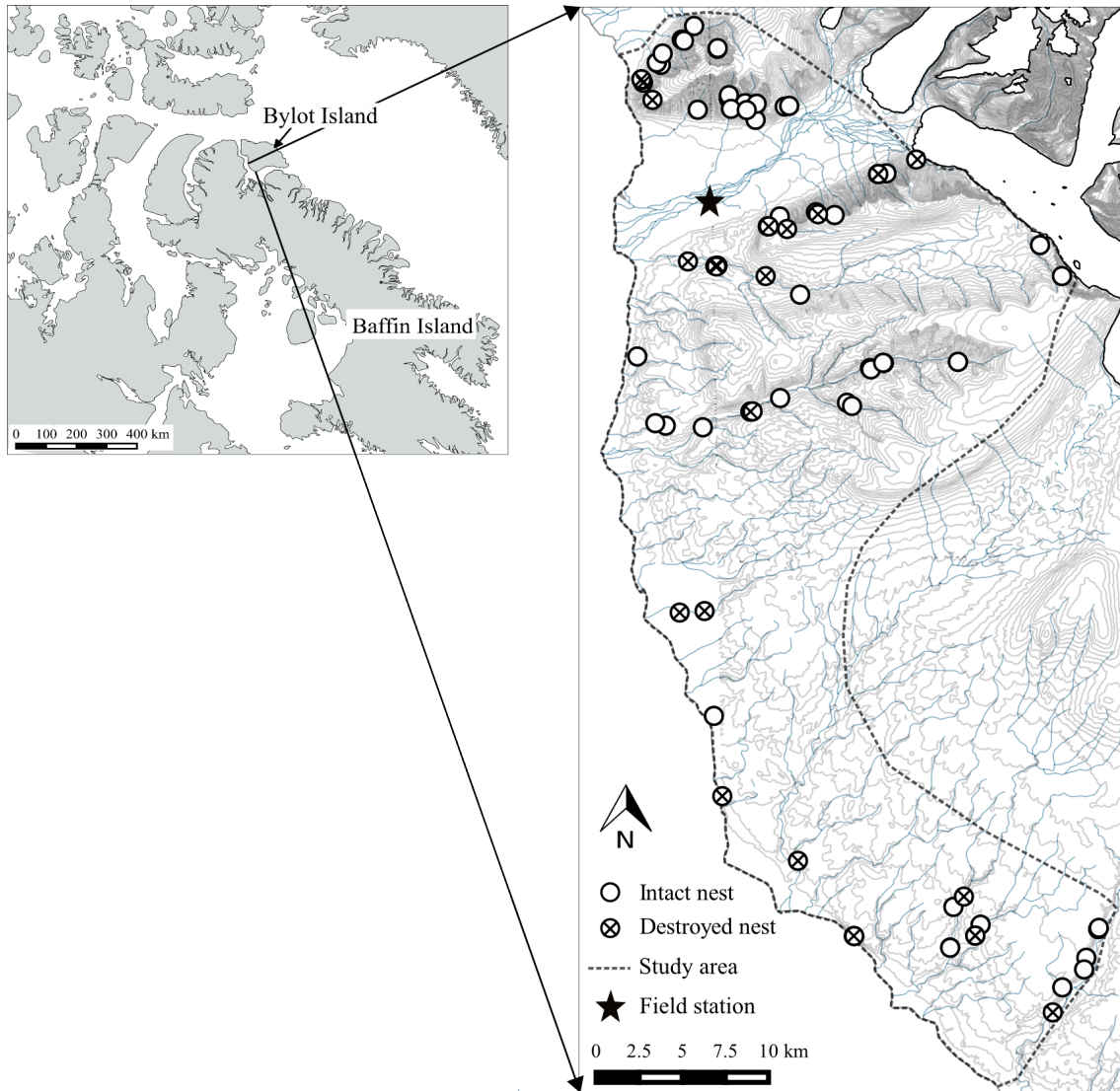
Figure 1.1 – Location of the study site on Bylot Island, Nunavut, Canada. Detailed study area is shown on the right, including positions of all known nesting structures (intact and destroyed nests at the end of the study, $n = 87$) monitored between 2007 and 2015. Spacing between contour lines is 20 m.
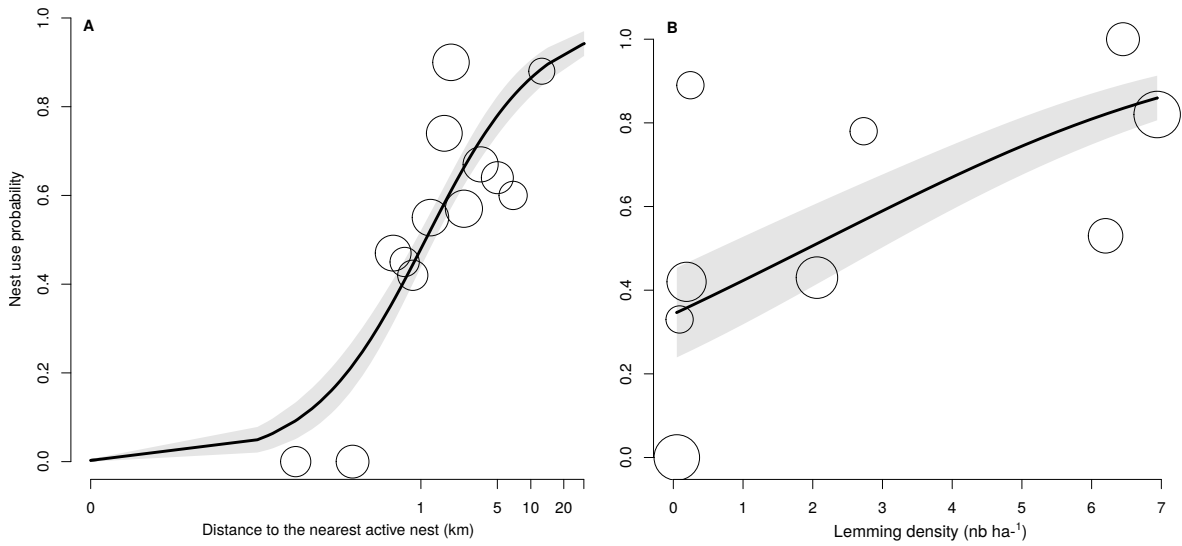
Figure 1.2 – Probability that a nesting structure was used by a rough-legged hawk breeding pair in relation to the distance to the nearest active nest (**A**) and lemming density (**B**). The gray band represents the $\pm 95\%$ CI of the regression. To illustrate observed values, each circle represents the proportion of used nest (circle size is proportional to the number of observations). The mean response for lemming density is based on the the most parsimonious models (Table 1.2 and A.1) after controlling for other model effects.
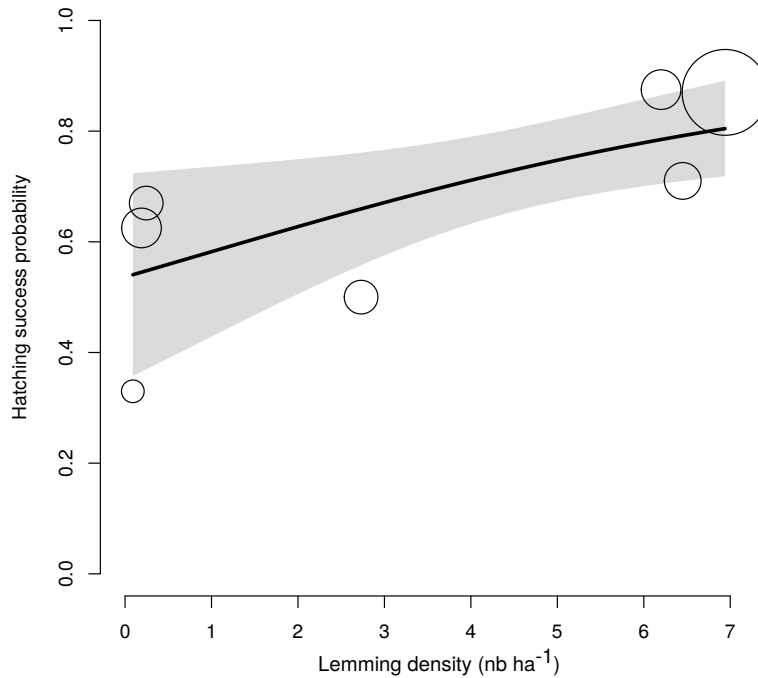
Figure 1.3 – Probability of hatching success by rough-legged hawks based on the most parsimonious models (Table 1.2 and A.2) in relation to lemming density. The gray band represents the ±95% CI of the regression. Circles illustrate observed data (circle size is proportional to the number of observations). The mean response after controlling for other model effects is shown.
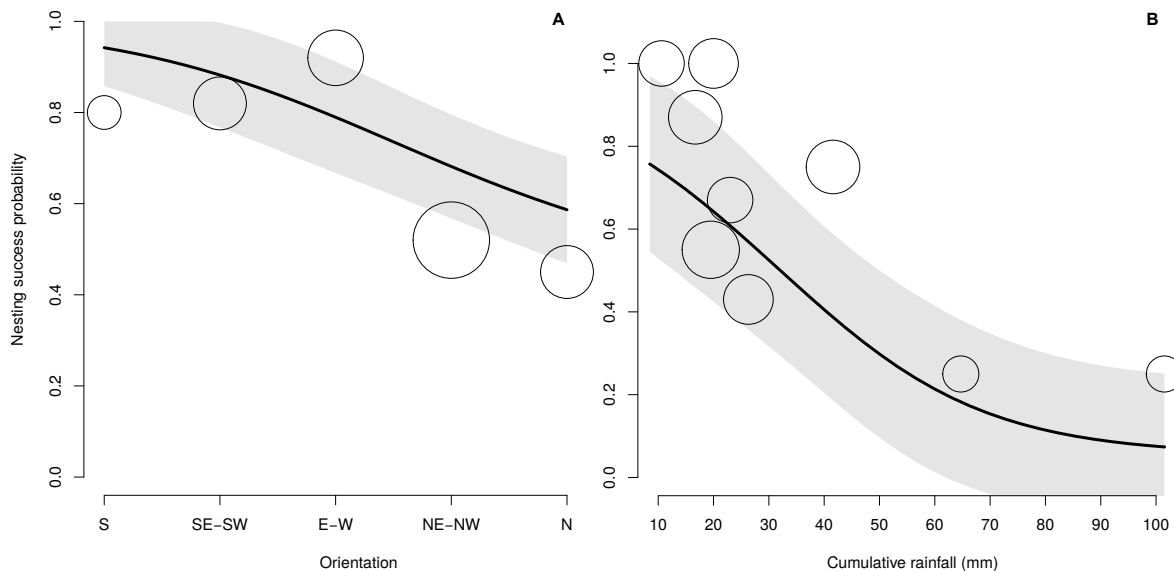
Figure 1.4 – Probability of nesting success by rough-legged hawks based on the most parsimonious models (Table 1.2 and A.3) in relation to nest orientation (**A**) and cumulative rainfall (**B**). The gray band represents the ±95% CI of the regression. Circles illustrate observed data (circle size is proportional to the number of observations). The mean response after controlling for other model effects is shown.
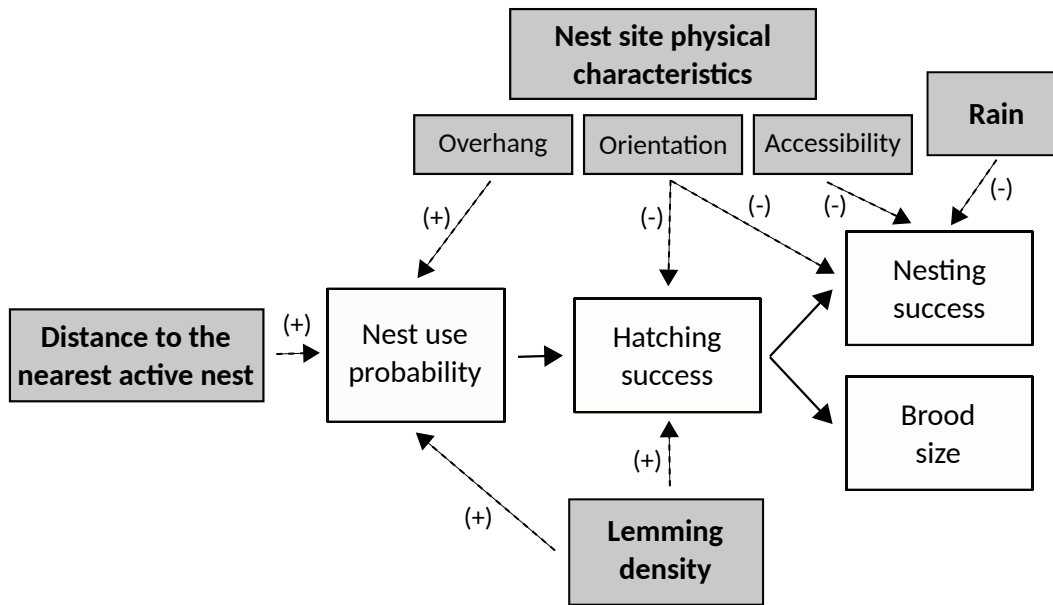
Figure 1.5 – Environmental variables (gray boxes) affecting different components of rough-legged hawk reproduction (white boxes). Arrows show links with various breeding parameters. Dashed arrows represent significant relationships along with their sign in parenthesis.

Chapitre 2

Vulnerability to geomorphological hazards of an arctic cliff-nesting raptor, the rough-legged hawk

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Résumé

La hausse des températures et des précipitations due aux changements climatiques peuvent augmenter le risque de destruction par des processus géomorphologiques de structures clées pour la reproduction de la faune arctique telles que des nids ou des tanières. Nous avons évalué la vulnérabilité des nids aux mouvements de masse (principalement aux ruptures de pente et chutes de blocs) et identifié les facteurs environnementaux associés à la persistance des nids de buses pattues (*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 ont été suivis entre 2007 et 2015. Près du tiers des nids connus ont été détruits pendant l'étude et parmi ceux encore intacts, la majorité sont à risque modéré et haut de l'être. La probabilité de destruction était élevée pour les nids construits sur des sédiments non consolidés et positivement associée aux fortes précipitations. La hausse anticipée des précipitations due aux changements climatiques est susceptible 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.

Abstract

Increase in temperature and precipitation associated to climate change may enhance the risk of destruction by geomorphological processes of key structures used by arctic wildlife such as nests or dens. We assessed nest vulnerability to mass movements (primarily slope failures and rockfalls) and identified environmental factors associated with the persistence of nesting structures in rough-legged hawks (*Buteo lagopus*), a species that typically nest on steep slopes or cliffs. The study was conducted on Bylot Island (Nunavut), where 82 hawk nesting structures were monitored from 2007 to 2015. Nearly a third of known nests were destroyed during the study and among those still intact, more than half are exposed to a moderate to high risk of being destroyed. The probability of nest destruction was high for nests built on unconsolidated sediments and positively associated with heavy rainfall. The anticipated increase in precipitation due to climate change is likely to increase the exposure of nest to mass movements which could ultimately reduce the availability of suitable sites for the reproduction of this raptor.

Introduction

Future weather patterns are predicted to be strongly modified in the wake 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 animal 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 landscape or habitat modifications (e.g., McCarty, 2001; Laidre et al., 2008).

Climate warming is expected to be faster and stronger in the polar regions compared to the rest of the globe, a phenomenon known as the polar amplification (Screen and Simmonds, 2010; IPCC, 2013; Pithan and Mauritsen, 2014). Increase in air and ground temperatures and changes in precipitation regime are already well documented in the Arctic (IPCC, 2013) and will have major impacts on the permafrost (Smith et al., 2010; AMAP, 2012), the universal defining characteristic of arctic landscapes. The rapid pace of warming and the corollary active layer deepening thus has a strong potential to cause perturbations to the geomorphology of the tundra and even be a source of hazards due to permafrost degradation (Harris et al., 2001; Haeberli and Burn, 2002; Harris, 2005; Rowland et al., 2010).

Mass movements are especially prevalent in the Arctic (French, 2007). Rainfall events and warm summer temperature are known to be triggering factors of various mass movements such as active layer detachment failures, retrogressive thaw slumps, debris flows or rockfalls (Lewkowicz, 1992; Can et al., 2005; Gruber and Haeberli, 2007; Lantuit and Pollard, 2008; Allen et al., 2009). A deepening of the active layer or increase in summer temperature and rainfall events are likely to augment the frequency and amplitude of such processes (Lewkowicz and Harris, 2005; French and Slaymaker, 2012). 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). These processes can result in the destruction or alteration of critical sites for wildlife species such as permanent nesting structures or dens (Gallant et al., 2014; Chapter 1), which could negatively affect the reproductive success and abundance of some arctic-breeding species.

Nesting structures have important ecological roles for birds, especially when they are reused over several breeding seasons such as in many raptor species (e.g., Sergio et al., 2011; Millsap et al., 2015). Nesting densities and ultimately breeding success of raptor species, especially those with specialized nesting habitat requirements, 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 nest persistence in species dependent on highly specific nesting structures. This is particularly relevant in the context of a warming climate, which will likely increase mass movement-related hazards for these species.

The rough-legged hawk (*Buteo lagopus*) is a long-lived raptor with a wide circumpolar distribution (Bechard and Swem, 2002). This species breeds on cliff edges, hoodoos or along steep hillsides in the tundra and often uses the same nesting structure for many years (Mindell 1983; Chapter 1). Those structures 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).

The objectives of this study 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 below and above the nest, because these characteristics are related to slope stability at high latitudes (Gruber and Haeberli, 2007; French, 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 and Harris, 2005; French and Slaymaker, 2012). 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, because mass movements can result in nest destruction, 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 to a higher reproductive success.

Methods

Study area

The study area, covering about 500 km^2 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 (Figure 2.1). The bedrock of the area is constituted of sedimentary rock (sandstone and shale) from the Lancaster formation of the Cretaceous and Tertiary periods (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. (2011*a*).

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 8-10x 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 (GPS) receiver and several photos 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.

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 a collapse of the 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, either due to the free fall of blocks breaking away from a cliff or rockwall, 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 from its grounding 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 active. We considered a nest active when a pair of hawks showed clear signs of territorial behavior (e.g., alarms calls, aproaches) or when direct evidence of breeding were found (e.g., an incubating adult at the nest, the presence of eggs or chicks). We visited active nests at least twice between early July and mid-August to determine nesting success and brood size. Nesting success was defined as the likelihood of producing at least one chick of 14 d of age. Brood size was defined as the number of chicks found in a nest between the 14th and the 21th day of chick rearing, excluding nests where no egg hatched. We estimated age of nestlings by the size of chicks and stage of feather development using a photographic guide developed for red-tailed hawks (*Buteo jamaicensis*; Moritsch, 1983), a similar-size species for which chicks fledged 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 of the slope can be different below and above the nest, we measured three geomorphological characteristics separately below and above the 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 (Figure A.1) 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 and shale) with very 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 refer to weakly-cemented sedimentary rocks that underwent a weak diagenesis and that can be easily 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 low (0-20%) or high (20-100%). 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 with a manual rain gauge near the weather station from June to August. A fully automated weather station located at 20 m above sea level recorded air temperature at 2 m all year round on an hourly basis(see CEN, 2014 for details).

Data analysis

We used Kaplan-Meier survival estimates to quantify survival rates of nests. Median lifespan was calculated as the time elapsed until half of the nests were destroyed (Kaplan and Meier, 1958). Nest persistence was calculated from the year the nest was found until the year it was destroyed or until the last census (2015). When the exact time of nest loss was unknown, the median date between two visits was used.

We used logistic regression to model nest status (intact = 0, destroyed = 1) according 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 build 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 or destroyed 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), model-averaged estimates and unconditional 95% confidence intervals were calculated with multi-model inference on the most parsimonious models (i.e. ΔAICc < 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 status 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 1 June to 17 August (duration of our presence at the site). Although summer precipitations are generally light 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 in rock material (Murton et al., 2006; Vedie et al., 2011). At our study site the average rainfall in days with 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 ≥ 7 mm per day, i.e. mean+1 SD, which represents 6% of all rainy events) each summer of the study. To evaluate the 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 during the 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 generalized linear mixed-effects models with a binomial distribution to model nest use probability and nesting success according to the risk index whereas we modeled brood size with a Poisson distribution. As rough-legged hawk is a territorial species, nests located <0.57 km from an active nest (the shortest distance ever recorded between 2 active nests on our study area) were excluded for investigating the effect of the risk index on nest use probability (Chapter 1). 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 R Statistical Environment (R Core Team, 2014). 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

The median lifespan of all monitored nesting structures was 7.6 years (Figure 2.2). From summer 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%; Figure A.2) and rockfalls (13%; Figure A.3). Finally, three (13%) nest destruction events were likely caused directly by extreme weather conditions, most probably very strong winds, since the nesting structures had tipped over and the geomorphological environment remained unchanged before and after the event.

Factors influencing nest persistence

Factors affecting the likelihood of nest destruction were very similar when considering either geomorphological characteristics below (Table 2.1) or above (Table A.5) 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 14.4 times greater than those built on consolidated and weakly altered rock. Nests built on consolidated and altered or poorly consolidated rock were respectively 5.6 and 7.5 times more likely of being destroyed than nests built on consolidated and weakly altered rock (Figure 2.3). The probability of nest destruction also tended to be lower when vegetation cover below the nest was high but this effect weakened as the slope became steeper (Table 2.1).

Based on the previous analysis, we characterized all known nests as being at a low (i.e. probability < 0.25), moderate (0.25-0.50) or high (> 0.50) risk of destruction (Figure 2.1). Among 59 nests still intact in summer 2015, 46% were at low, 38% at moderate, 16% at high risk of being destroyed by mass movement processes.

The probability that a nest was destroyed was positively associated to the number of days with heavy rain (≥ 7 mm) recorded during a given summer ($\beta = 0.42$, 95% CI $= 0.15$, 0.72; Figure 2.4). Similar results were found with thresholds of 3 mm ($\beta = 0.14$, 95% CI $= 0.03$, 0.25) and 5 mm ($\beta = 0.25$, 95% CI $= 0.08$, 0.43). No relationship was found between proba-

bility of nest destruction and summer cumulative thawing degree-days (β = 0.08, 95% CI = -0.64, 1.04).

Nest vulnerability, nest use and reproductive success

Nest use probability decreased slightly with an increase in the risk of destruction by geomorphological processes (β = -3.65, 95% CI = -7.24, -0.60, n = 190; Figure 2.5). We observed breeding failures directly caused by mass movements in two cases (in 2008 and 2014). We also documented in details a nest collapse that occurred in summer 2014 due to a slope failure following high precipitation events, which resulted in the death of chicks (see Figure A.4). However, the vulnerability of the nest did not explain variation in hawk nesting success (β = -1.99, 95% CI = -6.55, 1.99, n = 52) and brood size (β = -0.22, 95% CI = -1.17, 0.72, n = 35).

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 reproductive success of Arctic-breeding species. Mass movements have been suspected to influence the reproduction of various arctic cliff-nesting species(Cade, 1960; White and Cade, 1971; Poole and Bromley, 1988b). Studies in Russia and in western Canadian Arctic reported the destruction of hawk nests by such processes (White and Cade, 1971; Swem, 1996; Potapov, 1997; Gauthier et al., 2011b), but the mechanisms involved in such events remain largely unknown. Our study showed that mass movements were the main cause of destruction of rough-legged hawk nests and affected their lifespan. A high proportion of nesting structures was destroyed or exposed to a moderate to high risk of being destroyed. In addition, we found a strong influence of material type and summer precipitation on the risk of nest destruction. Mass movements were a minor cause of breeding failure and hawks tendend to avoid breeding in nesting strcuture more vulnerable to these movements. Our study thus provides a new perspective by integrating ecology and geomorphology to better understand nest persistence of an arctic top predator.

Our survival analysis suggests a shorter persistence of rough-legged hawk nesting structures

on Bylot Island (7.6 yrs on average) compared to other species such as forest raptors (median nest lifespan of 12 years; Jiménez-Franco et al. 2014*a*) or gyrfalcons (*Falco rusticolus*), for which nests may remain for hundreds of years (Burnham et al., 2009). Moreover, unlike other cliff-nesting raptors such as golden eagles (*Aquila chrysaetos*), where most breeding territories have 5 or more nests (Kochert and Steenhof, 2012), or bearded vultures (*Gypaetus barbatus*) where territories can have >10 nests (Margalida and García, 1999), most (58%, Chapter 1) rough-legged hawk territories contained only one nesting structure. Nesting structures are key resources for raptors (Jiménez-Franco et al., 2014*b*; 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 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).

Compared to other arctic cliff-nesting raptors and ravens, rough-legged hawks demonstrate considerable 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*) use mainly nesting sites sheltered by overhang providing protection from falling rock (White and Cade, 1971; Poole and Bromley, 1988*a*). Thus, the exposed nest placement characteristic of rough-legged hawks make them especially susceptible to nest destruction by mass movement processes 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 in slope underlain by unconsolidated sediments (French, 2007; Daanen et al., 2012) and nests build on unconsolidated sediments had the highest probability of being destroyed. The bedrock of our study area is mainly constituted of sedimentary rock (Jackson and Sangster, 1987; Klassen, 1993), which is more likely to contain ground ice and 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 very stable compared to sedimentary rocks. In contrast, raptor nests on Herschel Island, which are mostly

built on muddy or sandy cliffs, also suffer from a high lost rate likely due to coastal erosion and retrogressive thaw slump activity in this case (see Lantuit and Pollard, 2008; Gauthier et al., 2011*b*). High lost rate (25%) was also reported along Colville River in Alaska where nests are build mainly on unconsolidated sediments (Swem, 1996). Rough-legged hawk nest lifespan is thus likely to be strongly influenced by the local lithography and geomorphology.

Mass movements such as slope failure and rockfalls are heavily influenced by climatic factors (Can et al., 2005; Gruber and Haeberli, 2007; Lantuit and Pollard, 2008; Daanen et al., 2012; French and Slaymaker, 2012) and our results showed that heavy rain increased the risk of destruction of rough-legged hawk nesting structures. Heavy rain can trigger mass movements through many mechanisms. For instance, by reducing tensile strength due to water weight 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 sensible to precipitations through weathering processes (Hodgson and Nixon, 1998; French et al., 1986). Further increase in summer precipitation in northern areas as a result of ongoing climate warming (IPCC, 2013) is 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 a higher risk of destruction. The chilling effect of rainfall on young chick is known to be a key factor directly influencing reproductive success in arctic raptors (Potapov, 1997; Anctil et al., 2014). Our results showed 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 failure for active rough-legged hawk nests at our study site. 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) showed that 25% of breeding failure of rough-legged hawk in Alaska was related to mass movements, especially slope failure. These differences are likely due to variations in local geomorphology between sites. Otherwise, in our study, nest destruction could have been underestimated because most nests were monitored only until half-way through the chick rearing period. Nests could be more likely to be destroyed late in the nesting season because mass movements are more frequent in late summer (Mackay, 1981; Lewkowicz, 1992; French, 2007). Nest use probability decreased with an increase in the risk of destruction by mass movements but this effect was not very strong. Thus, despite a tendency of rough-legged hawks to avoid breeding in highly vulnerable nests, this effect may not be sufficient to compensate for a possible increase in the

exposure of nest to mass movements in the future.

To our knowledge, this study is the first empirical demonstrations of the link between geomorphological processes and nest persistence in a cliff-nesting species. Given that availability of suitable nesting sites is often limited in many raptor species (Newton, 1979; Restani, 1991; Kennedy et al., 2014), it is possible that a reduction in rough-legged hawk nest persistence due to anticipated increase in slope instability by ongoing climate change will result in future declines in nesting hawk density in some areas or even variations in distribution across its breeding range.

Acknowledgements

Table 2.1 – (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_i), log-likelihood values (LL) and R^2 are presented for each model. (b) Model-averaged parameter estimates from the most parsimonious models (ΔAICc < 4) and their 95% confidence intervals (CI). Estimates considered statistically significant are marked in bold.

a)

Variables in the model	k	Δ AICc	w_i	LL	R^2
Material[1], Vegetation[2]	5	0.00	0.30	-41.76	0.26
Material	4	0.03	0.30	-42.91	0.23
Material, Slope[3]	5	2.26	0.10	-42.89	0.23
Material Vegetation, Slope	6	2.33	0.09	-41.76	0.26
Material, Vegetation, Slope, Vegetation x Slope	7	2.65	0.08	-40.72	0.40
Vegetation, Slope, Vegetation x Slope	4	3.45	0.05	-44.62	0.26
Slope	2	4.42	0.03	-47.29	0.07
Vegetation, Slope	3	4.61	0.03	-46.31	0.11
Null	1	6.88	0.01	-49.57	0.00
Vegetation	2	8.05	0.01	-49.10	0.02

b)

Parameters	β	95% CI
Slope	-0.01	-0.05, 0.03
Vegetation	-3.68	-15.53, 8.17
Vegetation x Slope	0.13	-0.04, 0.65
Unconsolidated sediments	**2.49**	**0.81, 4.17**
Poorly consolidated rock	1.73	-0.04, 3.51
Consolidated and altered rock	**1.88**	**0.32, 3.45**

[1]Material: Consolidated and weakly altered rock (reference level), consolidated and altered rock, poorly consolidated rock and unconsolidated sediments.
[2]Vegetation: 0-20% (reference level) and 20-100 %
[3]Slope: Aspect (°)
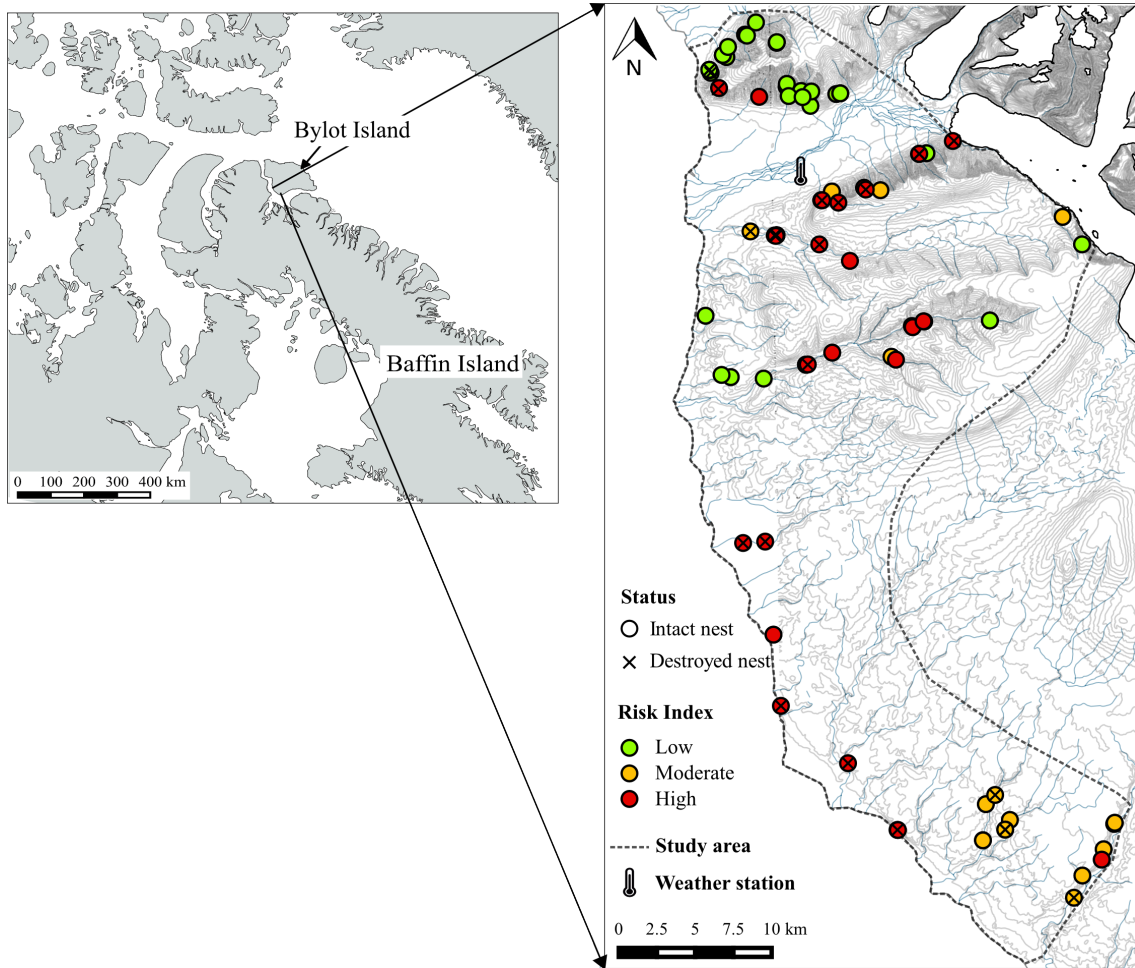
Figure 2.1 – Location of the study site on the southern plain of Bylot Island, Nunavut, Canada. The study area is shown on the right, including location of the weather station, position, status (i.e. destroyed during the study period or intact at the end) and risk index (probability of being destroyed according to our analysis; see results) of all rough-legged hawk nesting structures ($n = 82$) monitored between 2007 to 2015. Spacing between contour lines is 20 m.
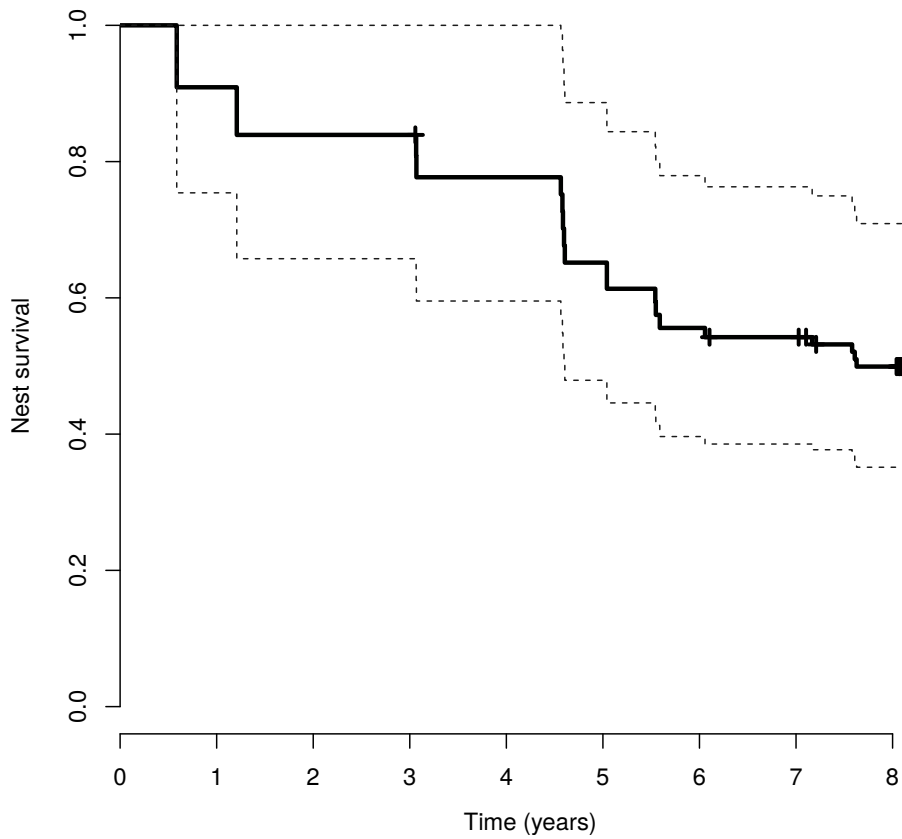
Figure 2.2 – Survival of rough-legged hawk nests on Bylot Island based on Kaplan-Meier estimates ($\pm$ 95% CI; errors lines). Each tick mark represents the time a nest was censored (i.e. the last time that an undestroyed nest was visited). Sample size range from 11 at time 0 to 51 at 8 years.
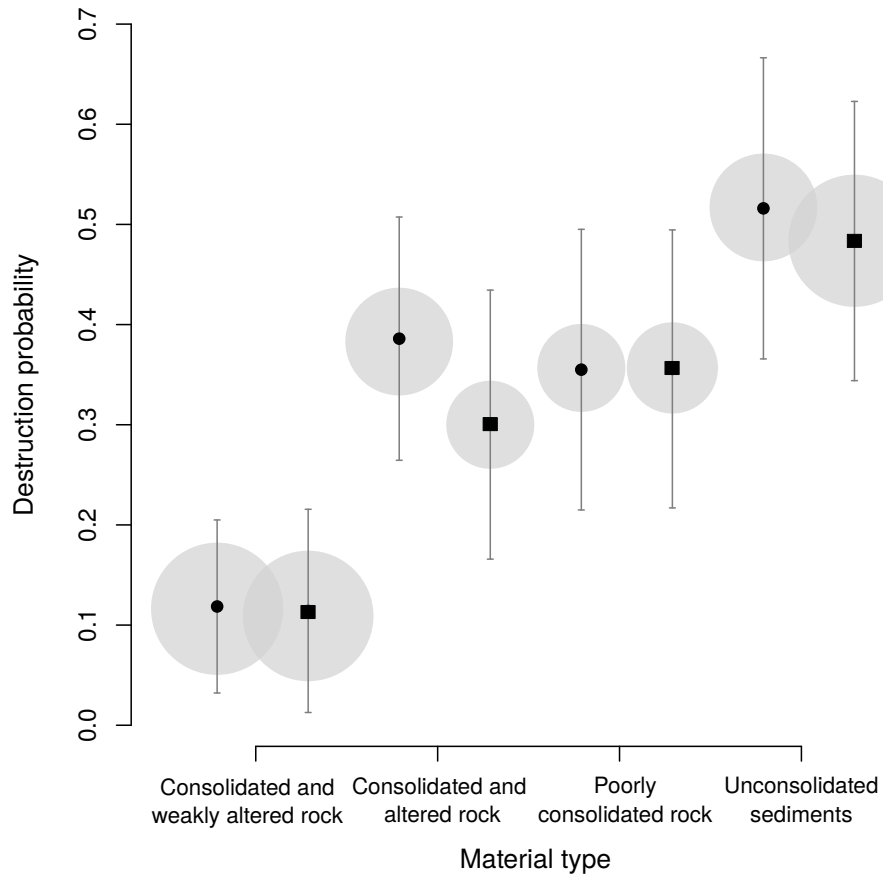
Figure 2.3 – Probability of destruction of rough-legged hawk nesting structures in relation to material type below (circles) and above (squares) the nest based on model-averaged estimates (Table 2.1 and A.5). Errors bars represent 95% confidence intervals and circle size is proportional to the number of observations.
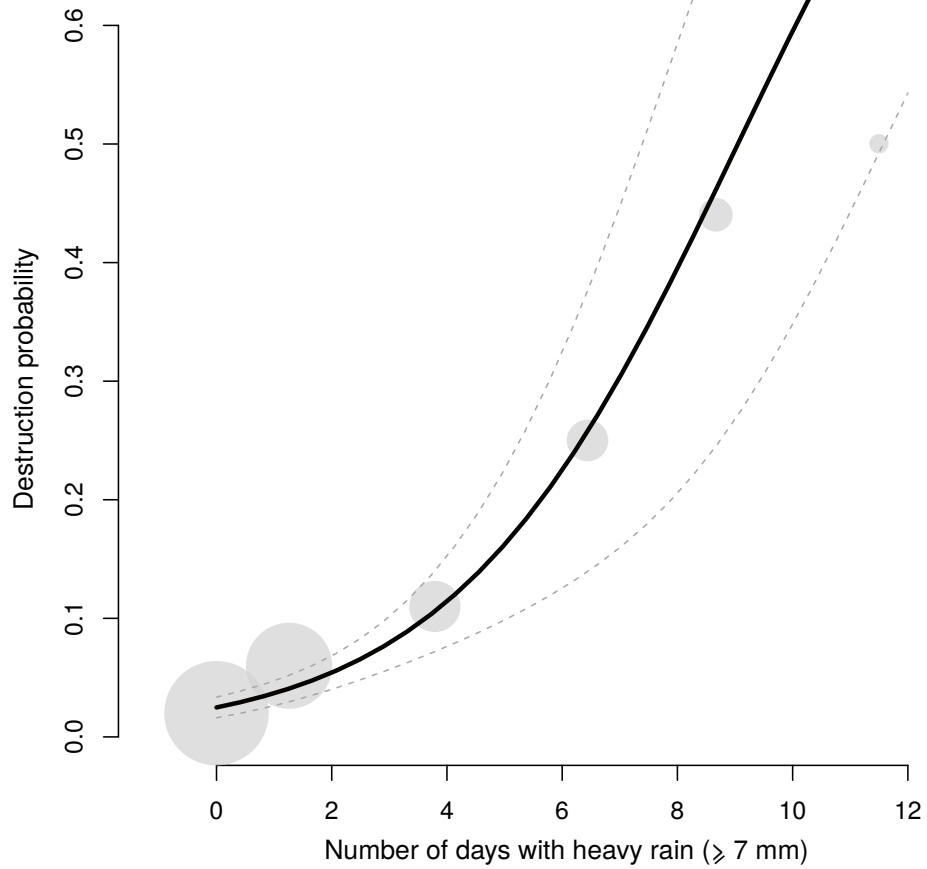
Figure 2.4 – Probability of destruction of rough-legged hawk nests in relation to the number of days with heavy rain ($\geqslant$ 7 mm). To illustrate observed values, each circle represents the proportion of destroyed nests grouped by similar number of days with rain (circle size is proportional to the number of observations). Dashed lines are the 95% confidence interval of the regression.
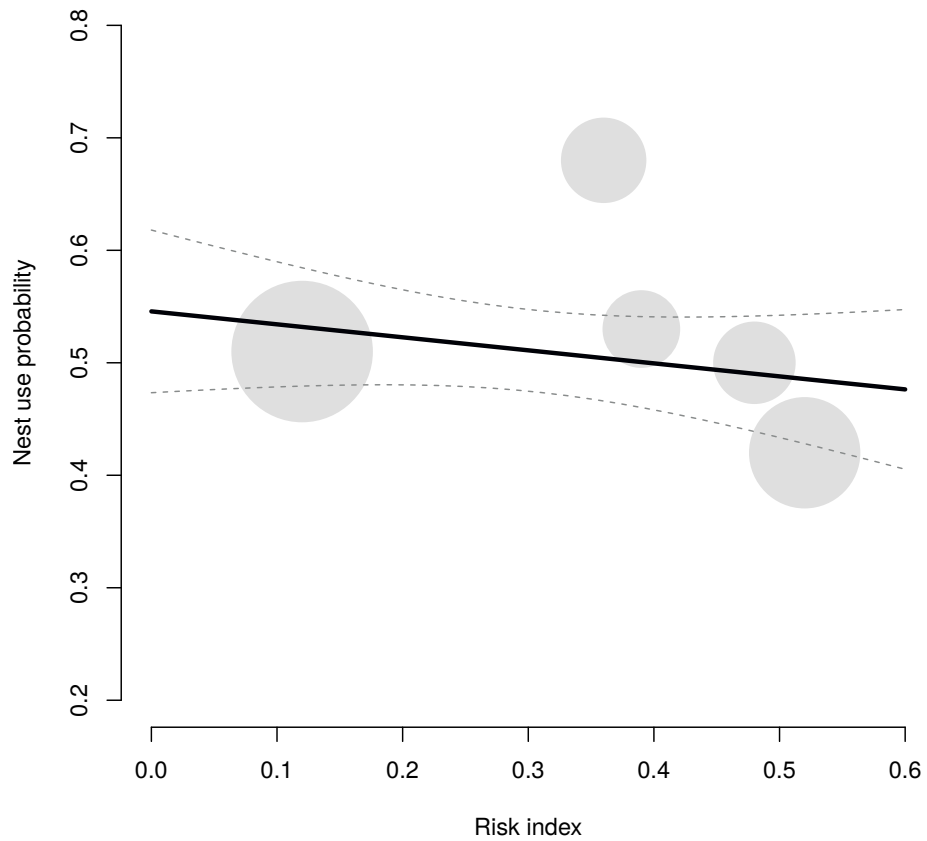
Figure 2.5 – Probability that a nest was used by a rough-legged hawk breeding pair according to the risk of nest destruction by a mass movement (risk index). To illustrate observed values, each circle represents the proportion of used nest grouped by similar risk index (circle size is proportional to the number of observations). Dashed lines are the 95% confidence interval of the regression.

Conclusion

Les prédateurs aviaires jouent un rôle clé au sein du réseau trophique de la toundra arctique et sont une des forces dominantes structurant ce réseau (Gauthier et al., 2011*a*; Therrien et al., 2014*a*). L'Arctique étant une région difficile d'accès, les connaissances demeurent toutefois limitées pour la plupart de ces espèces, en particulier en ce qui a trait à leur reproduction, une phase critique du cycle vital. Dans le cadre de ce mémoire, j'ai abordé différents aspects écologiques et géomorphologiques associés à la reproduction d'un rapace nichant dans le Haut-Arctique. Je me suis intéressée d'une part à mettre en évidence les liens possibles entre des facteurs environnementaux et différents paramètres de la reproduction de la buse pattue. Ensuite, j'ai évalué la vulnérabilité des nids de ce rapace aux risques géomorphologiques et j'ai identifié certaines caractéristiques géomorphologiques associées à la persistance des nids au fil des ans.

Contributions et limites de l'étude

En appui à ce qui a déjà été documenté chez cette espèce (Potapov, 1997; Wiklund et al., 1998; Hellström et al., 2014; Therrien et al., 2014*a*; Terraube et al., 2015), les buses ont démontré dans cette étude une forte réponse numérique aux fluctuations d'abondance de leur proie principale, les lemmings, résultant en de grandes variations interannuelles du nombre de nids actifs. Non seulement peu d'individus nichaient lorsque les densités de lemmings étaient faibles mais même parmi ceux-ci, qui étaient potentiellement des individus expérimentés, le succès reproducteur était réduit comparativement aux années de fortes abondances de nourriture. Sur l'île Kolguev en Russie, où les petits mammifères sont rares, la buse pattue peut apparemment se reproduire avec succès, en utilisant des proies alternatives comme des lagopèdes, des oisillons et des passereaux (Pokrovsky et al., 2015). Ainsi, la forte réponse numérique des buses sur l'île Bylot suggère que ces proies alternatives ne sont pas suffisamment abondantes pour permettre une reproduction réussie quand les lemmings sont rares.

L'utilisation d'habitats escarpés par les rapaces pour nicher est probablement une stratégie pour réduire le risque de prédation par voie terrestre (e.g., Ames and Mersereau, 1964; Ogden

and Hornocker, 1977; Roth and Marzluff, 1989; Anderson et al., 2015). Par exemple, dans les Aléoutiennes, le pygargue à tête blanche (*Haliaeetus leucocephalus*) utilise des nids accessibles aux renards arctiques seulement sur les îles où ceux-ci sont absents (Sherrod et al., 1977). En accord avec nos résultats, Swem (1996) a démontré que les nids de buses pattues, en Alaska, étaient plus susceptibles d'échouer lorsqu'ils étaient accessibles aux prédateurs terrestres. À l'île Bylot, il est bien documenté que les fluctuations annuelles d'abondance des lemmings, la proie préférée des renards arctiques, peuvent entraîner des variations annuelles de la pression de prédation par les renards sur d'autres proies (Bêty et al., 2002; Gauthier et al., 2015). Les oeufs ou les jeunes buses, dans les nids accessibles aux renards, pourraient ainsi être exposés à un risque de prédation plus élevé lorsque l'abondance des lemmings est faible et que les renards sont à la recherche de proies alternatives. Ainsi, l'effet de la disponibilité de la nourriture sur le succès reproducteur des buses documenté ci-dessus pourrait être expliqué non seulement par un effet trophique par le bas (*bottom-up*), soit une réduction de la disponibilité de la nourriture, mais aussi par un effet trophique par le haut (*top-down*) via la prédation intraguilde lors des années de faible densité de lemmings.

Les nids protégés d'un surplomb étaient davantage utilisés et ceux orientés autrement que vers le nord étaient associés à un meilleur succès reproducteur. Ces caractéristiques peuvent conférer des conditions microclimatiques favorables à la reproduction, d'une part en améliorant l'environnement thermique (Fortin et al., 2000; Fast et al., 2007) ou d'autre part en protégeant les oeufs et les jeunes des vents forts ou des précipitations (White and Cade, 1971; Anctil et al., 2014). Ces dernières sont considérées comme un facteur clé influençant la reproduction des rapaces en Arctique (Potapov, 1997; Lehikoinen et al., 2013; Anctil et al., 2014). Nos résultats montrent également que la survie des jeunes était négativement affectée par les fortes précipitations, ce qui corrobore les résultats des études antérieures chez la buse pattue (Potapov, 1997; Pokrovsky et al., 2012). Ces résultats confirment que les facteurs abiotiques peuvent être des déterminants importants du succès reproducteur chez les rapaces qui nichent dans l'Arctique.

Cette étude a démontré un haut taux de réutilisation des territoires précédemment occupés et des structures préexistantes ce qui suggère la fidélité des individus au site de nidification. De plus, les structures préexistantes pourraient agir comme un indicateur de la qualité de l'habitat lorsque des individus s'établissent dans un territoire. Ce résultat confirme également l'importance des structures existantes pour la reproduction, et on pourrait s'attendre à ce que la réutilisation d'une structure se reflète sur le succès reproducteur, par l'entremise,

par exemple, d'une réduction du temps et de l'énergie requis pour la reproduction. Nous n'avons toutefois pas trouvé d'évidences que la construction d'un nid entraîne des coûts sur la reproduction. En accord avec ces résultats, il semble que la majorité des études sur les rapaces n'ont pas démontré d'effet de la réutilisation d'un nid sur le succès reproducteur (Kochert and Steenhof, 2012; Jiménez-Franco et al., 2014*a,b*), bien que de telles études sont peu nombreuses. Toutefois, le succès d'éclosion et de nidification étaient plus élevés pour les nids dans les territoires précédemment occupés comparativement à ceux dans les territoires nouvellement occupés. Ce résultat suggère qu'une forte proportion des individus utilisant les nouveaux territoires étaient jeunes, moins expérimentés, lesquels ont généralement un moins bon succès reproducteur (Nielsen and Drachmann, 2003; Blas et al., 2009), ou bien que certains de ces territoires étaient de moins bonne qualité (Korpimäki, 1988*b,a*; Newton, 1989; Penteriani et al., 2003). Cependant, nos résultats ne nous permettent pas de trancher entre ces deux hypothèses.

Bien que les environnements nordiques soient considérés comme des milieux géomorphologiquement sensibles aux changements climatiques, les mécanismes reliant les processus géomorphologiques à la reproduction de la faune arctique sont très peu documentés. Les processus géomorphologiques ont été soupçonnés d'influencer la reproduction d'une variété d'espèces nichant sur les falaises en Arctique (Cade, 1960; White and Cade, 1971; Poole and Bromley, 1988*b*). Quelques études en Russie et dans l'ouest du Canada ont reporté des cas de destruction de nids de buses pattues (White and Cade, 1971; Swem, 1996; Potapov, 1997; Gauthier et al., 2011*b*). Cependant, les mécanismes impliqués dans ces événements demeurent inconnus. Cette étude a permis d'identifier que les processus géomorphologiques, tels que les ruptures de pente et les chutes de blocs, étaient la principale cause de destruction des nids de buses pattues et qu'ils influençaient leur persistance. Près du tiers des nids ont été détruits et parmi ceux encore intacts, plus de la moitié sont à risque modéré ou haut de l'être. La destruction d'un nid peut avoir des impacts directs sur la reproduction en influençant le succès de nidification et aussi indirects, à travers une réduction de la persistance des nids au fil des ans.

Nos résultats suggèrent que les processus géomorphologiques ont des effets directs mineurs sur la reproduction des buses dans notre système d'étude. Nous n'avons pas détecté de lien entre le risque de destruction d'un nid par des processus geomorphologiques et le succès de nidification et les buses avaient tendance à éviter la reproduction dans les nids plus vulnérables. Dans le Nord de la Sibérie, Potapov (1997) a reporté des résultats similaires soit que

4 % des échecs de la reproduction étaient liés à la destruction du nid. Cependant, en Alaska, les processus géomorphologiques étaient la cause de 25 % des cas d'échecs de la reproduction des buses (Swem, 1996). Ces différences peuvent être dues à des variations du contexte géomorphologique entre les sites. Toutefois, nous avons peut-être sous-estimé l'effet de la destruction du nid sur le succès reproducteur dans notre étude puisque les processus géomorphologiques sont particulièrement fréquents à la fin de l'été (Mackay, 1981; Lewkowicz, 1992; French, 2007) et que notre suivi de la nidification s'étendait rarement au-delà de la fin juillet.

Cette étude suggère que les nids de buses pattues persistent moins longtemps (espérance de vie médiane estimée à 7.6 ans) comparativement à d'autres espèces de rapaces. À titre comparatif, Jiménez-Franco et al. (2014*b*) ont obtenu, par la même méthode que la présente étude, une espérance de vie médiane d'environ 12 ans chez 3 espèces de rapaces forestiers. Également, contrairement à d'autres espèces de rapaces qui nichent sur les falaises telles que l'aigle royal, pour lesquels un territoire contient en moyenne 7 nids (Kochert and Steenhof, 2012), les territoires de buses pattues avaient en moyenne <2 nids et la majorité en contenait un seul (58%, chapitre 1). Les structures existantes sont une ressource importante pour la reproduction des rapaces (Jiménez-Franco et al., 2014*b*; Millsap et al., 2015), et la disponibilité de nids alternatifs au sein d'un même territoire peut avoir plusieurs rôles écologiques (Ontiveros et al., 2008). Par exemple, lorsque le nid est endommagé (e.g., enseveli, effondré, a basculé par des vents forts) tôt en saison de reproduction, le couple dispose d'un nid alternatif pour se reproduire (Newton, 1979; Kochert and Steenhof, 2012; Millsap et al., 2015). La destruction d'un nid a ainsi probablement plus d'impact dans un territoire contenant un seul nid comparativement à un territoire en contenant plusieurs (Kochert and Steenhof, 2012).

Le type de matériel, un facteur déterminant de la stabilité des pentes, avait une forte influence sur le risque de destruction d'un nid. La roche-mère de la plaine sud de l'île Bylot est constituée de roches sédimentaires (Klassen, 1993), qui sont plus susceptibles de contenir de la glace, plus sensibles au soulèvement cryogénique et à la gélifraction comparativement aux roches cristallines (Hodgson and Nixon, 1998; Dredge et al., 1999; Murton et al., 2006). Cet effet que nous avons détecté à l'île Bylot serait applicable aux sites avec une lithologie et des dépôts de surface similaires, mais ne pourrait probablement pas être généralisé à l'échelle de l'Arctique. Par exemple, les nids de buses le long de la côte ouest de la baie d'Hudson se trouvent principalement sur la roche cristalline (Laporte, 1975; Court, 1986) qui est très stable comparativement à la roche sédimentaire. En revanche, les nids de buses sur l'île Her-

schel et sur le long de la rivière Colville en Alaska semblent être sur un substrat plus similaire aux nids de l'île Bylot et un taux de destruction élevé a également été rapporté (Swem, 1996; Gauthier et al., 2011b). Ainsi, le contexte géomorphologique d'un site est susceptible d'avoir une forte influence sur la vulnérabilité des nids.

En plus de l'influence du type de matériel, le risque de destruction d'un nid était positivement associé aux événements de fortes précipitations. Il est bien documenté que les mouvements de masse sont fortement influencés par des facteurs climatiques tels que la température et les précipitations (Can et al., 2005; Gruber and Haeberli, 2007; Chiarle et al., 2011). Une augmentation de la fréquence et de l'amplitude de ces mouvements en lien avec les changements climatiques a été reportée par quelques auteurs (Lewkowicz and Harris, 2005; Lantuit and Pollard, 2008; French and Slaymaker, 2012). En conséquence, l'exposition des nids de buses aux mouvements de masse est susceptible d'être amplifiée dans le futur. Les structures existantes sont une ressource importante pour la reproduction des rapaces (Jiménez-Franco et al., 2014b; Millsap et al., 2015) et la disponibilité de sites de nidification de haute qualité semble être particulièrement limitée chez ces espèces (Newton, 1979; Restani, 1991; Kennedy et al., 2014). Une réduction de la disponibilité de ces sites pourrait ultimement influencer la répartition et l'abondance des buses dans certaines régions de l'Arctique, dépendamment du contexte géomorphologique de chaque région.

Perspectives futures

Cette étude a permis d'évaluer la vulnérabilité des nids de buses aux risques géomorphologiques et d'identifier certaines caractéristiques influençant leur persistance. Par contre, l'indice de risque assigné à chaque structure ne nous informe pas sur le temps que ce nid devrait persister. Cet aspect temporel manquant limite l'interprétation de nos résultats puisque les implications biologiques d'un nid qui persiste 1 an versus 10 ans sont différentes. Hors, il faudrait d'abord poursuivre le suivi de l'état des structures de nidification pour améliorer l'estimé de survie des nids. Puis, il faudrait mettre directement en relation les caractéristiques géomorphologiques et certaines variables climatiques avec la survie des nids en utilisant une approche par modèles de Cox (voir Edworthy et al., 2012; Jiménez-Franco et al., 2014a). Combinée avec des projections climatiques, cette approche pourrait ultimement permettre de prédire dans quelle mesure la survie des structures est susceptible d'être influencée par les

changements climatiques.

Il y a de plus en plus d'évidences que les oiseaux prédateurs sont un élément clé et structurant de l'écosystème terrestre arctique (Gilg et al., 2003 ; Krebs et al., 2003 ; Gauthier et al., 2011*a* ; Legagneux et al., 2014). Les facteurs influençant la répartition spatiale des prédateurs de la toundra demeurent toutefois peu connus bien que certains progrès ont été réalisés chez quelques espèces [e.g., harfang des neiges (Therrien et al., 2011, 2015) ; renard arctique (Lai et al., 2015), faucon pèlerin (Wightman and Fuller, 2006 ; Peck, 2015)]. Qu'est qui limite la répartition nordique des prédateurs ? Quelle est la relation entre la répartition spatiale de ces espèces et la disponibilité des habitats appropriés à leurs besoins ? Et quels sont les mécanismes proximaux qui guident les prédateurs dans leurs déplacements et lors de la sélection d'un site de nidification ? Concernant plus spécifiquement la buse pattue, l'étude des stratégies des déplacements de cet oiseau à l'aide d'individus marqués ou d'émetteurs satellitaires serait certainement une avenue de recherche fort intéressante. Tel que mentionné précédemment, le haut niveau de réutilisation des structures existantes par les buses suggère un certain degré de fidélité au site de nidification. Ce comportement est généralement associés aux prédateurs généralistes, comme le faucon pèlerin, qui démontrent des réponses numériques agrégatives plus faibles associées à une fidélité plus grande au site de reproduction (Sokolov et al., 2014 ; Smith et al., 2015). Cependant, la forte réponse numérique des buses aux fluctuations d'abondance des lemmings (Therrien et al., 2014*a*, Chapitre 1) suggère une faible fidélité aux sites de reproduction entre les années, une stratégie qui s'apparente plutôt à une espèce comme le harfang des neiges (Therrien et al., 2014*b*). Dans ce contexte, l'étude des stratégies de déplacements de cet oiseau suscite un intérêt particulier.

Finalement, la poursuite des suivis écologiques à long terme, tels que ceux réalisés à la station de recherche de l'île Bylot, devrait être encouragée. La présente étude contribue d'une part à l'avancement des connaissances d'une espèce peu étudiée mais d'autre part, ces travaux pourront être intégrés à d'autres réalisés à l'île Bylot et permettront ultimement une meilleure compréhension de l'écosystème global. Une telle intégration serait difficile sans un suivi écosystémique aussi détaillé.

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Annexes

Table A.1 – Variables, number of parameters (k), ΔAICc (difference between current model and the preferred model), AICc weight (w_i), log-likelihood (LL) and marginal R^2 of the candidate models explaining rough-legged hawk nest use ($n = 185$). Nest ID was included as a random effect in all models. See Table 1.1 for a description of each variable.

Variables	k	ΔAICc	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

Table A.2 – Variables, number of parameters (k), ΔAICc (difference between current model and the preferred model), AICc weight (w_i), log-likelihood (LL) and marginal R^2 of the candidate models explaining rough-legged hawk hatching success (n = 68). Nest ID was included as a random effect in all models. See Table 1.1 for a description of each variable.

Variables	k	ΔAICc	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

Table A.3 – Variables, number of parameters (k), ΔAICc (difference between current model and the preferred model), AICc weight (w_i), log-likelihood (LL) and marginal R^2 of the candidate models explaining rough-legged hawk nesting success ($n = 59$). Nest ID was included as a random effect in all models. See Table 1.1 for a description of each variable.

Variables	k	ΔAICc	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

Table A.4 – Variables, number of parameters (k), ΔAICc (difference between current model and the preferred model), AICc weight (w_i), log-likelihood (LL) and marginal R^2 of the candidate models explaining rough-legged hawk brood size (n = 38). Nest ID was included as a random effect in all models. See Table 1.1 for a description of each variable.

Variables	k	ΔAICc	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	-71.5	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	-71.9	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
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

Table A.5 – (a) Model selection among candidate models explaining destruction of rough-legged hawk nests in relation to geomorphological characteristics of the slope below the nest ($n = 78$). Number of parameters (k), ΔAICc values, AICc weights (w_i), log-likelihood values (LL) and R^2 are presented for each model. (b) Model-averaged parameter estimates from the most parsimonious models (ΔAICc < 4) and their 95% confidence intervals (CI). Estimates considered statistically significant are marked in bold.

a)

Variables in the model	k	Δ AICc	w_i	LL	R^2
Material[1]	4	0.00	0.38	-41.24	0.26
Material, Vegetation[2]	5	1.20	0.21	-40.70	0.27
Material, Slope[3]	5	2.19	0.13	-41.20	0.26
Slope	2	2.48	0.11	-44.68	0.13
Material, Vegetation , Slope	6	3.52	0.07	-40.68	0.27
Vegetation, Slope	3	4.18	0.05	-44.44	0.14
Material, Vegetation , Slope, Vegetation x Slope	7	5.89	0.02	-40.66	0.27
Vegetation, Slope, Vegetation x Slope	4	5.99	0.02	-44.24	0.15
Null	1	7.31	0.01	-48.14	0.00
Vegetation	2	9.37	0.00	-48.12	0.01

b)

Parameters	β	95% CI
Slope	-0.01	-0.05, 0.03
Vegetation	-0.79	-2.87, 1.28
Unconsolidated sediments	**2.67**	**0.78, 4.56**
Poorly consolidated rock	**2.02**	**0.00, 4.05**
Consolidated and altered rock	1.72	-0.39, 3.83

[1]Material: Consolidated and weakly altered rock (reference level), consolidated and altered rock, poorly consolidated rock and unconsolidated sediments.
[2]Vegetation: 0-20% (reference level) and 20-100 %
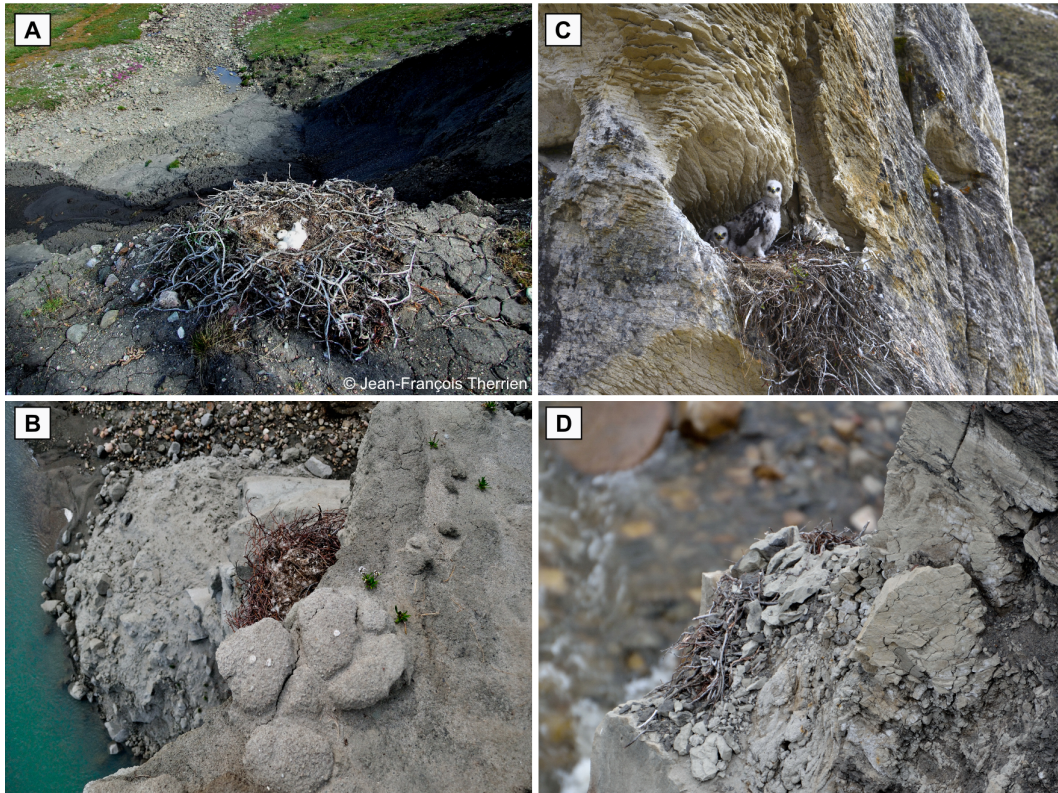[3]Slope: Aspect (°)

Figure A.1 – Material type classification: (**A**) unconsolidated sediments (diamicton essentially comprising 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.
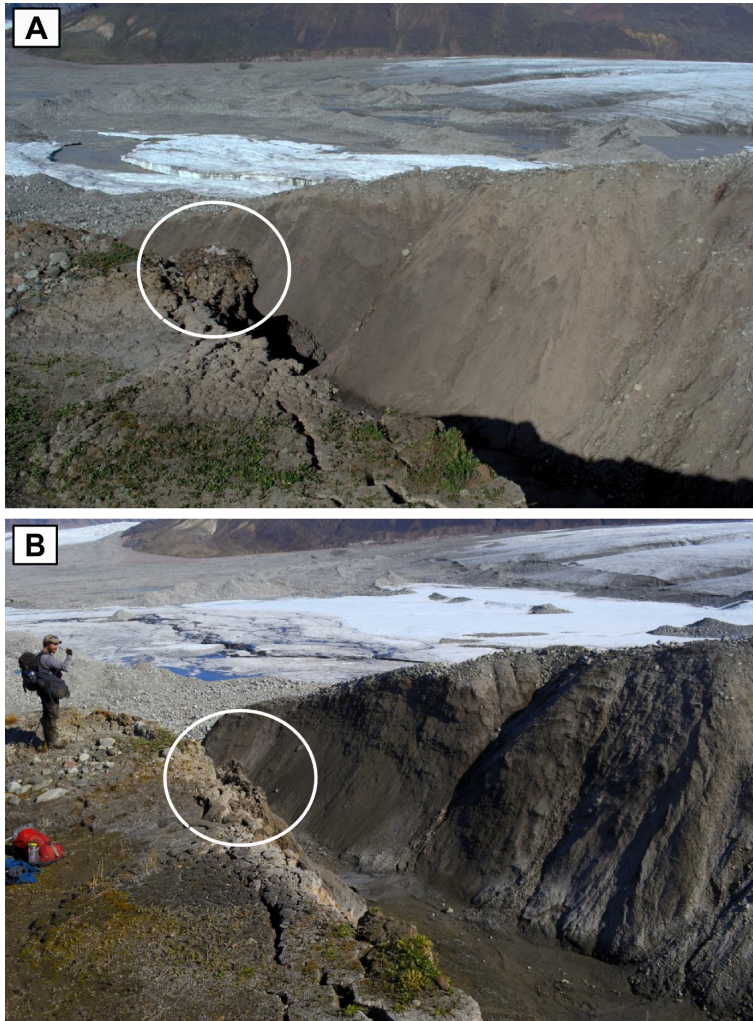
Figure A.2 – Photographs documenting the destruction of a rough-legged hawk nesting structure (circle) caused by a slope failure in glacial diamicton that occurred between July 2014 (**A**) and June 2015 (**B**). Note the tensile cracks in the surficial deposit.
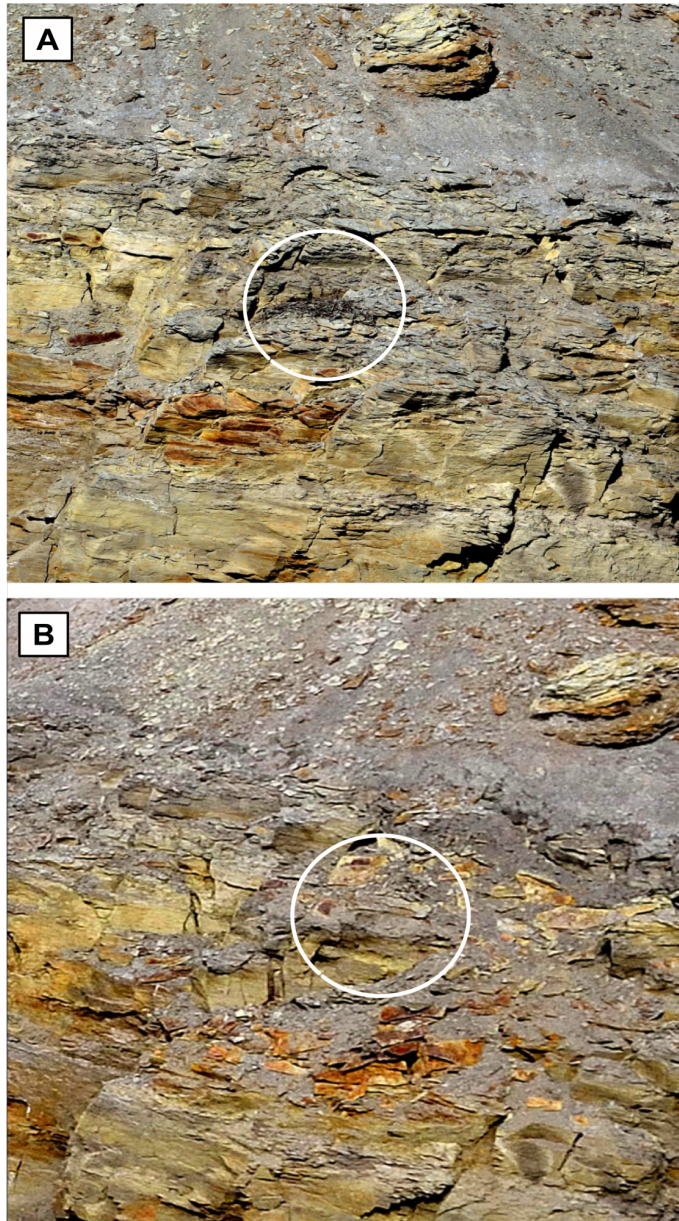
Figure A.3 – Photographs documenting the destruction of a rough-legged hawk nesting structure (circle) caused by a rockfall that occurred in 2013 between 14 June (**A**) and 30 July (**B**). (**A**) Note the unstable debris-covered apron over the nesting structure and in (**B**), fallen debris that accumulated close to the nest.
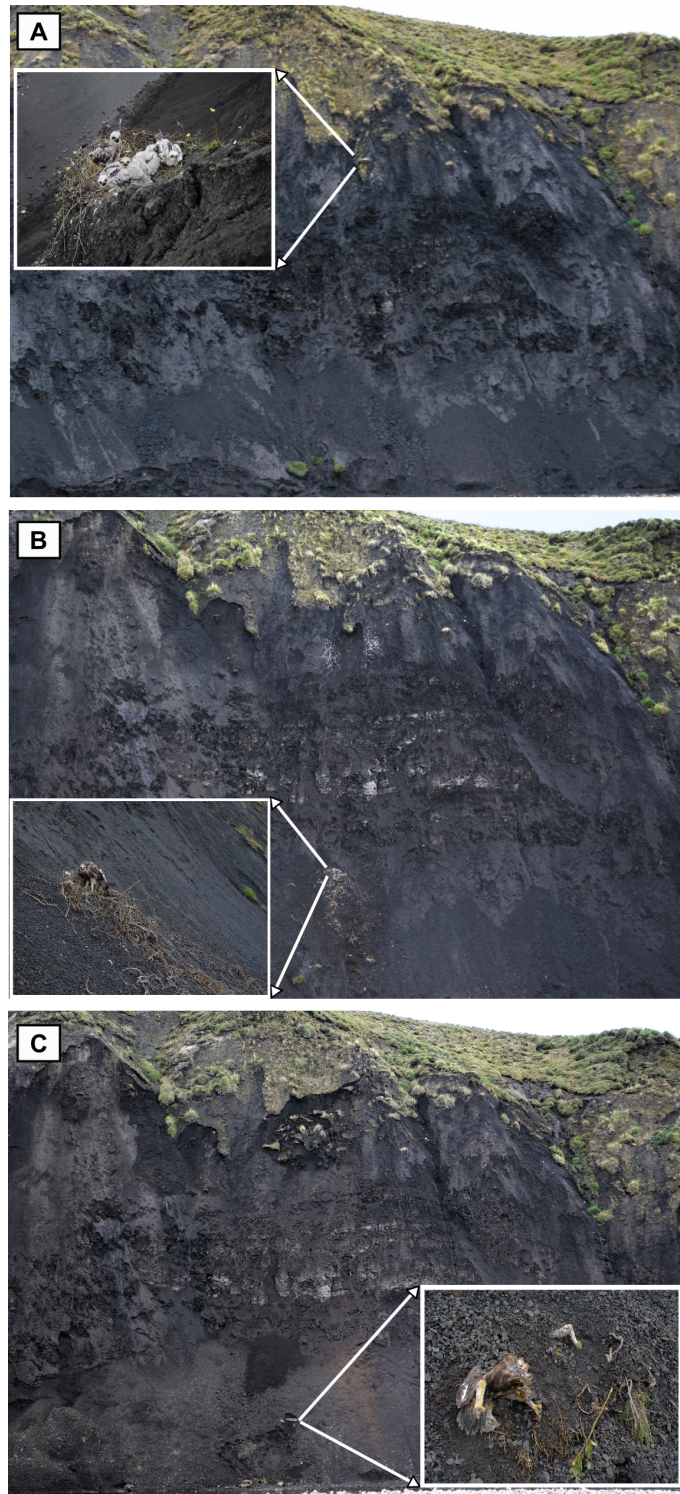
Figure A.4 – A photo-montage documenting the complete destruction of a rough-legged hawk nest caused by a slope failure in 2014. (**A**) Intact nest. (**B**) On 5 August, following 2 days of heavy rain (6.0 and 7.5 mm), the nest collapsed. (**C**) On 8 August the nest was buried with 3 dead chicks.