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APPLICATIONS OF AN UNMANNED AIRCRAFT VEHICLE AND REMOTE CAMERAS FOR STUDYING A SUB-ARCTIC ECOSYSTEM

by

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Bachelor of Science, University of British Columbia 2014

A Dissertation

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This dissertation, submitted by Andrew Barnas in partial fulfillment of the requirements for the Degree of Doctoral of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

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Andrew Barnas
December 4, 2019

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ABSTRACT

The midcontinent population of lesser snow geese (*Anser caerulescens caerulescens*) has increased dramatically since the 1960's due to changing agricultural practices in their southern wintering areas. The destructive foraging and continued population growth of lesser snow geese has resulted in cascading negative impacts on northern ecosystems. Studying remote sub-Arctic ecosystems is logistically challenging, but the advent of remote sensing technologies (such as drones and remote cameras) may assist ecologists in understanding snow goose ecology. Before these tools can be integrated into snow goose research programs, precursor "proof-of-concept" studies are required to validate tool use. The objectives of this study were to investigate the use of unmanned aircraft systems (hereafter "drones") and remote cameras for studying various aspects of lesser snow goose ecology within the sub-Arctic ecosystem of the Cape Churchill Peninsula, Manitoba, Canada.

We first evaluated impacts of drone surveys on wildlife by measuring drone-induced behavioural responses of nesting lesser snow geese using mini-surveillance cameras. We monitored 25 nests with cameras from 2015-2016, comparing behaviours of birds on days with drone surveys, and on days without surveys. Days with drone surveys resulted in decreased low-vigilance behaviours, and increased high-vigilance behaviours. Similarly, overhead vigilance behaviours increased from a baseline 0.03% of observation time to 0.56% when the drone was overhead, indicating birds were likely observing the drone as it flew overhead. Polar bears (*Ursus maritimus*) were also monitored via video recording during drone flights in 2016, and

they responded in a similar fashion to previously published tourism activity impact estimates (mean vigilance bout lengths during drone surveys = 18.7 ± 2.6 seconds).

We estimated goose habitat degradation using photointerpretation of drone imagery and compared estimates to those made with ground-based linear transects. We compared estimates between ground-based transects and those made from unsupervised classification of drone imagery collected at altitudes of 75, 100, and 120 m above ground level (ground sampling distances of 2.4, 3.2, and 3.8 cm respectively). We found large time savings during the data collection step of drone surveys, but these savings were ultimately lost during imagery processing. Based on photointerpretation, overall accuracy of drone imagery was generally high (88.8% to 92.0%) and Kappa coefficients were similar to previously published habitat assessments from drone imagery. Mixed model estimates indicated 75m drone imagery overestimated barren ($F_{2,182} = 100.03$, $P < 0.0001$) and shrub classes ($F_{2,182} = 160.16$, $P < 0.0001$) compared to ground estimates. Inconspicuous graminoid and forb species (non-shrubs) were difficult to detect from drone imagery and were underestimated compared to ground-based transects ($F_{2,182} = 843.77$, $P < 0.0001$).

Remote cameras were also used as a remote sensing tool to estimate impacts of Ursid predators on nesting lesser snow geese. From 2013-2018 we deployed 233 remote cameras on goose nests and reviewed images for occurrences of bears and associated avian predators. We recorded the amount of time that female geese spent on and of their nest on days with bears (bear-days), and the day before (control-days). Contrary to predictions, geese spent less total time off-nest on bear-days than control-days ($\beta = -0.32 \pm 0.13$, $P < 0.05$). Avian predators were observed more frequently on bear-days (13/18 days) than their paired control-days (2/18 days), and bear presence has a positive effect on avian predator occurrence ($\beta = 3.035 \pm 0.916$, $P <$

0.001). We suspect that geese spend more time on-nest in response to bears to defend nests from increased activity of avian predators, and we examined these behaviours using agent-based models. In mixed predator scenarios (bears and avian predators), birds that left their nest early would reduce the probability of nest loss by bears, but had increased risk by avian predators. This work demonstrates that the relationship between nesting geese and bear predators is more complex than commonly depicted, and provides a foundation for future examination of the continued impact of bears on nesting birds. This work demonstrates the value of remote sensing tools for understanding sub-Artic ecosystems and other regions where ecological research is logistically challenging.

CHAPTER I A PRIMER ON LESSER SNOW GOOSE ECOLOGY, DRONES, AND REMOTE CAMERAS

The midcontinent population of Lesser snow geese (*Anser caerulescens caerulescens*) has increased dramatically since the 1960’s, largely as a result of changing agricultural practices in the southern United States (R. Jefferies, Rockwell, & Abraham, 2004). Management efforts aimed at reducing adult survival have been largely unsuccessful at curbing population growth (Alisauskas et al., 2011; Koons, Aubry, & Rockwell, 2019; Koons, Rockwell, & Aubry, 2014), and as a result, snow goose populations have had detrimental impacts on vegetation communities throughout their Arctic breeding areas. This is especially well documented throughout the Hudson Bay lowlands, specifically the La Pérouse Bay region of Manitoba, where destructive foraging (e.g. grazing, grubbing, and shoot-pulling) by snow geese has had cascading negative impacts on vegetation (R. L. Jefferies, Jano, & Abraham, 2006; R. L. Jefferies & Rockwell, 2002), insects communities (Milakovic, Carleton, & Jefferies, 2001; Milakovic & Jefferies, 2003), and other bird species (Peterson, Rockwell, Witte, & Koons, 2014; R. F. Rockwell, Witte, Jefferies, & Weatherhead, 2003). The continued research and monitoring of snow geese in their nesting grounds is critical to inform management efforts and to better predict the outcome of continued population growth, along with forecasting the effects of recently founded satellite colonies in new areas (K. Abraham, Leafloor, & Lumsden, 1999; Burgess et al., 2017).

Unfortunately, studying complex systems in remote regions is challenging for several reasons. First, research in these regions is financially costly due to the lack of infrastructure (e.g. roads, commercial suppliers, etc.), and the need to import field equipment and supplies required for extended stays in the field (Mallory et al., 2018). Polar regions also typically have shorter operational windows due to inclement weather patterns; therefore researchers need to plan research activities appropriately, with little room for error (Loarie, Joppa, & Pimm, 2007; Malenovský, Lucieer, King, Turnbull, & Robinson, 2017). As such, researchers may become increasingly reliant on remote sensing technology in remote polar regions. These tools generally reduce the amount of time spent in the field by scientific personnel. Two important remote sensing tools are at the forefront of ecological research: drones (also known as unmanned aircraft vehicles, but see Chapman (2014)), and camera traps. Both of these tools have been heavily employed in wildlife research (Burton et al., 2015; Christie, Gilbert, Brown, Hatfield, & Hanson, 2016), but are relatively scarce in Arctic environments.

Drones and camera traps may be important tools for ecological inferences on nesting snow geese, but before these tools can be integrated into snow goose monitoring programs, precursor “proof-of-concept” studies are required to validate the use of such tools. The objective of this project is to determine the effectiveness, best practices, and implications of findings using camera technology to study an ecosystem currently undergoing rapid changes due to increasing snow goose populations and climate change.

Lesser Snow Goose Ecology

Lesser snow geese are large bodied migratory waterfowl which nest in colonies throughout the Arctic/sub-Arctic regions of Greenland, Russia, and Canada. Adult birds have a discrete plumage dimorphism and were previously thought to be comprised of two separate species (*Anser hyperborean and A. caerulescens*), but early research showed both colour morphs to belong to a single interbreeding species (G. Cooch, 1961; Cooke & Cooch, 1968). While lesser snow geese are currently classified in the genus *Anser*, they have undergone several taxonomic changes between the genera *Chen* and *Anser*, as have the closely related Greater snow goose (*A. c. atlanticus*) and Ross's goose (*A. rossii*) (Chesser et al., 2017).

The first records of snow geese nesting in the salt marshes of La Pérouse Bay (58°44'N, 94°28'W) were reported by Wellein and Newcomb (1953) and later confirmed by Foster (1957). Annual research and monitoring of this colony was established in 1968, during which time the colony contained approximately 2,000 breeding pairs (Cooke, Rockwell, & Lank, 1995). Benefiting from agriculture subsidies in their southern range (which reduced winter mortality rates), the La Pérouse Bay colony quickly expanded to near 20,000 breeding pairs. This massive population growth lead to overexploitation of the Bay's salt marsh, and quickly reduced nesting habitat quality (among other negative effects on conspecifics, see Ankney (1996); R. Jefferies et al. (2004)). As a result of this habitat loss, birds largely abandoned the La Pérouse Bay area and expanded to the east and southeast along the western Hudson Bay coast (Aubry et al., 2013; E. Cooch, Jefferies, Rockwell, & Cooke, 1993). Unchecked population growth and the ability to exploit new habitat types has led to the expansion of goose nesting along an approximately 150km stretch of the Hudson Bay coastline and up to 15km inland (R. Rockwell & Gormezano, 2009; R. F. Rockwell, Gormezano, & Koons, 2011; Winiarski, McWilliams, & Rockwell, 2012). The latest estimates of the population occupying this region are approximately 80,0000 breeding pairs (*Rockwell, unpublished data*).

The snow geese in this study primarily nest in a section of freshwater marsh approximately 3km east of the original La Pérouse Bay colony epicenter. Here, geese nest at densities much lower than previously observed in the original salt water marsh colony (Aubry et al., 2013; E. Cooch et al., 1993; E. Cooch, Lank, Rockwell, & Cooke, 1989). Although snow geese are highly philopatric with respect to nesting sites, they tend to return to the area they were originally raised in as goslings, rather than the specific site where they hatched (Cooke et al., 1995). The specific nesting sites are chosen by female geese, and typically consist of raised hummocks of vegetation which allow eggs to be laid above any potential snow-melt water (Cooke & Abraham, 1980). Once a nesting site is selected, geese enter an egg laying period, laying one egg approximately every 33 hours (Schubert & Cooke, 1993). Nest construction takes place during the egg laying period, with additional vegetation and insulating down feathers added over the course of several days (see Fig 2.6 Cooke et al. 1995). The number of eggs produced by a female is dependent on the nutrient reserves of female geese, most of which is transported to the colony along migration “stop-over” sites (Ankney & MacInnes, 1978). The mean clutch size is 4.2 eggs (SE =0.316, range: 1-7), although there is a strong negative correlation with later mean laying date (Cooke et al., 1995; Mineau, 1978). Apparent clutch size in a given year is also strongly influenced by habitat availability during the egg laying and early incubation period, which impacts nest parasitism rates by conspecifics. For a further discussion of this phenomenon see D. B. Lank, Cooch, Rockwell, and Cooke (1989).

Incubation of eggs commences following the laying of the last egg. Snow geese are uniparental incubators and the female incubates for an average of 23.6 days until hatch. During incubation, female snow geese are thought to remain on their nest for the majority of the day, although birds may take short (~1 hour) recess events (Cooke et al., 1995). Although detailed time budgets of lesser snow goose incubation behaviours are lacking, Greater snow geese have been shown to spend around 94% of their time on nest during incubation, with increases to 100% nest attendance during the last few days before hatch (Reed, Hughes, & Gauthier, 1995). This is consistent with the finding that Arctic nesting geese tend to have extremely high nest attendance rates, likely due to the inclement weather associated with northern latitudes (Thompson &

Raveling, 1987). While the female sits on eggs, the paired male generally remains in close vicinity to the nest (Ankney, 1977; Mineau, 1978), although he may take brief breaks to feed or pursue extra pair copulations (Mineau & Cooke, 1979a, 1979b).

During incubation there are several threats to eggs that geese must contend with. Nest abandonment is rare, but overly harsh weather conditions can prematurely deplete a female's energetic resources, which occasionally results in the death of birds on the nest (Ankney & MacInnes, 1978). Other geese can also be an issue as forced, extra-pair copulations by aggressive males on incubating females can result in damage to eggs in the nest bowl, as attendant females are reluctant to leave the nest (Mineau & Cooke, 1979a). Eggs "dumped" just outside of nest bowls by parasitic females are thought to be an indirect threat to nest, as these eggs raise the conspicuousness of nests to predators (David B Lank, Mineau, Rockwell, & Cooke, 1989).

The main cause of nest failure during incubation is predation, though it is suspected that the bulk of nest predation occurs during the egg laying stage before incubation begins (Cooke et al., 1995). If partial predation occurs during the egg laying stage, geese are likely to abandon their nest (Collins, 1993). Little is known about re-nesting attempts by females which abandon, as it is difficult to track individuals once they have left a nest bowl. A variety of species are known to consume Snow Goose eggs during incubation. The primary predators are considered to be Arctic foxes (*Vulpes lagopus*), Herring Gulls (*Larus argentatus*), and Parasitic Jaegers (*Stercorarius parasiticus*) (F. G. Cooch, 1958; Cooke et al., 1995; Ryder, 1969). Other, typically less important, predators include Sandhill Cranes (*Grus canadensis*), Bald (*Haliaeetus leucocephalus*) and Golden Eagles (*Aquila chrysaetos*), caribou (*Rangifer tarandus*), Arctic wolves (*Canis lupus*), red foxes (*Vulpes vulpes*) and even black bears (*Ursus americanus*) (K. F.

Abraham, Mineau, & Cooke, 1977; Cooke et al., 1995; Harvey, Lieff, MacInnes, & Prevett, 1968). Interestingly, periodic predation by polar and grizzly bears (*Ursus arctos horribilis*) has been documented on Snow Goose nests (K. F. Abraham et al., 1977), but in recent years this phenomenon has become more frequent along the Cape Churchill Peninsula (D. Clark, 2000; Gormezano, Ellis-Felege, Iles, Barnas, & Rockwell, 2017; D. Iles, Peterson, Gormezano, Koons, & Rockwell, 2013; R. Rockwell & Gormezano, 2009). Combined with the region's apparent population increase in Herring Gulls and Common Ravens (*Corvus corax*), Snow Geese must contend with a complex, and potentially interacting predator community (see Chapter VI). Nest defense by the male and female are usually successful against "classic" predators such as foxes or avian predators ((Cooke et al., 1995), *A.Barnas personal observation*), but geese are unable to defend against novel Ursid predators. Predator-swamping is also employed by snow geese as a method to overwhelm predator communities via highly synchronous hatch dates throughout the colony (Collins, 1993). As such, the nests most vulnerable to predation are those with extremely early or late nest initiation dates (Collins, 1993; Cooke et al., 1995)

Finally, if geese are able to successfully reach the breeding grounds, build a nest, produce a clutch of eggs, and incubate them for ~24 days, then goslings may hatch. Goslings may be lost during hatch, but parent geese typically remain extremely close to the nest during this period (Cooke, Bousfield, & Sadura, 1981; Thompson & Raveling, 1987). Within a nest, hatch is highly synchronous (Davies & Cooke, 1983), but some research has shown that laying and hatching sequence are highly correlated (Cargill & Cooke, 1981; Syroechkovsky, 1975). After approximately 24-hours post hatch, goslings are able to physically leave the nest and feed themselves. This is a critical period for gosling development, and mismatch between gosling hatch and available forage are detrimental to gosling growth and survival (Aubry et al., 2013; D.

T. Iles, Rockwell, & Koons, 2018). During this “brood rearing” stage, goslings feed continuously over the next 6-8 weeks until they develop flight feathers and eventually migrate south to the wintering areas in the southern United States (Cooke et al., 1995).

Drones in Wildlife Research

Drones are increasingly popular tools for wildlife research, and have notably been used for research and monitoring of several groups of wildlife, including: marine mammals (Andrew F. Barnas, Felege, Rockwell, & Ellis-Felege, 2018; Hodgson, Peel, & Kelly, 2017; Koski et al., 2015), large terrestrial mammals (Su et al., 2018; Vermeulen, Lejeune, Lisein, Sawadogo, & Bouché, 2013), small terrestrial mammals (Bushaw, Ringelman, & Rohwer, 2019), primates (Van Andel et al., 2015; Wich, Dellatore, Houghton, Ardi, & Koh, 2015), birds (Chabot & Bird, 2012; Junda, Greene, & Bird, 2015; Sardà-Palomera, Bota, Padilla, Brotons, & Sardà, 2017), insects (Kim, Park, & Lee, 2018), and reptiles (Elsey & Trosclair III, 2016; Rees et al., 2018; Thapa et al., 2018). The popularity of drone use in wildlife sciences has been documented by multiple literature reviews (Christie et al., 2016; D. W. Johnston, 2019; Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015), and there are several characteristics of drones that are consistently cited as reasons for this increased use. One commonly cited benefit of drones are that they are thought to be a safer alternative to occupied aircraft flights (Jones, 2003; Jones, Pearlstine, & Percival, 2006), which accounted for 66% of job related mortality in wildlife researchers from 1937-2000 (Sasse, 2003). The absence of onboard human operators allows drones to fly at lower altitudes and speeds, which increases the quality of remotely sensed imagery through higher resolution. Flight paths of drones are often georeferenced, allowing researchers to conduct repeat surveys with little variation as a result of human error. Data collected by drones is also able to be archived, allowing for repeat analyses and eliminating common researcher biases such as observer fatigue in occupied aircraft based surveys (Andrew F Barnas, Darby, Vandeberg, Rockwell, & Ellis-Felege, 2019; Linchant et al., 2015; Stapleton et al., 2014). Finally, one of the most commonly cited advantages of drones is the reduced disturbance introduced by drones as a survey tool compared to other survey techniques (A. Barnas et al., 2018; A. F. Barnas et al., 2018; Brunton, Bolin, Leon, & Burnett, 2019; Mulero-Pázmány et al., 2017; Rümmler, Mustafa, Maercker, Peter, & Esefeld, 2015; Vas, Lescroël, Duriez, Boguszewski, & Grémillet, 2015). However findings of minimal disturbance to wildlife are difficult to generalize, and responses to drone surveys are likely context- and species-specific (McEvoy, Hall, & McDonald, 2016; Mulero-Pázmány et al., 2017). Increasingly so, research is showing that drone surveys may adversely affect some wildlife species (Brisson-Curadeau et al., 2017; Brunton et al., 2019; Ditmer et al., 2015; Weimerskirch, Prudor, & Schull, 2017), further dampening the generalization that drones are a non-invasive methodology. As such, it is generally recommended that users investigate potential negative impacts of drones on their study species (or closely related surrogates) either before- or as a part of drone based research (A. Barnas et al., 2018).

The success of drones in wildlife research is partly due to the diversity of drone platforms, sensors/payloads, and technological modifications that can be made to suit specific applications. As a result, drones have been used for relatively simple purposes such as wildlife counts (Chabot & Bird, 2012; Vermeulen et al., 2013) or habitat evaluations (Michez et al., 2016; Puttock, Cunliffe, Anderson, & Brazier, 2015), but also a growing suite of innovative uses. Drones have been tested in management practices such as performing maritime surveillance of marine protected areas (Brooke et al., 2015), detecting African rhinoceros poachers (Mulero-Pázmány, Stolper, Van Essen, Negro, & Sassen, 2014), evaluating power line electrocution risk to raptors (Mulero-Pázmány, Negro, & Ferrer, 2013), and detecting illegal crab traps to supplement fisheries operations (Bloom et al., 2019). While many of these applications have made use of consumer-level drones and sensors (i.e. Red-Blue-Green cameras), there are several unique applications that have been tested with in-house modifications to payloads. Wilson et al. (2017) attached a small acoustic recorder to a quadcopter drone to record songbirds and estimate species diversity. Rodríguez et al. (2012) combined the use of GPS loggers on Lesser Kestrels (*Falco naumanni*) with drone technology, by having a drone follow similar flight paths of the GPS-tracked kestrels to understand habitat preferences. Drones have also been used to collect or deliver biological material, such as assessing whale health through nasal "blow" (Geoghegan et al., 2018; Pirotta et al., 2017) or delivering baits as a method of pest species control (M. Johnston, McCaldin, & Rieker, 2016).

Since drones are so versatile in their implementation within wildlife research, generalizations of findings for a particular drone/sensor/environment combination are difficult. As such, the bulk of recent publications are necessarily "proof-of-concept" papers, whereby researchers rigorously test their chosen drone for a specific application, often with surrogate species or objectives. There are many common pitfalls to the current state of drone technology in wildlife research that have been reported in the literature, which represent significant obstacles for the future use of drone use. Currently, one of the most common limitations on drone use is the inability to operate drones Beyond Visual Line Of Sight (BVLOS), as operators in the U.S. and Canada are required to maintain visual contact with their drone during flight unless granted a special waiver. Further, the most commonly used platforms for wildlife research do not have the capabilities (e.g., communication or battery life) to have extended flights BVLOS. This greatly restricts the operational range of drones, limiting the potential large-scale data collection ability of drones.

Despite these shortcomings, drones remain an attractive tool for wildlife research, with special attention given to colonial nesting birds. Colonial nesting birds are especially prone to disturbance, making on-the-ground methods a problematic approach for research (Götmark, 1992). Further in remote regions these colonies can be difficult to access, restricting the abilities of researchers to conduct measurements of nests at appropriate spatial scales. Given the increasing population of snow geese along the Cape Churchill Peninsula (Koons et al., 2019), and dispersal of birds away from their traditional nesting grounds (Aubry et al., 2013), drones may be an appropriate technology to add to the toolkit of snow goose researchers. Drone imagery has been used extensively to research colonial nesting birds (Chabot, Craik, & Bird, 2015; McClelland, Bond, Sardana, & Glass, 2016; Ratcliffe et al., 2015; Sardà-Palomera et al., 2012) and has already been demonstrated as adequate to count individual snow geese on their wintering grounds (Chabot & Bird, 2012).

Remote Cameras in Wildlife Research

Remote cameras are a tool that has proliferated throughout wildlife research, most commonly used for estimates of wildlife density or relative abundance (Burton et al., 2015; Rowcliffe & Carbone, 2008), but also for elucidating aspects of wildlife behaviour such as bird nest attendance (Stechmann, 2019), hunting associations (Thornton et al., 2018), and novel hunting behaviours (Gormezano et al., 2017; Stempniewicz & Iliszko, 2010).The most common form of remote cameras in wildlife ecology are based on the acquisition of still-images based on the detection of wildlife with an infrared trigger, but video cameras are also being used to investigate subtle ecological phenomenon, especially in nesting birds (Andes et al., 2019; Burnam et al., 2012; Burr, Robinson, Larsen, Newman, & Ellis-Felege, 2017).

Similar to drones, one of the most commonly cited benefits of using remote cameras is the ability to non-invasively collect data by removing researcher presence from sampling sites. Since researcher presence may bias the movement or detection of wildlife at sampling sites, cameras overcome a large obstacle to studying animals in the wild by largely removing this bias (Ellis-Felege & Carroll, 2012). However, the camera systems themselves may introduce their own biases into the study system. Camera equipment placed around bird nests has been shown to induce nest abandonment by females (Stake & Cimprich, 2003), but may also impact nest predation rates by either attracting or repelling predators (Richardson, Gardali, & Jenkins, 2009). The infrared trigger mechanisms used in many camera systems may also impact behaviour of wildlife, since some species may be sensitive to the infrared light and noises produced by these systems (Meek, Ballard, Fleming, and Falzon (2016); P. D. Meek et al. (2014), but see Gibeau and McTavish (2009)). Further difficulties associated with using cameras include the overwhelming amount of collected data to organize and sort, which is especially relevant to cameras collecting 24-hour video (Cox, Pruett, Benson, Chiavacci, & Frank III, 2012). Given the breadth and diversity of camera types and operation available, researchers must also ensure proper reporting of methodologies is done (Burton et al., 2015; P. Meek et al., 2014).

In Arctic regions, remote cameras offer an especially convenient method to collect data, as these areas often lack transportation infrastructure. Researchers can place cameras in the field and leave them for months (or up to a year) to operate remotely. Such methods may be attractive for studying wide-ranging Arctic species which would otherwise be difficult or financially costly to obtain (D. A. Clark et al., 2018; Laforge et al., 2017). Further, cameras produce attractive images of wildlife which may be used to facilitate citizen scientist participation (Desell et al., 2013; Mattingly et al., 2016) and potentially incentivize funding opportunities through public outreach. Currently along the Cape Churchill Peninsula, remote cameras are being used to broadcast “live-feeds” of polar bears on land to the public (Lafontaine, 2015), but also to document their presence at remote research camps (D. A. Clark et al., 2018; Laforge et al., 2017). However, these technologies could also be used to address more complex ecosystem processes, such as the changing predator community of the region. For lesser snow geese, the increased presence of Ursid predators has potential to impact reproductive output, but also influences the nesting behaviour of female geese. Studying this phenomenon would be difficult by observers in the field, as researcher presence would influence bird behaviour (Götmark, 1992) and put researchers at risk in the presence of foraging bears (Cooke et al., 1995). As such, remote cameras offer an ideal technology for studying snow goose nesting behaviour and their changing predator community.

Project Objectives

In the following chapters, I make use of drones and remote cameras systems to investigate several aspects of Lesser Snow Goose ecology of the Cape Churchill Peninsula. In chapters II and III, I first evaluate the behavioural responses of geese and polar bears (a focal predator species in this research) to drone surveys. I then make use of classified drone imagery to evaluate Snow Goose impacts on vegetation communities in chapter IV. In chapter V, I use remote trail cameras to describe novel Ursid predators of Snow Goose nests, and then describe the indirect effect of these novel predators on Snow Goose nesting behaviour and secondary avian predators in chapter VI. Finally in chapter VII, I conclude with a simulation based approach to understanding how goose nest attendance patterns are impacted by the mixed predator environment described in the previous chapter.

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CHAPTER II EVALUATING BEHAVIOURAL RESPONSES OF NESTING LESSER SNOW GEESE TO UNMANNED AIRCRAFT SURVEYS

Abstract

Unmanned aircraft systems (UAS) are relatively new technologies gaining popularity among wildlife biologists. As with any new tool in wildlife science, operating protocols must be developed through rigorous protocol testing. Few studies have been conducted that quantify impacts that UAS may have on unhabituated individuals in the wild using standard aerial survey protocols. We evaluated impacts of unmanned surveys by measuring UAS-induced behavioural responses during the nesting phase of lesser snow geese (Anser caerulescens caerulescens) in Wapusk National Park, Manitoba, Canada. We conducted surveys with a fixed-wing Trimble UX5 and monitored behavioural changes via discreet surveillance cameras at 25 nests. Days with UAS surveys resulted in decreased resting and increased nest maintenance, low scanning, high scanning, head cocking and off nest behaviours when compared to days without UAS surveys. In the group of birds flown over, head cocking for overhead vigilance was rarely seen prior to launch or after landing (mean estimates 0.03% and 0.02%respectively) but increased to 0.56% of the time when the aircraft was flying overhead suggesting that birds were able to detect the aircraft during flight. Neither UAS survey altitude or launch distance alone in this study were strong predictors of nesting behaviours, though our flight altitudes (> 75 m above ground level) were much higher than previously published behavioural studies. The diversity of UAS models makes generalizations on behavioural impacts difficult and we caution that researchers should design UAS studies with knowledge that some minimal disturbance is likely to occur. We recommend flight designs take potential behavioural impacts into account by increasing survey altitude where data quality requirements permit. Such flight designs should consider *a priori* knowledge of focal species behavioural characteristics. Research is needed to determine whether any such disturbance is a result of visual or auditory stimuli.

Keywords: behaviour, Anser caerulescens, disturbance, drone, nest camera, non-invasive, unmanned aircraft system, waterfowl

Introduction

Unmanned Aircraft Systems (UAS) have gained popularity as a tool for research in wildlife ecology, particularly in ornithological studies (Anderson & Gaston, 2013; Christie, Gilbert, Brown, Hatfield, & Hanson, 2016). These technologies are relatively novel, yet have evolved rapidly to fit a wide variety of avian research questions and applications. Early work focused on the feasibility of using UAS for bird related research and addressed questions of detectability (Jones, 2003; Jones, Pearlstine, & Percival, 2006; Watts et al., 2008; Watts et al., 2010). Colony and flock size estimates have been conducted for staging flocks of geese (Chabot & Bird, 2012), breeding populations of black headed gull *Chroicocephalus ridibundus* (Sardà-Palomera et al., 2012), penguins (*Pygoscelis sp*.) in Antarctica (Goebel et al., 2015; Ratcliffe et al., 2015) and sandhill crane *Grus canadensis* flocks along their migratory routes (USGS 2011) . UAS have been used for monitoring coastal habitat use of mixed waterbird flocks (Drever et al., 2015), measuring habitat quality for threatened least bitterns *Ixobrychus exilis* (Chabot & Bird, 2013; Chabot, Carignan, & Bird, 2014), and understanding habitat selection of lesser kestrels *Falco naumanni* (Rodríguez et al., 2012). Other applications used UAS to conduct maritime surveillance in a marine protected area used by seabird colonies (Brooke et al., 2015) and to evaluate powerline electrocution risks for nesting raptors (Mulero-Pázmány, Negro, & Ferrer, 2013).

Another popular application of UAS is the ability to monitor birds during their reproductive period at multiple spatial scales. Unmanned aircrafts have been deployed at the landscape level to survey greater sage-grouse *Centrocercus urophasianus* leks (Hanson, Holmquist-Johnson, & Cowardin, 2014) and estimate nesting density of common terns *Sterna hirundo* (Chabot, Craik, & Bird, 2015). Other studies have shown UAS to be an effective method for determining nesting status of several raptor species including osprey *Pandion haliaetus,* bald eagle *Haliaeetus leucocephalus,* ferruginous hawk *Buteo regalis,* red-tailed hawk *Buteo jamaicensis* (J. Junda, Greene, & Bird, 2015), and Stellar's sea eagle *Haliaeetus pelagicus* (Potapov, Utekhina, McGrady, & Rimlinger, 2013). Weissensteiner et al. (2015) found that UAS can be efficiently used to save time in checking nest contents of canopy-nesting birds by eliminating the need for surveyors to climb trees for such inspections. Other authors have noted similar benefits of using UAS for studying birds, such as the relatively low cost, ease of use, and time savings (Anderson & Gaston, 2013; Jones et al., 2006; Watts et al., 2010).

Across the variety of applications, the most commonly cited benefit of UAS for wildlife research is that these technologies are low impact or have a reduced disturbance effect when compared to manned aircraft surveys or researchers on the ground (Christie et al., 2016; Ward, Stehn, Erickson, & Derksen, 1999). The low impact factor of UAS on birds is poorly documented and is often based on anecdotal observations or general impressions of behaviour (Brooke et al., 2015; Chabot & Bird, 2012; Goebel et al., 2015; Grenzdörffer, 2013; Kudo, Koshino, Eto, Ichimura, & Kaeriyama, 2012; Potapov et al., 2013; Ratcliffe et al., 2015; Weissensteiner, Poelstra, & Wolf, 2015). Some studies have attempted to document behavioural responses using dedicated spotters (Chabot et al., 2015; Drever et al., 2015; Hanson et al., 2014) or post-hoc analysis of imagery (Dulava, Bean, & Richmond, 2015; Sardà-Palomera et al., 2012), though they are not inclusive of a study design that rigorously evaluate behavioural responses. Several studies have attempted to quantify bird behaviour in response to UAS but often lack controls for baseline behavioural patterns or use flight designs that do not represent standard survey protocols such as line transects (J. H. Junda, Greene, Zazelenchuk, & Bird, 2016; McEvoy, Hall, & McDonald, 2016; Rümmler, Mustafa, Maercker, Peter, & Esefeld, 2015; Vas, Lescroël, Duriez, Boguszewski, & Grémillet, 2015; Weimerskirch, Prudor, & Schull, 2017). More importantly, these designs do not account for habituation of individuals to repeated flights, thus masking any behavioural signals that may be apparent to novel stimuli but are lost with repeated exposures. The increasing trend of using UAS for avian research warrants a robust quantification of potential impacts to the wildlife species being studied, which is currently lacking in the field of UAS for wildlife studies (Christie et al., 2016; Crutsinger, Short, & Sollenberger, 2016; Hodgson & Koh, 2016; Smith et al., 2016).

Several recent reviews of UAS use for wildlife research have concluded that UAS surveys result in minimal disturbance, though this is likely dependent on a variety of factors such as aircraft type, flight patterns, and taxa (Borrelle & Fletcher, 2017; Chabot & Bird, 2015; Christie et al., 2016). Mulero-Pázmány et al. (2017) found that birds were more prone to behavioural responses [during UAS surveys] than other taxa, and expressed the need for standardized experiments to evaluate causes of disturbance during UAS surveys. Quantification of behavioural impacts can be difficult given that observers on the ground are likely to miss short-lived or ephemeral behaviours. Collected videos of individual birds allows for the review and characterization of a wider spectrum of behaviours than is available to real-time observers.

The objective of this study is to remotely characterize and quantify the behavioural responses of nesting waterfowl to unmanned aircraft surveys by using nest camera footage. Specifically we examine (1) if behaviours are affected by presence of UAS survey flights, and (2) which factors associated with UAS flights may play a role in bird behaviour.

Methods

Study Species and Area

Given the increased use of UAS for monitoring colonial nesting birds, flights and behavioural observations were conducted on lesser snow geese *Anser caerulescens caerulescens* (hereafter LSGO) during incubation. The widespread distribution of LSGO nesting colonies in remote arctic locations makes this species a good candidate for future UAS studies and applications.

Study sites were located in Wapusk National Park (WNP) in northeastern Manitoba and research was based out of a remote field camp (N 58.725388^o, W -93.464288^o). Topography in this region is uniformly low-lying with little overhead cover for nesting waterfowl. With the exception of researcher activity, there is restricted access to the vast majority of WNP, leaving these study sites relatively free of anthropogenic influences during the waterfowl incubation season.

Behaviour monitoring

Ground searches were conducted to locate nests approximately halfway through the incubation period to avoid disrupting birds during nest-initiation. Initiation was determined by floating goose eggs in water and measuring the position eggs held when submerged (Westerskov, 1950). Nests were randomly selected for behavioural monitoring provided individual nests were greater than 75m away from the nearest monitored nest as measured by handheld Garmin eTrex-

20 and 64S GPS (Garmin, Olathe, KS). We established a minimum nest-distance to increase the likelihood that individual nest behaviours were independent of neighboring nest behaviours. For ease of flight operations, nests were grouped into clusters with a 500m buffer between groups to ensure UAS flights over groups did not inadvertently affect birds not intended to be flown over.

To monitor behaviour of nesting birds during UAS surveys, video surveillance cameras were deployed at nests to record continuous video (Burr, Robinson, Larsen, Newman, & Ellis-Felege, 2017). Cameras were powered by 12-V, 36 amp batteries and equipped with 32GB SD cards, allowing individual systems to operate and record for 5-9 days without need of researcher maintenance and minimizing disturbance to birds. Cameras were set up 1m from the nest and a 25m cable connected them to a DVR housed inside a camouflaged, waterproof box and connected to the battery. The bulk of camera equipment (DVR, batteries etc.) was stored far from the nest to reduce potential influences on the hen's behaviour, and also reduce the chance of attracting curious predators.

Flight Operations

Flights were conducted using a Trimble UX5 (colour: black, wingspan: 100 cm, weight: 2.5kg, cruise speed: 80 km/h, see Appendix A Figure 1), a fixed-wing rear-propelled aircraft powered by removable lithium polymer batteries (14.8V, 6000 mAh). UX5 takeoffs are initiated using an elastic catapult launcher. Once the flight area has been covered, the UX5 begins its descent and eventually belly lands as the aircraft lacks skid gear of any kind. Take-offs and landings were done at a minimum of 325m from monitored nests. All flight plans were pre-programmed line-transects using Trimble Access Aerial Imaging V2.0.00.40 (Trimble, Sunnyvale, CA) and georeferenced in real-time using the UX5's built in GPS system with 80% overlap of adjacent images. Flight path directory and angle of approaches are dictated by environmental factors such as wind speed and direction. Still images are automatically taken with a Sony NEX-5R 16.1 MP camera (Sony Corporation of America, New York, NY) along flight paths. Imagery is downloaded following completion of a flight and used to create landscape mosaics from which habitat characteristics and nest density can be evaluated.

Between June 11-18, 2015 and June 3-16, 2016, flights were conducted at altitudes of 75, 100 and 120m above ground level (AGL). Flight paths were designed to fly over groups of monitored nests at specified altitudes, such that other monitored nests (non-targets) were not flown over at the same time. A control group of monitored nests was never flown over with the UAS to serve as baseline behavioural comparisons.

Video Review and Behavioural Classifications

SD cards were retrieved from monitored nests during nest checks and after completion of UAS flights. Video files were downloaded to a hard drive. A single observer (AB) reviewed video using Windows Media Player (Microsoft, Seattle, WA). Time stamps on video files were matched with flight operation times, and behavioural observations were made continuously from 30 minutes prior to takeoff and until 60 minutes after the aircraft had landed. We selected 30 minutes prior to takeoff to include more than the team’s average setup time of 20 minutes. We selected 1 hour after landing to allow time to examine bird behaviour to residual effects of the flight. Behaviours were classified into six broad categories: resting, nest maintenance, low scanning, high scanning, head cocking, and off nest (Figure 1). Resting was comprised of mostly sleeping but also included heads tucked back into the body while still awake. Nest maintenance involved activities such as contributing vegetation to nest bowls, egg-turning or self-preening. Low scanning was a very low activity behaviour wherein birds seemed to be passively observing their environment, in stark contrast to high scanning in which birds were attentively observing by means of rapid head movement or raised necks. Head cocking was distinctly different from high scanning and was classified by birds tilting their head to observe overhead. Off nest was recorded upon birds standing and leaving their nest. We further categorized off nest to include whether or not birds covered their eggs with insulating down before leaving the nest. Since individual flight times varied throughout flight operations, behaviours were calculated as relative proportions rather than absolute time durations.

Data Analysis

To determine the effects of flight operations on nesting birds we constructed generalized linear mixed models examining the proportion of time birds engaged in each of the six different behaviour classifications using PROC GLIMMIX in SAS Studio 3.7 (Cary, NC). Each behaviour was analyzed as a separate response to test for effects of factors on specific components of behaviour. To facilitate the use of linear models we logit-transformed (log(y/[1-y])) our proportion data which is bounded between 0 and 1 (Warton & Hui, 2011). To ensure logit transformed data did not contain any undefined values, we used an empirical logit transformation by adding or subtracting a small value (0.0001) to proportion values of 0 or 1 respectively (Iles, Salguero-Gómez, Adler, & Koons, 2016; Peterson, Rockwell, Witte, & Koons, 2013). To avoid model dredging and allow comparison of a restricted number of models, we selected factors of interest and relevant possible interactions prior to statistical analyses (Burnham & Anderson, 2002; Zuur, Ieno, & Elphick, 2010).

As we were first interested in whether UAS flights played any role in bird behaviours, we constructed candidate models [Equation (1)] with the fixed effects *day of flight operation* (categorical with two levels: flight or no-flight), treatment *group* (categorical with two levels: surveyed birds and control birds with no flights overhead), and the interaction term *day* x *group*.

To incorporate dependency among observations at the same nest and period of observation, we used *nest_id* and *flight_id* as random effects with an autoregressive covariance structure to account for decay in correlation with increased distance and time between observations (Barnett, Koper, Dobson, Schmiegelow, & Manseau, 2010).

$$\text{Response}_{ijk} \sim \text{Gaussian}(\mu_{ijk})$$

$$\text{E}(\text{Response}_{ijk}) = \mu_{ijk}$$

$$\text{Logit}(\mu_{ijk}) = \text{Day}_{ijk} + \text{Group}_{ijk} + \text{Day}_{ijk} \text{ x } \text{Group}_{ijk} + \text{Nest}_{i} + \text{Flight}_{j}$$

$$\text{Nest}_{i} \sim \text{Gaussian}(0, \sigma^2)$$

$$\text{Flight}_{j} \sim \text{Gaussian}(0, \sigma^2)$$

(Eqn 1)

A separate set of models was then constructed to examine which factors within UAS flight operations influence bird behaviour on flight days only [Equation (2)]. Fixed effects were treatment *group* (categorical with two levels: surveyed birds and control birds with no flights overhead), flight *altitude* (categorical with four levels: 75, 100, 120 meters above group, and a 0 category for control birds), and *launch distance* (Euclidean distance of individual nest to UAS launch site, range 325-2100m). Also included was the categorical fixed effect of *period* within flight operation with three levels: 30 minutes before UAS launch (Pre), the duration of the flight (Air), and 60 minutes post landing (Post). We included the interaction terms *group* x *period* as we felt it was import to examine how behaviours between groups vary depending on whether the aircraft was in the air or not. For both model sets, we were unable to include predator presence as a covariate due to our long distances from focal nests. As with our previous models, *nest_id* and *flight_id* were included as random effects with an autoregressive covariance structure.

$$\text{Response}_{ijk} \sim \text{Gaussian}(\mu_{ijk})$$

$$E(\text{Response}_{ijk}) = \mu_{ijk}$$

$$\text{Logit}(\mu_{ijk}) = \text{Group}_{ijk} + \text{Altitude}_{ijk} + \text{Launch Distance}_{ijk} + \text{Group}_{ijk} \text{ x } \text{Period}_{ijk} + \text{Nest}_i + \text{Flight}_j$$

$$\text{Nest}_i \sim \text{Gaussian}(0, \sigma^2)$$

$$\text{Flight}_j \sim \text{Gaussian}(0, \sigma^2)$$

(Eqn 2)

In all models, Response_{ijk} is the *k*th observation at Nest_i (i=1…25) and Flight_j (j=1…13). Individuals in treatment *group* were only included in the control group if they had never been flown over with the UAS. For all model sets, we included a null model that included the intercept and random effects only. Models were evaluated using Akaike Information Criterion (AICc) for small sample sizes (Akaike, 1998; Burnham & Anderson, 2002). Model assumptions were assessed by visually examining probability plots of the residuals for global models of each response behaviour (Burnam et al., 2012; Suraci, Clinchy, Dill, Roberts, & Zanette, 2016). Since linear models are relatively robust to non-normality, visual inspections are a good method to assess whether a candidate set of models adequately describes the variability of data (Raudenbush & Bryk, 2002; Zuur et al., 2010). We assessed model fit by examining the deviance of candidate models in comparison to null deviance. For top models we back-transformed estimates and 95% confidence limits to the original data scale for presentation (Jørgensen & Pedersen, 1998; Vander Yacht et al., 2016).

Results

We conducted 26 LSGO flights in 2015 and 2016 and deployed cameras for behavioural observations at 32 LSGO nests. Not all flights and nests were included in analyses due to logistic or technical difficulties (e.g. nest predation, nest-camera failures). Of the birds flown over, we collected behavioural data for 18 LSGO from 13 flights. Control data were collected from 7 LSGO nests. Average UAS flight duration was 32 mins (range: 13 – 42 minutes).

Effect of UAS flight presence

Our best model (lowest AICc score) for all behaviours was the interactive model of *day* x *group* (Table 1). For all behavioural responses, the top model possessed >65% AICc weight, and the second best models had a minimum ΔAICc > 2.0 (see Appendix A Table 1).Visual inspection of the global model residuals did not reveal substantial deviations from normality, which is expected as a result of the logit transformed data (Appendix A Table 1). We back-transformed estimates of behaviour proportions and 95% confidence limits (Figure 2) for each behavior. In control birds, sleeping decreased on days of UAS flight operations while all other behaviours increased. For birds in the UAS treatment group, sleeping and low scanning decreased on flight days, while nest maintenance, high scanning, head cocking, and off nest behaviours increased (Figure 2). In all cases of LSGO leaving the nest during observation periods, birds covered their nest with insulating down.

Effect of factors within UAS flight operations

The top two models for all behaviours was either the model of *altitude* + *period*, or the interactive model *group* x *period*. Nest maintenance, high scanning, and head cocking had high support for their top model *group* x *period*, with weights of 0.85, 0.75, and 0.92, respectively (see Appendix A Table 2). Resting, low scanning, and off nest had low ΔAICc and similar weights between the two top models, indicating that similar amounts of variation are explained by both models (Burnham & Anderson, 2002). Since the covariate *altitude* had a built in group component (0 m altitude for birds not flown over [controls]), this suggests that treatment group plays some role in both top models, as does *period*. For simplicity we report results for *group* x *period* as the best model for explaining behavioural responses on flight days (Table 2).

Resting and nest maintenance behaviours decreased in both groups once the aircraft was in the air (Table 3). In the control groups low and high scanning decreased during the Air period, but increased during the Post period. In the UAS group, scanning behaviours increased throughout flight operations. For both the control and UAS group, head cocking increased while the aircraft was in the air, though this increase was greater in the UAS group. Mean estimates for head cocking in control birds increased from 0.0001 to 0.0012 when the aircraft launched, while birds flown over increased from 0.0003 to 0.0056, suggesting that birds were engaging in increased overhead vigilance regardless if the UAS was directly overhead. The amount of time birds spent off nest increased in the post flight period for both groups, again this increase was greater in the UAS group. Large confidence intervals around estimates suggest high variability in individual behavioural response.

Distance between the nest and launch site ranged from 325 – 2,100m, and we suspected launch distances would influence behaviours. However, we did not find this to be an important predictor of behaviours as *launch distance* was the least supported model for all behaviours (Appendix A Table 2). Model deviances are reported in Appendices A Table 1 and B Table 2.

Discussion

Our study addressed key weaknesses of previous work by quantifying behavioural observations of a waterfowl species using replication and controls. Here we also included baseline observations to demonstrate changes in behaviour, a metric lacking in previous studies (Rümmler et al., 2015; Vas et al., 2015). Our results demonstrate there is a quantifiable change in behaviour of nesting waterfowl during UAS surveys compared to non-survey days. However we acknowledge there was considerable variation in responses between individual birds, and as such results should be interpreted with caution. On days with surveys, birds in both groups spent less time resting at the nest and were more likely to participate in active behaviours suggesting higher levels of alertness. Previous studies have shown anthropogenic disturbances reduce time spent feeding by geese, resulting in a net loss of energetic intake (Bélanger & Bédard, 1990; Owens, 1977). Several species of geese have been shown to lose 11.4 - 27.1% of their body mass by the end of incubation. Additional energetic losses through reduced feeding or increased activity at the nest have the potential to reduce reproductive fitness and should be avoided if possible. Our results suggest that the increased activity during UAS surveys could result in changes in energetics and should be a focus of future research and consideration.

Arctic nesting geese heavily invest in nest attendance by spending greater than 90% of their time on the nest during incubation (Reed, Hughes, & Gauthier, 1995; Thompson & Raveling, 1987). Here we documented slightly increased time spent off nest on days with UAS surveys, which puts LSGO nests at risk of predation by arctic foxes *Vulpes lagopus* and aerial predators (Samelius & Alisauskas, 2001). Though again, off nest responses were highly variable. We did not observe any predation events during any observation periods and in all off nest events birds covered their eggs with insulating down before leaving the nest. Though aerial predators are frequently spotted in our field site, we were unable to account for predator presence near nests in this study due to the limited field of view for nest cameras to focus on individual behaviour. It is possible that increased disturbance by UAS has the indirect effect of increasing an individual’s vigilance, reducing the ability of predators to ambush nesting hens, though future analyses would be required to determine the long term effects of UAS surveys on nest success. In contrast, investigator disturbance by researchers on the ground significantly increases the risk of nest attack in a greater snow goose colony (Bêty & Gauthier, 2001). When birds flushed off nest because of researchers only 32 - 47% of birds covered their eggs with nest material, leaving the nest exposed (Bêty & Gauthier, 2001).

During UAS flights, the period of flight operations when the aircraft was flying accompanied increased levels of head cocking, indicating birds were noticing the aircraft as it surveyed. Similar aerial vigilance behaviours have been noted in Antarctic birds surveyed with a microcopter UAS (Rümmler et al., 2015; Weimerskirch et al., 2017) and several species of waterfowl surveyed with various UAS models (McEvoy et al., 2016). However, the increased aerial vigilance was observed in both the UAS and control treatment groups suggesting that either 1) birds were visually aware of the aircraft at >500m lateral distance or, 2) birds were responding to an auditory disturbance produced by the aircraft. While the indication that birds are aware of the aircraft, the biological relevancy of this behaviour is likely minimal since the highest estimate of head cocking accounted for less than 2% of the observation period. The small proportion of time is likely due to the ephemeral nature of head cocking events, though we feel it is a strong indication of birds being able to detect the unmanned aircraft. Discerning between visual and auditory disturbance of UAS surveys is difficult and future work should address this; however, we suspect the geese are detecting the sound of the aircraft and then searching for the source of the sound.

Differences in size and wing profiles of different fixed-wing UASs can influence the behavioural responses of waterfowl (McEvoy et al., 2016; Mulero-Pázmány et al., 2017). Our small unmanned fixed-winged aircraft may resemble the silhouette of raptor species, leading to a higher perceived threat to bird species that are typical prey of raptors, thus leading to potential disturbance issues (McEvoy et al., 2016). Future experimentation with shapes resembling common raptors and non-predatory birds should be planned to further inform the design of low-disturbance aircrafts. Using rotary-wing UAS may decrease the likelihood of these predator resemblance responses, though such aircraft are accompanied with higher dB output and shorter battery endurance for flight operations (McEvoy et al., 2016). Increased dB levels have been shown to elicit increased disturbance and alert behaviours in sea birds (Brown, 1990) and nesting osprey (Trimper et al., 1998), though small UAS operations conducted higher than 100m AGL have reduced impacts from noise disturbance (Mulero-Pázmány et al., 2017). For our future purposes of estimating nesting LSGO densities, rotary wing quadcopters are likely unable to cover the large areas given the limited endurance of these platforms.

Launch distance (and thus direct influence of human operators) was not in our top models influencing behaviour as expected, though most launch distances were substantially farther than previous behavioural studies which were often within 100m from the study organisms (J. H. Junda et al., 2016; Rümmler et al., 2015; Vas et al., 2015). Several observations of LSGO near the launch site (< 50m) indicated that individuals were more alert to our presence upon arrival though quickly habituated. Thus, our launch distance limited inference on human activity near the nests, but may be an important consideration in future UAS protocols aimed at being less invasive.

Our study found survey altitude alone to be a poor predictor of behavioural changes, contrary to previous studies which generally found increased responses with lower survey altitude (Rümmler et al., 2015; Vas et al., 2015). However, our lowest flight altitude was greater than the highest altitude presented in these previous studies, likely rendering differences in our survey altitudes to be negligible for nesting birds. There likely exists a threshold altitude where wildlife respond proportionately to any decreases in UAS survey altitude, though we did not find such any such threshold. Thus, we suggest using UAS sensors that enable users to fly at least

75m AGL to further reduce the risk of impacting species of interest while maintaining sufficient data quality. Understanding data resolution needs and selecting an appropriate sensor to meet those needs at specific altitudes during planning will be an important survey design consideration to minimize wildlife disturbances.

Although it is clear that UAS surveys result in some minimal changes in waterfowl behaviour, this should not dissuade the use of these novel technologies for ecological applications surrounding waterfowl and other wildlife. Results from this study demonstrate that UAS offer a relatively low impact survey method for surveying nesting waterfowl. The diversity of UAS models currently available makes generalizations on behavioural impacts difficult. We caution that researchers should design UAS studies with the knowledge that some disturbance is likely to occur and make efforts to minimize it. Further it should be noted that different aircraft models and flight designs will be needed to fit species-specific data needs, and that some aircraft may be inappropriately utilized if prior considerations for study design are not taken. It is up to individual researchers to balance the need for high quality data with the potential for species impact. As such, *a priori* knowledge of a focal species should be taken into consideration before selection for a UAS study to avoid potential negative impacts.

Future research is needed to determine whether any such disturbance is a result of visual or auditory stimuli, and how development of UAS for wildlife research should proceed. Direct comparisons of disturbance between UAS and ground-based surveys are needed, but any future studies should be designed to match actual survey protocols that would be used for data collection, rather than methods that would not be reproduced as a part of standard UAS use. However, as UAS technology and practices are still developing, potential users should cautiously consider the appropriate aircraft and flight design to meet data needs before adopting these tools.

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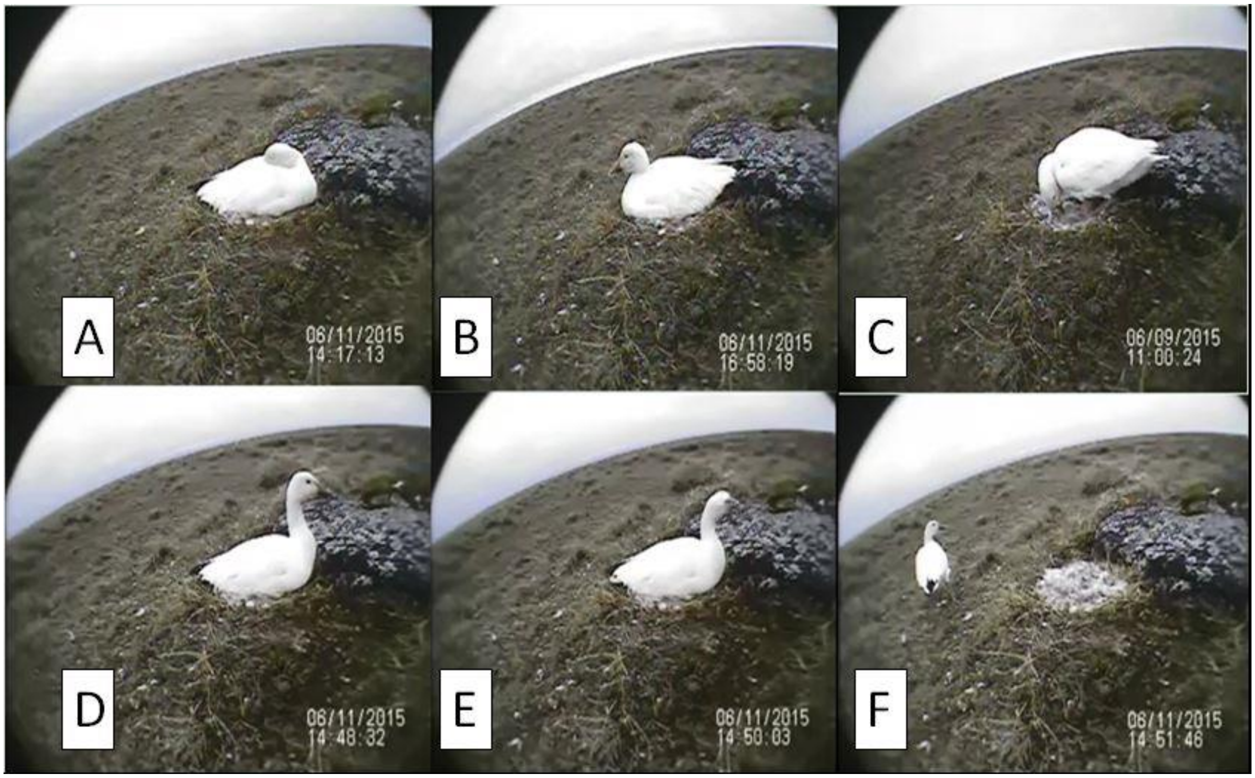

Figure 1 Behavioural classifications for nesting waterfowl (Lesser snow goose pictured above). A) Resting, B) Low Scan, C) Nest Maintenance, D) High Scan, E) Head Cock, F) Off Nest.

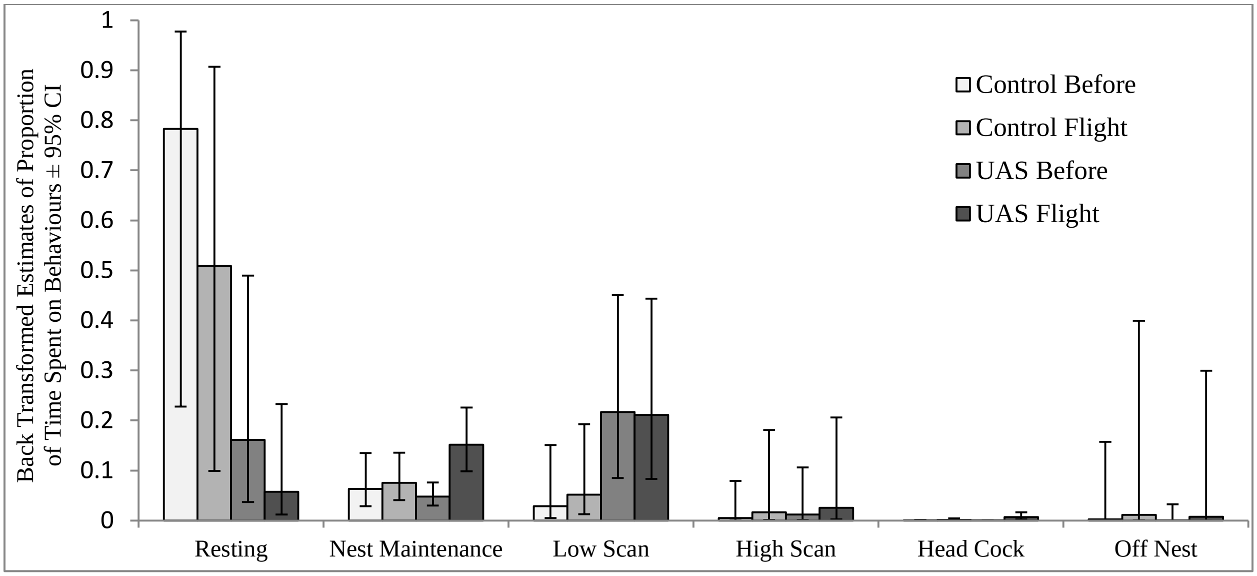

Figure 2 Back-transformed estimates and 95% confidence intervals of proportion of time Lesser snow geese spent on individual behaviours within treatment groups (Control vs UAS) and between days (Before vs Flight). Behavioural data from 67 observations at 25 nests across 13 UAS flights.

Table 1 Beta estimates from top model (*day* x *group*) for the proportion of time[1] spent on behaviours of nesting LSGO relative to whether or not a UAS survey flight occurred (*day* where UAS = birds flown over, CTRL = birds not flown over) and treatment (*group*). Estimates obtained from 67 observations at 25 nests across 13 UAS flights.

Behaviour	**w**	**Intercept β±SE**	**UAS x Day before[2] β±SE**	**UAS x Flight day[2] β±SE**	**CTRL x Flight day[2] β±SE**
Resting	0.721	1.2817 ± 1.2308	-2.9303 ± 1.4037	-4.0790 ± 1.4037	-1.2454 ± 0.9626
Nest Maintenance	0.798	-2.6915 ± 0.4102	-0.2941 ± 0.4762	0.9673 ± 0.4762	0.1821 ± 0.5213
Low Scan	0.651	-3.5310 ± 0.8857	2.2476 ± 1.0566	2.2148 ± 1.0566	0.6231 ± 0.9838
High Scan	0.683	-5.2956 ± 1.3980	0.8755 ± 1.2612	1.6563 ± 1.2612	1.1973 ± 1.1458
Head Cock	0.854	-8.5943 ± 0.7616	0.1109 ± 0.8842	3.5994 ± 0.8842	1.9785 ± 0.9680
Off Nest	0.786	-5.9746 ± 2.1128	-1.4177 ± 1.4067	1.1342 ± 1.4067	1.5029 ± 1.4014

[1] Note β and SE estimates remain on logit transformed scale

[2] Baseline comparisons are to the control group of birds the day before flight operation

Table 2 Estimates from the model (*group* x *period*) for the proportion of time[1] spent on behaviours of nesting LSGO during UAS survey flight days relative to treatment *group* where (UAS = birds flown over, CTRL = birds not flown over) and flight operation *period* where (PRE = 30 minutes before launch, AIR = the period in which the UAS was airborne, and POST = 1 hour after landing). Estimates obtained from 114 observations at 25 nests across 13 UAS flights.

Behaviour	**w**	**Intercept** β±SE	**CTRL x AIR**[2] β±SE	**CTRL x POST**[2] β±SE	**UAS x PRE**[2] β±SE	**UAS x AIR**[2] β±SE	**UAS x POST**[2] β±SE
Resting	0.721	-0.6063 ± 1.9195	-0.8059 ± 1.6957	-0.8428 ± 1.6957	-1.6995 ± 2.0630	-4.0738 ± 2.0630	-3.1931 ± 2.0630
Nest Maintenance	0.798	-4.3628 ± 0.9116	-1.1186 ± 1.2352	1.5177 ± 1.2352	0.1261 ± 1.0981	1.2784 ± 1.0981	2.6975 ± 1.0981
Low Scan	0.651	-4.9940 ± 1.2461	-1.0968 ± 1.0964	2.2643 ± 1.0964	1.5884 ± 1.3376	2.2023 ± 1.3376	4.0999 ± 1.3376
High Scan	0.683	-5.9157 ± 1.2153	-0.6418 ± 0.9291	1.5720 ± 0.9291	0.1849 ± 1.2308	1.4040 ± 1.2308	1.4409 ± 1.2308
Head Cock	0.854	-8.9180 ± 0.7296	2.1538 ± 1.0318	1.3113 ± 1.0318	0.8319 ± 0.8995	3.7308 ± 0.8995	0.5481 ± 0.8995
Off Nest	0.786	-6.3329 ± 1.5767	-0.4442 ± 1.4328	0.9327 ± 1.4328	-2.0708 ± 1.6124	-0.8054 ± 1.6124	0.7456 ± 1.6124

[1] Note β and SE estimates remain on logit transformed scale

[2] Baseline comparisons are to the control group of birds during the period before the aircraft is in the air (CTRL x PRE)

Table 3 Back-transformed estimates and 95% confidence intervals from the model (*group* x *period*) for the proportion of time spent on behaviours of nesting LSGO during UAS survey flight days relative to treatment *group*, and flight operation *period*. Estimates obtained from 114 observations at 25 nests across 13 UAS flights.

Behaviour		**CTRL X PRE**	**CTRL x AIR**	**CTRL x POST**
Resting	µ	0.3529	0.1959	0.1901
	95%CI	0.0118<µ<0.9614	0.0053<µ<0.9176	0.0051<µ<0.9148
Nest Maintenance	µ	0.0126	0.0041	0.0549
	95%CI	0.0021<µ<0.0726	0.0007<µ<0.0249	0.0094<µ<0.2631
Low Scan	µ	0.0067	0.0023	0.0612
	95%CI	0.0006<µ<0.0750	0.0002<µ<0.0264	0.0054<µ<0.4382
High Scan	µ	0.0027	0.0014	0.0128
	95%CI	0.0002<µ<0.0294	0.0001<µ<0.0157	0.0012<µ<0.1274
Head Cock	µ	0.0001	0.0012	0.0005
	95%CI	0.0000<µ<0.0006	0.0003<µ<0.0049	0.0001<µ<0.0021
Off Nest	µ	0.0018	0.0011	0.0045
	95%CI	0.0001<µ<0.0394	0.0000<µ<0.0256	0.0002<µ<0.0944

Table 3 Continued.

Behaviour		UAS x PRE	UAS x AIR	UAS x POST
Resting	µ	0.0906	0.0092	0.0219
	95%CI	0.0059<µ<0.6245	0.0006<µ<0.1341	0.0013<µ<0.2719
Nest Maintenance	µ	0.0142	0.0438	0.1591
	95%CI	0.0038<µ<0.0517	0.0120<µ<0.1473	0.0477<µ<0.4166
Low Scan	µ	0.0321	0.0578	0.2903
	95%CI	0.0053<µ<0.1712	0.0098<µ<0.2762	0.0616<µ<0.7179
High Scan	µ	0.0032	0.0109	0.0113
	95%CI	0.0005<µ<0.0202	0.0017<µ<0.0652	0.0018<µ<0.0675
Head Cock	µ	0.0003	0.0056	0.0002
	95%CI	0.0001<µ<0.0009	0.0020<µ<0.0157	0.0001<µ<0.0007
Off Nest	µ	0.0002	0.0008	0.0037
	95%CI	0.0000<µ<0.0026	0.0001<µ<0.0093	0.0003<µ<0.0422

CHAPTER III A PILOT(LESS) STUDY ON THE USE OF AN UNMANNED AIRCRAFT SYSTEM FOR STUDYING POLAR BEARS

Abstract

Unmanned aircraft systems (UAS) are increasingly popular tools for studying wildlife ecology. The noninvasive aspect of UAS and the ability to collect a large amount of high resolution imagery should be of interest to polar bear (*Ursus maritimus*) researchers who face logistic challenges with field work and developing minimally invasive methods. We opportunistically observed the behavioural reactions of three adult male polar bears during UAS surveys in the summer of 2016. We recorded vigilance behaviours and compared them to previously published vigilance behaviours during wildlife-viewing activities by Dyck and Baydack (2004). The number of vigilance events was 13.4±3.7 (SE) and vigilance bout lengths was 18.7±2.6s (SE), which is similar to reported results by Dyck and Baydack (2004). To estimate detection probabilities of polar bears from UAS imagery, we had two independent observers review mosaics and 80% of known bear locations were identified. Our preliminary results suggest UAS are capable of detecting polar bears using RGB imagery in a relatively non-invasive manner. Before UAS can be integrated into large scale polar bear studies, further research is required to formally assess behavioural impacts with unhabituated individuals in the wild, and model factors influencing detection probabilities.

Keywords: Unmanned aircraft, polar bear, remote sensing, behaviour, drone

Introduction

Measuring the distribution and abundance of species is fundamental to ecological research and monitoring (Smith, Smith, & Waters, 2012). Therefore, understanding how species distributions and abundances change over time is pivotal to understanding the effects of climate change. This is especially pertinent in the Arctic where climate change is occurring faster than in other regions of the world, leading to changes in species' abundance and spatiotemporal distributions (Higdon & Ferguson, 2009; Kovacs, Lydersen, Overland, & Moore, 2011; Stroeve, Holland, Meier, Scambos, & Serreze, 2007). For some subpopulations of polar bears (*Ursus maritimus*), climate change has been directly linked to decreased population numbers, decreased body size, and reduced cub recruitment (Obbard, Thiemann, Debruyn, & Peacock, 2010; Regehr, Lunn, Amstrup, & Stirling, 2007; Stirling & Derocher, 2012). The declines have been largely attributed to increased temperatures leading to decreased sea ice extent during late spring to early fall which limits polar bear access to their primary prey species, ringed seals (*Pusa hispida*) (Stirling & Derocher, 2012). In other subpopulations the effects of climate change are not yet apparent, as indicated by long term stability or increases in abundance (Jon Aars et al., 2017; Stapleton, Peacock, & Garshelis, 2016). Monitoring of both areas with declining and increasing populations is essential for understanding how polar bears are responding to changes in habitat and prey species associated with climate change.

Total censuses of polar bear subpopulations are impractical, though abundance estimates and details on habitat use are valuable to conservationists and wildlife managers. In the western Hudson Bay, such estimates are largely based on mark-recapture studies in which bears are anesthetized from a helicopter (Derocher & Stirling, 1995; Jonkel, Kolenosky, Robertson, & Russell, 1972; Lunn et al., 2016). While evidence suggests these capture techniques have minimal long term impact on the bears (Messier, 2000; Ramsay & Stirling, 1986; Thiemann et al., 2013), these operations are financially costly and often do not align with cultural values of Arctic residents (Peacock, Derocher, Thiemann, & Stirling, 2011; Stapleton, Atkinson, Hedman, & Garshelis, 2014; Wong et al., 2017). Polar bear abundance estimates can be made using distance sampling from aircraft which excludes the need to physically capture bears (J Aars et al., 2009; Stapleton, Atkinson, et al., 2014; Stapleton et al., 2016). However, this method still burdens researchers with the expenses and logistic difficulties of manned aircraft flights. Additionally, manned aircraft flights pose a significant safety risk to researchers and may disturb wildlife due to their low altitude and slow speeds (Sasse, 2003). Other remote sensing methods such as satellite imagery show promise for studying polar regions, but remain subject to error based on limited imagery resolution and cloud cover (LaRue, Stapleton, & Anderson, 2017; LaRue et al., 2015; Loarie, Joppa, & Pimm, 2007; Stapleton, LaRue, et al., 2014).

With the risks associated with manned flights and the current limitations of satellite imagery in mind, the rising technology of unmanned aircraft systems (UAS) has great potential for studying polar bears and aspects of their ecology. Decreasing costs of UAS and subsequent increasing commercial availability are making these tools more accessible to researchers (Anderson & Gaston, 2013; Chabot & Bird, 2015; Christie, Gilbert, Brown, Hatfield, & Hanson, 2016; Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015). UAS have been shown to be effective at surveying large mammals in a variety of environments, including African savanna elephants (*Loxodonta africana*) (Vermeulen, Lejeune, Lisein, Sawadogo, & Bouché, 2013), leopard seals (*Hydrurga leptonyx*) (Goebel et al., 2015), and humpback whales (*Megaptera novaengliae*) (Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016). These tools can collect a large amount of high-resolution imagery very quickly which also provides a digital archive for future analyses and researchers (Hodgson, Kelly, & Peel, 2013). Moreover, UAS are largely cited as a less invasive survey methodology than traditional manned aircraft flights (Linchant et al., 2015; Vermeulen et al., 2013).

The noninvasive aspect of UAS technology should be of extreme interest to polar bear researchers as they seek to develop minimally invasive management efforts to increasingly comply with aboriginal traditions and institutional animal care protocols. However, a recent review of UAS studies revealed that some species are more likely than others to show behavioural responses to UAS surveys (Mulero-Pázmány et al., 2017). Research has shown polar bears are prone to anthropogenic disturbances (Andersen & Aars, 2008; Dyck & Baydack, 2004; Smultea et al., 2016), so it is not unreasonable to suggest polar bears may have adverse reactions to UAS surveys. An additional challenge facing UAS is the ability to discriminate polar bears from their background environment in imagery (snow, ice, gravel beach ridges). Preliminary research has shown that the spectral signatures of polar bear pelts are sufficiently different from clean snow to allow discrimination (Leblanc, Francis, Soffer, Kalacska, & de Gea, 2016). Yet the primary difficulties encountered with high resolution satellite imagery were the identification of false-positives and inability to developed automated detection based on reflectance (LaRue et al., 2015). UAS could provide higher resolution imagery to ameliorate these problems while offering variability in sensor capability (e.g. thermal, near infrared, multispectral, ultraviolet) to suit research-specific needs (Anderson & Gaston, 2013; Berni, Zarco-Tejada, Suárez, & Fereres, 2009). Before unmanned aircraft can be used for large scale studies of polar bears, operating protocols must be developed that demonstrate minimal disturbance levels while facilitating high detection probabilities of polar bears.

In the summer of 2016 during coastal UAS surveys, we were able to opportunistically observe three adult male polar bears and capture them in UAS imagery. Here we describe the behavioural reactions of three bears to UAS surveys, and calculations of detection probabilities for potential future use in UAS studies. We also detail some of the logistic and technological considerations for the future use of UAS for study polar bear ecology.

Methods

Study Area

This study took place on the Cape Churchill Peninsula, within Wapusk National Park, Manitoba, Canada (Figure 3). Flight operations were conducted over tidal flats, sand bars and beach ridges along the coast of Hudson Bay. This area is predominately low-lying, with the exception of sand bars and glacial beach reaches made up of gravel with intermittent shrub patches (*Salix sp*., *Betula glandulosa*, *Myrica gale*).

Aircraft Specifications and Flight Parameters

Flights were conducted using a Trimble UX5 (colour: black, wingspan: 100 cm, weight: 2.5 kg, cruise speed: 80 km^{hr}, operational temperature range: -25 °C to 55 °C, maximum operational wind speed: 50km^{hr}), a fixed-wing rear-propelled aircraft powered by removable lithium polymer batteries (14.8 V, 6000 mAh). UX5 takeoffs are initiated using an elastic catapult launcher. Once the flight area has been covered, the UX5 begins its descent and eventually belly lands as the aircraft lacks skid gear of any kind. All flight plans were pre-programmed line-transects using Trimble Access Aerial Imaging V2.0.00.40 (Trimble, Sunnyvale, CA) and georeferenced in real-time using the UX5’s built in GPS system with 80% overlap of adjacent images. In-flight stability and thus image quality are optimized by flying crosswind, rather than into a headwind or with a tailwind, therefore flight path direction and angle of approaches are dictated by environmental factors such as wind speed and direction. Still images were collected in true colour (3 visible bands: Red Blue Green) and were taken at systematic intervals along flight paths with a Sony NEX-5R 16.1 MP camera (Sony Corporation of America, New York, NY). Pictures were taken by trigger approximately once every second while on flight paths, and were saved in JPEG format automatically to the camera's SD card. At an altitude of 75 m AGL, the image footprint is 118 × 78 m. At 100 m AGL, the footprint is 157 × 104 m. Camera settings for all flights were as follows: no flash, exposure time 1/4000, automatic white balance, and automatic ISO. Imagery was downloaded following completion of individual flights and used to create landscape mosaics. Flights were conducted on 26 July 2016 from 1123 to 1715.

Transportation to and from the study site was by helicopter (Bell 206L-3). Following standard safety protocols, polar bears were located by observers in the helicopter at 150m (approximately 500ft) above ground level (AGL) to minimize disrupting the bears upon arrival. To avoid carry over effects of behavioural changes due to helicopter landing, we waited approximately 25 minutes before commencing UAS flights. UAS operations consisted with initial surveys of two bears at 120m AGL, followed by 75m AGL surveys of the same two bears. We then surveyed a third bear at 75m AGL, but were unable to complete a 120m AGL survey for this individual due to time constraints (five flights total).

Behavioural Observations and Classifications

Bear behaviour was recorded by a single observer (C. Felege) using a Leica 20-60 × 72mm spotting scope (Leica Camera, Wetzlar, Germany). Video was recorded through the spotting scope using a Samsung Galaxy S7 smartphone (Samsung Group, Seoul, South Korea) during UAS surveys. Video was reviewed by a single observer (A. Barnas) on Windows Media

Player (Microsoft, Redmond, WA). Behaviours were recorded and categorized following procedures provided by Dyck and Baydack (2004). We classified behaviours as either non-vigilant (sleeping, laying, walking, sitting etc.) or vigilant. Vigilance was assumed when the bear was seen lifting its head to shoulder level or above while laying down (Dyck & Baydack, 2004), but we also included obviously raised heads while sitting or walking as vigilant. We recorded the number of seconds individual bears spent on behaviours, as well as the number of individual behaviour events. Video was reviewed for individual bears from the time of unmanned aircraft takeoff until landing.

Imagery Analysis

UAS imagery was downloaded from the aircraft after each flight. Mosaics were created using Pix4Dmapper Pro (Pix4D, Switzerland, V3.3). For survey altitudes of 75 and 120m AGL, the nominal ground sampling distance of imagery was 2.4 and 3.8 cm, respectively. Individual mosaics were loaded into ArcGIS 10.4 (ESRI, Redlands, CA) and a search grid composed of 100x100m cells was placed over the imagery to facilitate search efforts and reduce the chance of missing areas during searches. Cells with missing imagery (black patches) and obvious discolouration as a result of the mosaic creation process were removed from the search area. It should be noted that majority of anomalies are located at the edge of the mosaic far away from the survey plot of interest, thus should have little impact on the search process. Cells which contained people were also eliminated from the search area, since this would influence observers to suspect no bears were within the cell.

We used a hybrid double observer method to calculate the detection probability for polar bears from UAS imagery (Griffin et al., 2013; Lubow & Ransom, 2016). Two observers were asked to first independently review the UAS imagery. These observers were selected based on previous experience of identifying polar bears from aircraft, though neither were present during UAS operations, nor had any prior information on the number or location of bears in the imagery. For each observer, total search time was recorded for each 100x100m cell. Note that each bear in the imagery occupied it's own cell (i.e. bears were not clustered as a family group, which would influence detection). Following completion of searches, observers were then allowed to compare identifications. By doing so, false-positives and false-negatives are reduced, though false-negatives would remain if both observers failed to identify a bear that was present in the imagery.

Data Analysis

Comparison of relatively short periods of behavioural observations to previously-published long-term activity budgets of polar bears (see Stirling, 1974) would likely lead to erroneous conclusions. Instead we restrict ourselves to comparing descriptive statistics (specifically, mean and SE) of vigilance estimates to those found by Dyck and Baydack (2004), who observed individual bears for similarly short bouts of time (approximately 30 mins for each individual) during periods of tundra vehicle activity. Specifically, we report the number of head-ups (vigilance), the length of individual vigilance events, and the length of the period between individual vigilance events, for comparison with Dyck and Baydack (2004).

Detection probabilities were calculated based on observer's ability to detect and correctly identify bears as a proportion of the number of known bears in the imagery. Mean time to search cells with SE was calculated from the pooled times from both observers.

Results

In 2016, we conducted five UAS survey flights; average flight time was 28.4±0.68 minutes (n=5). Since bear observations were made from takeoff to landing, the mean observation time for bears is identical to mean flight time. For all UAS flights, the average number of head-ups during flights was 13.4±3.7, which falls within the results observed by Dyck and Baydack (2004) for both paired and unpaired polar bears (Table 4). Vigilance bout length during UAS flights were higher on average (18.7±2.6 seconds) than Dyck and Baydack (2004), as were the between bout intervals (101.0±18.1 seconds, Table 4). There appears to be small differences in vigilance responses to UAS survey altitude, though we are careful to restrict inferences here due to small sample sizes, repeated exposures, and lack of controls. For a complete breakdown of individual responses during each UAS flight, see Appendix B Table 1.

There were 148 cells searched, totaling 1.48 km^2 searched by each observer. Observer 1 took 49 minutes, 55 seconds to search the entire area, while Observer 2 took 1 hour, 2 minutes and 41 seconds. Mean search time for $0.01km^2$ cells was 22.8±0.91 seconds (n=296, range: 5-106). Polar bears were detected with 80% success (n=5) by observers after review. Substantial variation existed between observers in initial search results (Table 5). Observer 1 correctly identified the bear in 4 of 5 mosaics (Figure 4a-d), had 1 false-positive, and 0 false-negatives. The second observer correctly identified 3 bears, had 4 false-positives (Figure 4f) and 2 false-negatives. After review both observers agreed on 4 of the identified bears and correctly eliminated the false-positives, though both observers missed the same bear resulting in a shared false-negative (Figure 4e). For both observers the lower altitude surveys (75m AGL) yielded more correct identifications, and had a lower mean search time for cells (Table 5).

Discussion

In general we found behavioural responses similar to those observed near polar bear tourism vehicles by Dyck and Baydack (2004), indicating similar levels of disturbance to a common-place practice in the region. Though notably there was moderate individual variation in response to UAS operations (Appendix B Table 1), flights did not appear to adversely affect polar bears by inciting any flee-responses as documented in response to snowmobiles (Andersen

& Aars, 2008). Though bears did not physically appear to be adversely impacted by UAS surveys, there is some support that small rotory-wing UAS at much lower survey altitudes (20m AGL) may cause short term physiological responses (increased heart rates) in black bears (Ditmer et al., 2015). We were unable to account for possible UAS noise disturbance in this study. Larger gasoline powered UAS models may introduce significant noise disturbance, but smaller electric models in windy polar regions have demonstrated noise attenuation at altitudes greater than 30m AGL (Goebel et al., 2015). The lack of any flee-responses by surveyed bears is a strong indication that UAS surveys produced less disturbance than traditional mark-recapture methods. We do caution that the bears occupying our study site are commonly flown over by both helicopters and fixed-wing aircraft during polar bear tourism activities, so it is possible that these bears were habituated to anthropomorphic stressors.

Several issues remain regarding the detection of bears from UAS imagery. We found that by using multiple observers to search for polar bears, we were able to eliminate false-positives and some false-negatives, corroborating findings of Stapleton, LaRue, et al. (2014). However, the long search time required to complete all the grid cells implies manual searches of imagery will be ineffective for larger scale studies. Search times were faster in lower altitude surveys, but lower altitudes require longer flight times and will likely increase the disturbance. Future small scale projects using UAS imagery to locate polar bears should employ multiple observers, and we recommend employing those who have experience detecting polar bears from aircraft or imagery. Further, we recommend the use of reference imagery to improve detection, considering that once Observer 2 detected the first true-positive, they claimed their ability to detect bears greatly improved. In our imagery, the false-negative that both observers missed was a bear laying on beach ridge gravel, resulting in little contrast between the bear and it’s background (Figure

4e). To facilitate future large scale UAS studies of polar bears, formal analyses should be done to determine the relative importance of various factors (e.g. UAS sensor type, environmental background, image processing method) on detection, as has been done for other taxa (Chabot & Bird, 2012; Hodgson et al., 2013; Linchant et al., 2015). Any large-scale studies should explore the use of additional sensors coupled with automated detection software to reduce manual search times. Previous research using infrared indicates that polar bears should be detectable with such sensors, and future work should explore the use of thermal and multispectral images (Amstrup, York, McDonald, Nielson, & Simac, 2004; Brooks, 1972; Preciado et al., 2002).

We stress that while our findings are novel and have implications for the future use of UAS in polar bear research, we recognize the limited scope of our study and that much work is needed before UAS can be efficiently implemented. Current unmanned aircraft regulations in Canada restricted us to flying the UX5 within line-of-sight, which is a major impediment to the spatial coverage required to survey polar bears in the wild and requires proximity of researchers to bears on the ground. Aircraft specifications regarding battery life and platform design (fixed-wing versus rotary-wing) will be an important consideration for researchers to ensure sufficient flight time is met to cover study areas of interest. Moreover, depending on the time of year, the field site where we conducted our study can be heavily populated by aircraft engaged in polar bear tourism activities. The future development of unmanned aircraft for polar bear research will need to carefully follow evolving government protocols, and researchers will have to work closely with industry aircraft operations in study regions to prevent conflicts.

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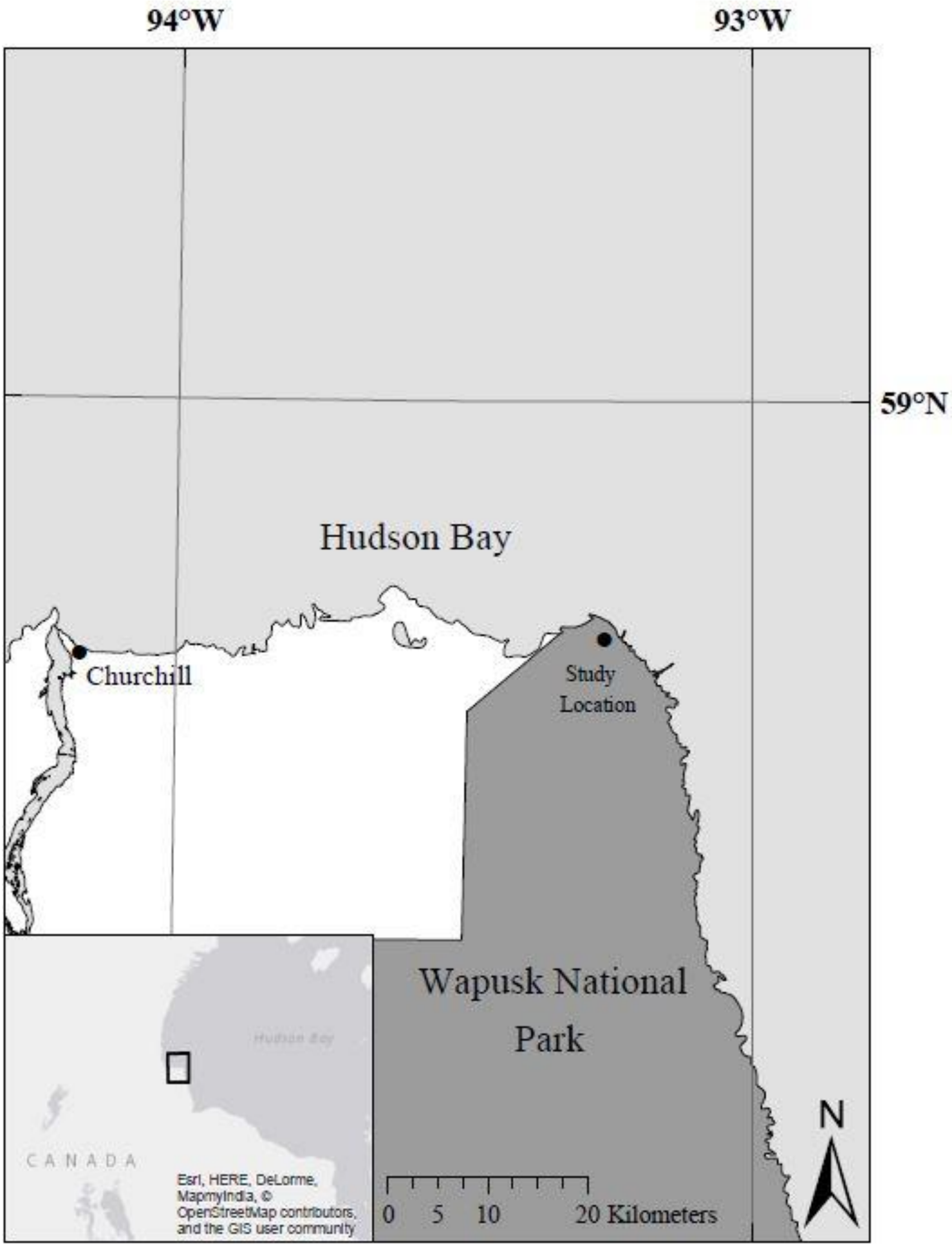

Figure 3 Map of Wapusk National Park, Manitoba, Canada.

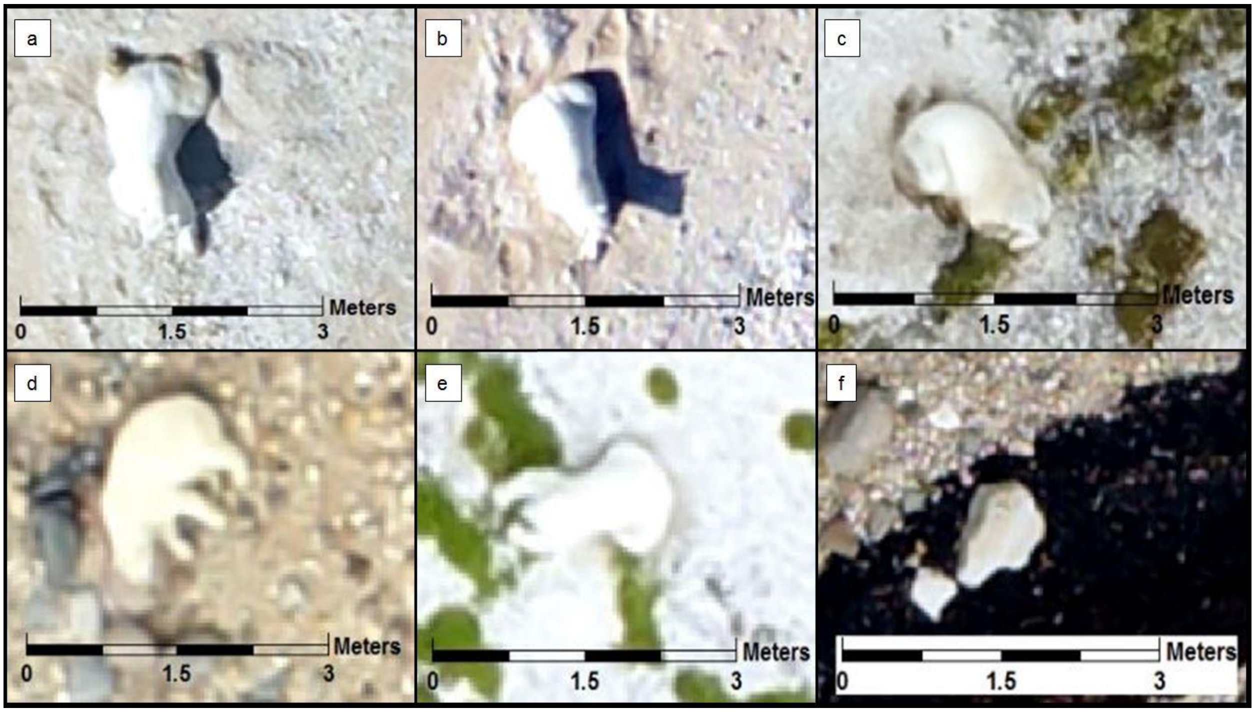

Figure 4 Trimble UX5 UAS imagery of polar bears from survey flights. Boxes a, b, and c are taken at 75m above ground level (AGL), while d and e are at 120m AGL. Box f is an example of a rock identified as a false-positive by an observer at 75m AGL.

Table 4 Descriptive statistics of adult male polar bear (n=3 individuals) behaviour during UAS flights presented as mean± SE (range), for the number of head-ups (HU), vigilance bout length in seconds (VBL), and between bout interval in seconds (BBI). Also included are comparable behavioural data from Dyck and Baydack (2004: Table 1) on male polar bears (n= 29 individuals) observed in the presence of Tundra Vehicles.

	Unmanned Aircraft Flights			**Tundra Vehicles Present (Dyck and Baydack 2004)[a]**	
	All Flights (n=5)	75m AGL (n=3)	120m AGL (n=2)	Unpaired Males (n=23)	Paired Males (n=6)
HU (#)	13.4±3.7 (7-27)	15.0±6.0 (8-27)	11.0±4.0 (7-15)	12.9±1.5 (4-33)	17.0±1.9 (11-24)
VBL (s)	18.7±2.6 (2-141)	16.0±1.9 (2-52)	24.2±6.9 (3-141)	13.2±1.9 (4.8-50.6)	17.8±4.8 (7.8-40.7)
BBI (s)	101.0±18.1 (5-813)	94.4±23.2 (6-813)	114.1±28.9 (5-572)	93.2±11.1 (24.6-184.1)	81.3±8.9 (52.6-104.4)

[a] Unpaired males were bears that were observed only when tundra vehicles were present, whereas paired males had observations during tundra vehicle activity (reported here), and during periods without tundra vehicle activity which is not reported here, see Dyck and Baydack (2004).

Table 5 Search summary statistics for two independent observers identifying polar bears from UAS imagery at 75 and 120m AGL (Above Ground Level).

	Observer 1	**Observer 2**
75m AGL		
Mean Search Time per cell (s) ± SE	18.8±1.2	19.2±1.4
Correct Identifications	3	2
False-Negatives	0	1
False-Positives	0	0
120m AGL		
Mean Search Time per cell (s) ± SE	21.7±1.4	31.6±2.6
Correct Identifications	1	1
False-Negatives	1	1
False-Positives	0	4

CHAPTER IV A COMPARISON OF DRONE IMAGERY AND GROUND-BASED METHODS FOR ESTIMATING THE EXTENT OF HABITAT DESTRUCTION BY LESSER SNOW GEESE IN LA PÉROUSE BAY

Abstract

Lesser snow goose (*Anser caerulescens caerulescens*) populations have dramatically altered vegetation communities through increased foraging pressure. In remote regions, regular habitat assessments are logistically challenging and time consuming. Drones are increasingly being used by ecologists to conduct habitat assessments, but reliance on georeferenced data as ground truth may not always be feasible. We estimated goose habitat degradation using photointerpretation of drone imagery and compared estimates to those made with ground-based linear transects. In July 2016, we surveyed five study plots in La Pérouse Bay, Manitoba, to evaluate the effectiveness of a fixed-wing drone with simple Red Green Blue (RGB) imagery for evaluating habitat degradation by snow geese. Ground-based land cover data was collected and grouped into barren, shrub, or non-shrub categories. We compared estimates between ground-based transects and those made from unsupervised classification of drone imagery collected at altitudes of 75, 100, and 120 m above ground level (ground sampling distances of 2.4, 3.2, and 3.8 cm respectively). We found large time savings during the data collection step of drone surveys, but these savings were ultimately lost during imagery processing. Based on photointerpretation, overall accuracy of drone imagery was generally high (88.8% to 92.0%) and Kappa coefficients were similar to previously published habitat assessments from drone imagery. Mixed model estimates indicated 75m drone imagery overestimated barren ($F_{2,182} = 100.03$, $P < 0.0001$) and

shrub classes ($F_{2,182} = 160.16$, $P < 0.0001$) compared to ground estimates. Inconspicuous graminoid and forb species (non-shrubs) were difficult to detect from drone imagery and were underestimated compared to ground-based transects ($F_{2,182} = 843.77$, $P < 0.0001$). Our findings corroborate previous findings, and that simple RGB imagery is useful for evaluating broad scale goose damage, and may play an important role in measuring habitat destruction by geese and other agents of environmental change.

Introduction

Light goose populations (lesser snow *Anser caerulescens caerulescens*, greater snow *A. c. atlanticus*, and Ross's geese *A. rossii*) have grown rapidly since the 1960's, predominately as a result of modernized agricultural practices in the southern extent of their ranges (Alisauskas et al., 2011; Ankney, 1996; R. Jefferies, Rockwell, & Abraham, 2004a). In their northern staging and summer breeding areas, growing numbers of light geese have dramatically altered vegetation communities through increased foraging pressure, resulting in a loss of above ground primary productivity (K. F. Abraham, Jefferies, & Alisauskas, 2005; R. Jefferies, Rockwell, & Abraham, 2004b). These impacts are especially well documented in colonies of lesser snow geese (hereafter snow geese), which have been formally designated as an overabundant species in Canada (Alisauskas et al., 2011). While snow goose foraging has direct impacts on vegetation communities, the indirect effects of this biomass loss have resulted in apparent trophic cascades in Canadian Arctic ecosystems with important consequences for sympatric species (Flemming, Calvert, Nol, & Smith, 2016; R. Jefferies et al., 2004b). Previous studies have linked growing snow goose colonies with decreased song bird nest occurrence (Peterson, Rockwell, Witte, & Koons, 2014; Rockwell, Witte, Jefferies, & Weatherhead, 2003), reduced small mammal abundance (Samelius & Alisauskas, 2009) and reduced invertebrate community species richness (Milakovic, Carleton, & Jefferies, 2001; Milakovic & Jefferies, 2003).

Continued monitoring and assessments of snow goose habitat damage is critical to management efforts to better predict the outcome of continued population growth, along with forecasting the effects of recently founded satellite colonies in new areas (K. Abraham, Leafloor, & Lumsden, 1999; Burgess et al., 2017). Assessing plant-goose interactions is typically done using ground-based sampling designs (linear transects, quadrat sampling etc.), which offer high resolution data but are time consuming and logistically challenging in the remote regions where geese stage and breed (K. F. Abraham, 2014; Alisauskas, Charlwood, & Kellett, 2006). Further, in heterogeneous or highly degraded landscapes these logistically limited sampling methods may not adequately capture spatial variation in vegetation communities. As a result, local ecosystem processes may be poorly delineated, leading to weak inferences on regional patterns and trends. Remote sensing technologies such as satellites can offer opportunities to create broad regional indices such as the Normalized Difference Vegetation Index (NDVI) to quantify vegetation cover and have been used to study the relationships between geese and their forage plants (Hogrefe et al., 2017; Jano, Jefferies, & Rockwell, 1998; R. L. Jefferies, Jano, & Abraham, 2006). These methods offer wide spatial coverage, but miss out on fine scale data that can be collected on the ground such as species assemblages or plant demographic information. Fortunately, satellite imagery resolution is continually improving. For example WorldView-03 (Satellite Imaging Corporation, Houston, Texas) offers panchromatic imagery at 0.31m/pixel and has been used for ecological research (LaRue & Stapleton, 2018), but this imagery can be expensive and prone to interpretation errors (LaRue et al., 2015). More importantly, the quality of satellite imagery is dictated by prevailing atmospheric conditions such as cloud cover surrounding study sites, potentially limiting the repeatability of image acquisition and appropriate timing to address rapid landscape changes (Loarie, Joppa, & Pimm, 2007).

One solution to the problem of sampling scale and repeatability is the advent of drone (Chapman, 2014) technology for ecological research (Anderson & Gaston, 2013; Chabot & Bird, 2015). Drones are increasingly being used by ecologists to address questions involving vegetation communities and habitat assessments (Chabot, Carignan, & Bird, 2014; Cruzan et al., 2016; Marcaccio, Markle, & Chow-Fraser, 2016). These platforms are able to rapidly collect high resolution imagery that can be easily archived for future analyses, and flight paths are highly repeatable over areas of interest which allows users to conduct repeated surveys with minimal variation. While recognizing that drone operations are still limited by environmental conditions (precipitation, high winds), smaller models can be rapidly deployed in the field when conditions become suitable, dampening logistic difficulties of organizing manned aircraft flights. This is especially relevant for research in polar regions with more persistent cloud cover, as drones are able to operate at low altitudes during cloudy conditions (Malenovský, Lucieer, King, Turnbull, & Robinson, 2017). Clearly drones have great potential for monitoring the impact of snow geese and other agents of environmental change, which will ultimately help alleviate the high financial costs of research in the Arctic (Mallory et al., 2018) .

While studies in ecology featuring drones are on the rise, the many of these have been tested with small aircraft at restricted spatial scales(Andrew F. Barnas, Felege, Rockwell, & Ellis-Felege, 2018; Fortune et al., 2017; Hanson, Holmquist-Johnson, & Cowardin, 2014; Rümmler, Mustafa, Maercker, Peter, & Esefeld, 2015). Studies in wildlife featuring drones are currently restricted to flying within visual line-of-sight, but regulatory agencies are making strides towards relaxing these restrictions (Christie, Gilbert, Brown, Hatfield, & Hanson, 2016).

Indeed there are several examples of large-scale studies that have successfully used drones with beyond-visual-line-of-sight (BVLOS) flight plans (Ferguson et al., 2018; Patterson, Koski, Pace, McLuckie, & Bird, 2015; Sykora-Bodie, Bezy, Johnston, Newton, & Lohmann, 2017; Zmarz et al., 2018) However, any aircraft models capable of very long distance surveys are not likely affordable to lone PIs or even collaborative research groups. For example, an increasingly popular long-range drone system, the ScanEagle (Insitu Inc., a subsidiary of The Boeing Company), costs an estimated $3.2 million US. Further, the operation of these aircraft requires a high degree of technical training, which is unlikely to be feasible for the average ecologist. Therefore, the future of large scale ecological research with drones is more likely to be outsourced to commercial operations, similar to satellite technology or even manned aircraft flights.

Some ecological studies have tested the capacity of long-range aircraft to acquire imagery at restricted spatial scales (Hodgson, Kelly, & Peel, 2013; Koski et al., 2015; Moreland, Cameron, Angliss, & Boveng, 2015), setting the stage for routine acquisition and analysis of imagery collected BVLOS. The analysis of drone-based imagery collected by commercial operators may become analogous to methods used for satellite imagery, whereby the imagery is collected and ecological experts later interpret the imagery. This is not an unrealistic option for the future of assessing habitat degradation by snow geese at broad scales, given the high financial cost of field studies in the Arctic (Mallory et al., 2018). However before drones can be readily integrated into the toolkit of ecological researchers, validation studies are a necessary precursor to understand how interpretation of drone imagery by ecological experts compares to estimates made by field-based methods.

The objective of this study was to estimate the extent of habitat degradation in an area historically damaged by lesser snow geese using drone imagery. Specifically, we examine the composition of broad vegetation land cover classes using a standard field-based linear transect approach, and compare estimates to those made from the analysis of drone imagery via methods analogous to interpretation of commercially acquired imagery. We suspect that high resolution drone imagery will result in similar estimates of land cover estimates when compared to field-based sampling, which would therefore lead to similar inferences on biological processes. Further, we hypothesize that lower altitude flights with better image resolution will result in classifications of higher accuracy (based on photointerpretation) than flights at higher altitudes.

Methods

Study Area

This study was conducted at a long-term remote research camp within Wapusk National Park, Manitoba, Canada (Figure 5). This area is a coastal supratidal salt marsh, southwest of La Pérouse Bay along the western coast of Hudson Bay. The area is part of the Hudson Bay Lowlands physiographic region (Shilts, Aylsworth, Kaszycki, & Klassen, 1987) and is characterized by a vegetation community predominately composed of dwarf shrub (*Salix sp. Betula glandulosa, Myrica gale*) and graminoid (e.g. *Puccinellia phryganodes, Festuca rubra, Triglochin sp*.) species. For a more detailed account of the region's plant community and natural history see (R. Jefferies et al., 2004b).

Field Derived Estimates of Land Cover

We conducted ground-based linear transects within five rectangular study plots of varying size to evaluate vegetation (Appendix C Table 1 for further details on plot specifications). Each plot consisted of a grid system of adjacent 50x50m cells (92 cells, 23 ha total). Following methods established by previous habitat assessment studies in these plots, two linear transects were walked in each cell diagonally from northwest to southeast, and northeast to southwest corners (Peterson, Rockwell, Witte, & Koons, 2013; Rockwell et al., 2003; Weatherhead, 1979). Vegetation and landscape cover data along transects were collected following a modified step-point method whereby dominant composition was recorded underfoot approximately every meter (Evans & Love, 1957; Owensby, 1973). Vegetation was recorded to the genus or species level for target species of interest (Appendix C Table 2 for a complete list of classifications). Bare soils, waterways or ponds lacking vegetation, dried waterways or ponds, and dead willows were classified as barren. Dwarf shrub species in the genus *Salix*, *Betula*, and *Myrica* were classified as shrubs. All other plant species (predominately graminoids) were classified as non-shrubs. A single observer and a dedicated recorder conducted surveys from 12-19 July 2016.

Drone Data Collection

We conducted drone flights using a Trimble UX5 (color: black, wingspan: 100 cm, weight: 2.5kg, cruise speed: 80 km/h), a fixed-wing rear-propelled aircraft powered by removable lithium polymer batteries (14.8V, 6000 mAh). The UX5 uses an elastic catapult launcher to initiate flights and engage the motor. We programmed the UX5 to follow a pre-defined flight path established by the operator based on the vegetation survey grids to be covered, the survey altitude needed for a specific resolution, and wind conditions at the time of the flight using Trimble Access Aerial Imaging V2.0.00.40 (Trimble, Sunnyvale, CA). Using the UX5's built in GPS system, a flightlog recorded georeferenced images with 80% forward and horizontal overlap. Still images were collected in true color (3 visible bands: Red Blue Green) and were automatically taken with a Sony NEX-5R 16.1 MP camera (Sony Corporation of

America, New York, NY) along flight paths. Relevant camera settings for all flights were as follows: no flash, exposure time 1/4000, automatic white balance, and automatic ISO. Pictures were taken by automatic trigger approximately once every second while on flight tracks and were saved in JPEG format to an onboard 16GB SD card. Once the flight area had been covered, the UX5 returned to a pre-defined landing zone and belly landed. Imagery and flight logs were downloaded following completion of individual flights. All flights were done on 14 July 2016 between the hours of 0900 and 1200. Study plots were surveyed at 75, 100, and 120 m above ground level (AGL), resulting in a ground sampling distance (linear distance between center points of adjacent pixels) of 2.4, 3.2 and 3.8 cm, respectively.

We were also interested in any differences in wind conditions during flight operations which could affect aircraft stability and thus image quality. Therefore, we examined weather data which was collected throughout the field season by a consumer-level AcuRite weather station (Chaney Instrument Co, WI). Windspeed measurements were recorded every 12 minutes (default settings), along with the peak windspeed during the 12 minute window.

Raw images were stitched together using Pix4Dmapper Pro (Pix4D, Switzerland, V3.3) to create high resolution mosaics of study plots, which were loaded into ArcGIS 10.6 (ESRI, Redlands, CA) for image classification, and the areas of interest were clipped out. Mosaics were separately classified into 30 class types using an unsupervised classification approach (Lillesand, Kiefer, & Chipman, 2014) and classes were manually inspected and reclassified into barren, non-shrub, or shrub categories. We selected to employ unsupervised classifications based on preliminary accuracy results when compared to both supervised and random forest classifiers during data exploration. This approach also allowed us to test a simple classification method that requires relatively little technical training and is useful for ecologists with access to a widely used program. Study plots were classified separately to account for any variation in light conditions between plots or any natural variation in land cover type reflectance across the study area. High resolution imagery is often associated with a “salt-and-pepper” effect, where individual pixels are incorrectly classified as different from their majority neighbors (Feng, Liu, & Gong, 2015). To account for this effect, post processing was done using methods in Chabot and Bird (2013) (Chabot & Bird, 2013). This was done by applying a majority filter and boundary clean tools, followed by the removal of patches <0.25m^2, which were replaced based on the values of nearest neighbours.

We calculated proportion cover as the proportion area represented by each class in relation to the total area surveyed across all plots from classified images for the three flight altitudes. We assessed classification accuracy by generating 100 randomly stratified points within each plot, where the number of points generated for each class is proportional to the relative area occupied by each class. This was repeated for each survey altitude (100 points in each plot, 500 total for each altitude). Standard convention for accuracy assessments is to use georeferenced ground-truth data as the comparative standard for site-specific accuracy assessments, but this can present a problem for very high resolution imagery. Commonly used consumer grade GPS units can vary by several meters in their horizontal accuracy (Arnold & Zandbergen, 2011; Wing, Eklund, & Kellogg, 2005), which could result in biased accuracy assessments in heterogeneous land cover habitats. Survey grade GPS units would overcome this problem, but these are financially costly for researchers and were unavailable for this project. Further, each point of ground data collected in this study was not georeferenced and thus unable to be used for creation of an accuracy assessment confusion matrix.

To assess our imagery accuracy in a manner similar to that of commercially purchased imagery, the true classification for assessment points was assessed via visual inspection (manual photointerpretation) of each altitude’s respective high resolution RGB mosaics, which allows relatively clear identification of land cover type for each point. Similar practices with high resolution drone imagery have previously been reported in the literature (Chabot & Bird, 2013; Pande-Chhetri, Abd-Elrahman, Liu, Morton, & Wilhelm, 2017; Su & Gibeaut, 2017). It should be noted that visual inspection of imagery is not likely to be 100% accurate, but given the high resolution nature of the imagery, we have a high degree of confidence in correct vegetation class identification. We calculated overall accuracy and kappa coefficients for each flight altitude.

Statistical Analysis

To compare estimates between ground-based linear transects and drone imagery, we examined proportional cover data within cells. Proportional data from ground-based linear transects within cells was obtained by taking the number of data points (steps) for each type (barren, non-shrub, and shrub) and dividing by the total number of data points in each cell. Drone proportional data was produced with two approaches. First, we extracted the proportion of each land cover class within each cell as the number of pixels for each class type divided by the total number of pixels for each respective cell. While this is a common approach to land cover assessments from remotely sensed imagery, any differences between estimates from this method and the field-based transects may simply reflect differences in sampling technique (i.e. assessing the entire cell using the drone vs sampling a small proportion on the ground). To address this discrepancy, we also replicated ground-based data collection by overlaying approximately the same ground-based linear transects within cells in the classified drone imagery. We extracted classification values every meter along the two drone transects within each cell and calculated proportion land cover class for each cell using the number of data points for each class type divided by the total number of data points within each cell.

We calculated Pearson’s correlation coefficients in R v3.4.3 (R Core Team, 2017) comparing the three methods of data acquisition (ground transects, drone transects, and drone pixel counts) for each cover type. Each method has its own value for a cover type within an individual cell and data are measured on the same scale; therefore deviation from a 1:1 relationship should represent a difference in measurement between methods.

We then used a modified version of the generalized linear mixed model presented in Peterson et al. (2013) to estimate the proportion of land cover type (barren, non-shrub, and shrub) across our five study plots. Models were constructed using PROC GLIMMIX in SAS Studio 3.7 (Cary, NC). We modeled proportional land cover assuming a beta distribution for data constrained between 0 and 1 (Eskelson, Madsen, Hagar, & Temesgen, 2011; Ferrari & Cribari-Neto, 2004). To accommodate cells with values of 0 or 1, we transformed data according to Smithson and Verkuilen (2006),

$$y' = \frac{y \times (n - 1) + 0.5}{n}$$

where n is equal to the number of data points collected for each method within each cell (i.e. the number of transect points or pixels within a classified cell), y is the original proportion cover estimate for each cell, and y' is the adjusted value. By doing so 0’s or 1’s are respectively modified by the gain or loss of one-half the detection limit for each cell. We used a logit link function and a variance components covariance structure. Since we were first interested in the estimates between different drone survey altitudes, we constructed separate models for each drone method (drone pixel counts vs drone transects). These models were produced for each cover type, and only examined the fixed effect of *altitude* (3 levels: 75 m, 100 m, and 120 m

AGL). We then constructed another set of models examining the difference between ground estimates, and those from our highest accuracy drone survey altitude. These models included only the single fixed effect of *method* (three levels: ground based transects, drone based transects, and drone pixels counts). For all models we included the random effect of *cell_id* (n=92). Model fit was assessed via Generalized Chi-Square/DF as a measure of dispersion, and we generated Conditional Pearson's and Studentized residual plots for each model.

Results

In July 2016 ground-based assessments were completed by surveying 184 transects in 92 cells, taking approximately 72 researcher-hours. To survey the same plots, drone surveys took 61 min at 75 m AGL (2 flights), 28 min at 100 m AGL (1 flight), and 26 min at 120 m AGL (1 flight). While drone surveys were initially quicker than the ground based field work, post-flight image processing (data management, mosaic creation, image classification, etc.) took approximately 50 hours. Wind conditions during drone flights were mostly similar. The 75 m flights had a mean windspeed of 5.86 km h^{-1} (SD = 1.22, peak speed = 8.70), the 100 m flight had a mean of 5.19 km h^{-1} (SD=0.72, peak speed = 8.08), and the 120 m flight had a mean of 8.08 km h^{-1} (SD=1.78, peak speed = 10.56).

Drone Image Classification

Unsupervised classifications in ArcGIS produced similar proportion cover results for each altitude based on total enumeration of pixels across the study area, and there were minor differences in overall accuracy and kappa coefficients (Table 6). Notably, the mean accuracy and kappa coefficients decreased with increasing drone survey altitude, but the range of values for both measures overlapped between the three altitudes (Table 6). The lowest altitude surveys at

75m AGL produced the highest mean ± SD overall accuracy of 92.0±0.019%, followed by 90.8±0.036% at 100m AGL, and 88.8±0.024% at 120m AGL.

Visual inspection of the RGB mosaics and classified images revealed several consistent errors remaining despite post processing efforts (Figure 6). Distinctions between relatively darker mats of graminoid vegetation (non-shrubs such as *Puccinelia sp.*, *Rannunculus sp.*) and darker soils proved difficult for the pixel based classifiers as indicated by higher errors of omission and commission at all altitudes (see Confusion Matrices in Appendix C Table 3). Further, larger shadows from rocks and vegetation were often classified as shrub patches (Figure 6), although smaller shadows were often successfully eliminated via post-processing tools.

Ground vs Drone Cover Estimates

We chose to examine correlations using drone estimates from the 75 m AGL flight, which had the highest mean overall accuracy (Table 6). Generally barren and shrub cover types had higher agreement among the three methods of measurement (Figure 7). Non-shrub cover was poorly measured by both drone methods when compared to ground transects (Pearson's r = -0.036 for drone transects, and r = 0.028 for drone pixel counts), indicating the drone RGB imagery is inadequate for detecting the inconspicuous graminoid and forb species that dominate the non-shrub category. However, both drone methods had high agreement in measurements for all three classes (Figure 7 G-I).

Drone pixel count models indicated significant differences in measurements for barren ($F_{2,182}$ = 16.24, P<0.0001) and non-shrubs ($F_{2,182}$ =18.56, P<0.0001), but not for shrubs ($F_{2,182}$ =3.02, P=0.051) (Table 7). Similarly, drone transects also indicated significant differences in measurements for barren ($F_{2,182}$ = 10.17, P<0.0001) and non-shrubs ($F_{2,182}$ = 10.49, P<0.0001), but not for shrubs ($F_{2,182}$ = 1.30, P=0.275) (Table 8). Our third set of models examining differences between ground and drone methods indicated that drone methods overestimated barren and shrub categories, but underestimated non-shrubs (Table 9). We plotted model estimates of proportion land cover from only the 75m drone survey in comparison to ground estimates (Figure 8). Mixed model estimates from all three methods indicate higher proportion cover of barren area when compared to shrubs and non-shrub cover (Figure 8). Models showed no evidence of over- or underdispersion. Inspection of residual plots revealed no clear violation of model assumptions.

Discussion

Here we show that by using a fixed-wing drone we were able to survey our study area much faster than ground-based methods, but these savings came at the cost of increased time spent during image processing and classification steps. Cruzan et al. (2016) had similar findings on time management and importantly noted that increases in imagery resolution will require concordant investment in computer processing time and power (Cruzan et al., 2016). Indeed, Fraser et al. (2016) reported drone imagery processing times of up to 10 days when producing ultradense point clouds from highly overlapping imagery (Fraser, Olthof, Lantz, & Schmitt, 2016). As such, longer flight durations to survey larger areas and ultimately process larger amounts of data may present a limit on the scalability of drone technology in ecological research. Fortunately, the efficiency and time savings gained during the data collection step are likely more relevant to researchers in polar regions where ecological field studies are often limited by shorter operational field seasons (Malenovský et al., 2017).

Our simple unsupervised classification approach with RGB imagery was moderately successful when compared to ground-based methods. Overall accuracy assessment and kappa coefficients of the RGB mosaics were relatively high with little difference between altitudes and were quantitatively similar to previous vegetation assessments with fixed-wing drones (Laliberte, Herrick, Rango, & Winters, 2010; Marcaccio et al., 2016; Mora, Vieira, Pina, Lousada, & Christiansen, 2015). We expected accuracy of classifications to increase with lower altitude surveys (higher image resolution), which was supported by our findings (see Table 6). Accuracy and kappa coefficients appeared to increase with higher resolution imagery, but we considered these differences between altitudes to be minimal as the difference between the highest and lowest resolution's mean overall accuracy was only 3.2%. This likely reflects the minimal difference in ground sampling distances between each altitude, and we suspect that advantages gained by higher resolution RGB imagery were simply not realized by our simple classification approach. Consequently, if similar methods were to be used in the future, we encourage higher altitude drone flights which are more efficient at surveying larger study areas (Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015). It is worth noting that our highest survey altitude was the highest allowed under our drone operation permit, and higher altitude flights would require additional permitting.

It is important to consider that differences in environmental conditions between flights could have played a role in image quality and subsequent classifications. Our measurements of wind speed were examined post-hoc study design, and in the future, more fine scale environmental measurements should be collected to formally account for differences among flight operations (i.e. every minute). Although our coarse data indicated slightly higher wind speeds during the 120 m flight, we considered these differences to be minimal and likely played little role in differential image quality between flights. Time-of-day has been shown to be an important consideration for drone image acquisition, due to the differential presence of shadows throughout the day (Patterson et al., 2015). Although we did not measure cloud cover during this study, our period of flight operations used for classifications all occurred within a three hour window, so changes in light conditions likely did not play a large role in image quality differences between flights. Considerations for light conditions will be important in future drone studies, and researchers may benefit from obtaining images on overcast days to minimize the presence of shadows. This, however, will require high quality sensors to compensate for reduced light conditions (Fraser et al., 2016; Patterson et al., 2015).

We caution that although we were confident in our visual inspection of RGB imagery for each land cover class, it is possible that accuracy was artificially inflated due to researcher biases. As such, results should be interpreted with care. The lack of georeferenced ground-truthed data in this study represents an obstacle for the future of long-range drone surveys in ecology. If BVLOS surveys become routine in ecology, researchers will not always be present at field sites to validate imagery collected by drones. Therefore, efforts should be made to test aircraft capable of BVLOS flights on smaller scale where comparisons compare estimates between traditional and drone methods for ecological parameters of interest are conducted as we did in this study.

Although our model results appeared to overestimate barren and shrub cover while underestimating non-shrubs, similar findings have been reported in the literature (Breckenridge, Dakins, Bunting, Harbour, & Lee, 2012; Mora et al., 2015). Similar spectral signatures of shrubs and non-shrub species likely played a large role in our misclassifications, which lends support to the apparent need for additional layers of input data (hyperspectral, textural, etc.) to achieve fine-scale classifications (Turner, Lucieer, Malenovský, King, & Robinson, 2018). While we recognize that our drone imagery was inadequate at capturing inconspicuous graminoid and forb species (see Figure 7), the use of bare ground coverage has been shown to be a reliable metric for measuring snow goose habitat degradation (R. L. Jefferies & Rockwell, 2002). As such, our simple drone imagery should be reliable at determining the impact of snow geese on Arctic vegetation communities at a coarse scale. Further, our high altitude drone estimates corroborate the findings of Fraser et al. (2016), who found drone imagery to be a useful method for measuring Arctic shrub communities by combining spectral and structure-from-motion data inputs into their classifiers with an overall accuracy of 82% (Fraser et al., 2016). These findings support the notion that simple RGB imagery from drones may be more effective for identifying broad scale patterns of conspicuous features, but delineation between more inconspicuous species remains a challenge. Despite post-processing efforts undertaken in ArcGIS, Chabot et al. (2013) suggests that incorporating texture information could help differentiate between classes of land cover with similar spectral properties (Chabot & Bird, 2013). More sophisticated techniques such as object based image analysis or random forest classifiers have been used for vegetation assessments from drone imagery and may yield more accurate results, but will come at the cost of increased processing time and requires proficiency in more advanced image analysis techniques (Feng et al., 2015; Laliberte et al., 2010; Turner et al., 2018).

Our estimates of land cover from all three methods generally agree with most recent habitat assessments in the La Pérouse Bay region and that the majority of study plots remain dominated by barren ground, likely as a result of hypersaline conditions (Peterson et al., 2013; Rockwell et al., 2003). Experimental evidence indicates that in the absence of goose foraging and presence of suitable soil conditions, degraded habitats may recover their graminoid assemblages (K. Abraham, Jefferies, Alisauskas, & Rockwell, 2012). While there is some evidence of re-vegetation in long term goose exclosures in supratidal marsh areas at La Pérouse Bay (Rockwell unpublished data 2008-2018), widespread vegetation re-establishment is not yet apparent when compared to historical assessments (Weatherhead, 1979). Our classifications were restricted to three broad classes of land cover, keeping in-line with previous assessments in the region that used a similar approach (Peterson et al., 2013; Rockwell et al., 2003). It is possible that increasing the number of classes in our study may produce different accuracy statistics, but consistency in classification types allows us to attempt integration of novel drone technology into long-term ground based datasets. Further, initial inspections of RGB mosaics revealed difficulties in differentiating between several distinct shrub species (e.g. *B. glandulosa, S. planifolia, S. candida*), indicating that coarse classifications may be more successful. While we did not attempt to distinguish between different species of shrubs, graminoids or forbs in this study and were not the primary objective of this study, the development of drone models and sensors may still play an important role in understanding the impacts of snow geese within their ecosystem, with respect to changing plant communities. Logistic and financial constraints can often prevent repeat surveys by researchers on the ground, but drone flights are easily repeatable and may assist in future monitoring protocols (Sardà-Palomera, Bota, Padilla, Brotons, & Sardà, 2017). Ground based approaches may also have their own associated biases such as researcher fatigue or experience level in identifying plants. Drones may help overcome the fatigue bias due to the ability to archive data and spread data collection (image interpretation) over several shorter sessions. In plant community studies where higher spatial coverage is often required for landscape-level inferences, fixed-wing drones may be more advantageous than quadcopter models (Cruzan et al., 2016; Marcaccio et al., 2016). If one of the goals of snow goose monitoring involves repeat surveys of vegetation communities, drones may prove a useful tool for quickly surveying larger areas to collect coarse landscape level data. However, ground-based fieldwork will likely still be required if fine-scale data is desired.

Here we have detailed the application of a fixed-wing drone using RGB imagery and a relatively simple classification method for evaluation of snow goose habitat damage. Applications of similar methods have played an important role in understanding polar vegetation (Fraser et al., 2016; Lucieer, Turner, King, & Robinson, 2014; Malenovský et al., 2017) but may also be used to research other types of habitat degradation and landscape changes. Potential applications might include changes in salinity, overgrazing, beetle infestations of forests, land-use conversions, and changes in ephemeral wetland coverage. Although we used a simple technique here, future studies could explore the use of more sophisticated multispectral sensors in drones, which have previously been used in fine-scale plant ecology studies (Ahmed et al., 2017; Knoth, Klein, Prinz, & Kleinebecker, 2013; Strecha, Fletcher, Lechner, Erskine, & Fua, 2012). Multispectral sensors in drones have been heavily employed in precision agriculture for applications such as measuring the Leaf Area Index in vineyards(Mathews & Jensen, 2013) and estimating nitrogen status in sunflowers (*Helianthus annuus*) (Agüera, Carvajal, & Pérez, 2011), while miniaturized hyperspectral sensors have been used for detecting water stress in plants(Zarco-Tejada, González-Dugo, & Berni, 2012) and estimating plant biomass(Pölönen, Saari, Kaivosoja, Honkavaara, & Pesonen, 2013). These sensor types offer unique insights into aspects of plant ecology beyond measuring abundance and distribution, potentially allowing researchers to address a wide variety of ecology phenomenon using drones. The natural progression of these technologies from industry applications to academic research is assisted by decreasing costs and accessibility of miniaturized sensors(Berra, Gaulton, & Barr, 2017). However such specialized sensors generally require field calibrations, which may necessitate further expenditures and validation experiments in the field (Tay, Erfmeier, & Kalwij, 2018). Any such experiments should consider paired survey designs (see Ahmed et al. 2017) that explicitly compare performance between competing sensors and aircraft design to better facilitate comparisons (Ahmed et al., 2017).

The implementation of drones for ecological research in polar regions will ultimately depend on the specifics and scale of the scientific questions being asked. Current government and technological limitations prevent drone use at broad spatial scales, and several studies have noted limitations of current drone based research due to within line-of-sight flight regulations (Anderson & Gaston, 2013; Andrew F. Barnas et al., 2018; Christie et al., 2016; Hodgson et al., 2013). However if the operation of long-range drone models is eventually outsourced to commercial operations, these regulations may be more easily overcome by industry partners with aircraft regulation expertise. To better facilitate the development of drones for ecological research, we recommend researchers report specifics of their aircrafts as seen in Zweig et al. (2015) and Vermeulen et al. (2013). The benefit of this reporting will better inform researchers considering drones as methods for research and monitoring projects in the future.

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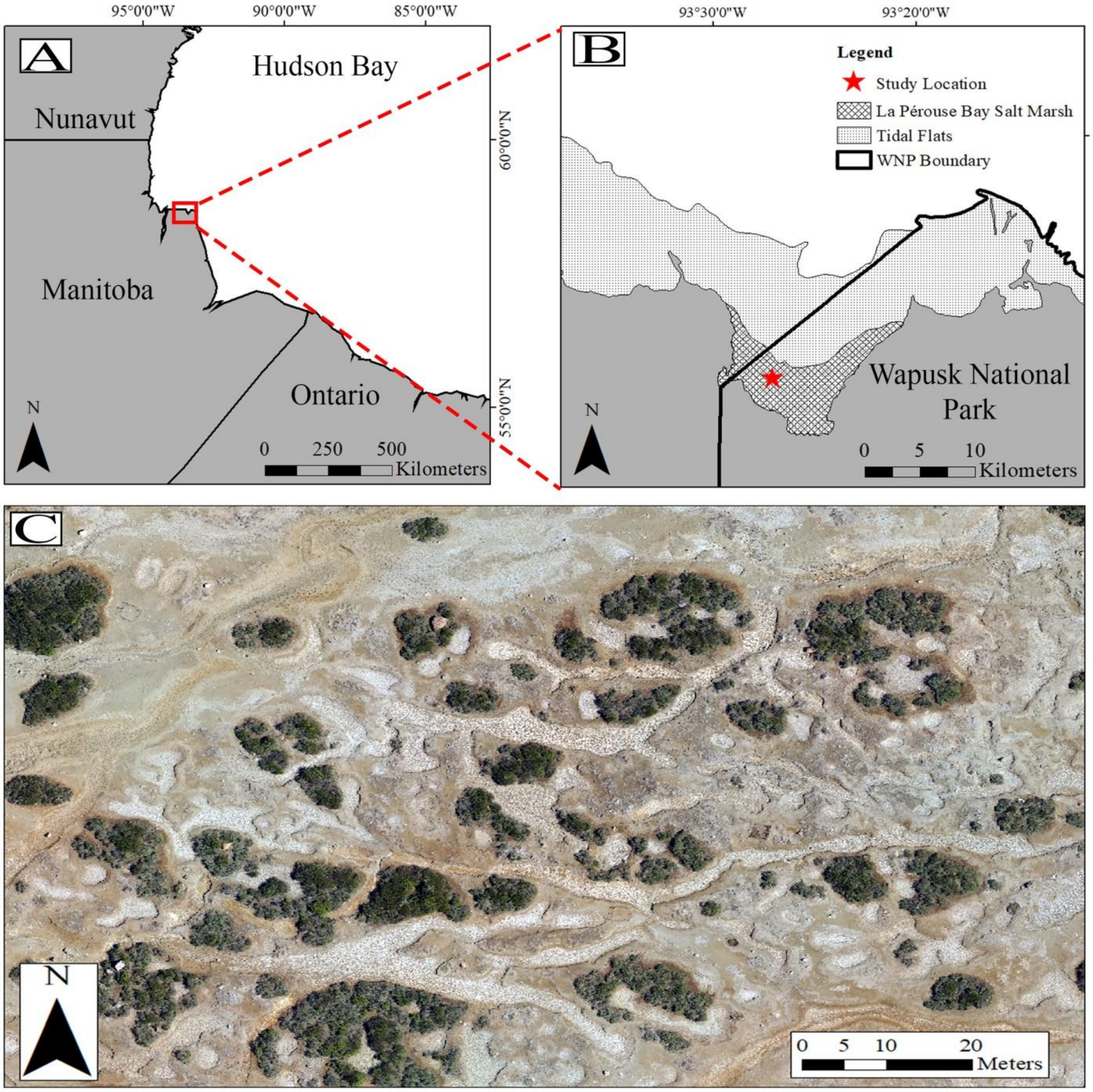

Figure 5 Map of study location (A) Extent indicator of study location in northern Manitoba, (B) supratidal salt marsh study location within Wapusk National Park, (C) sample RGB photo of habitat surveyed by drone. Image acquired at 75 m above ground level.

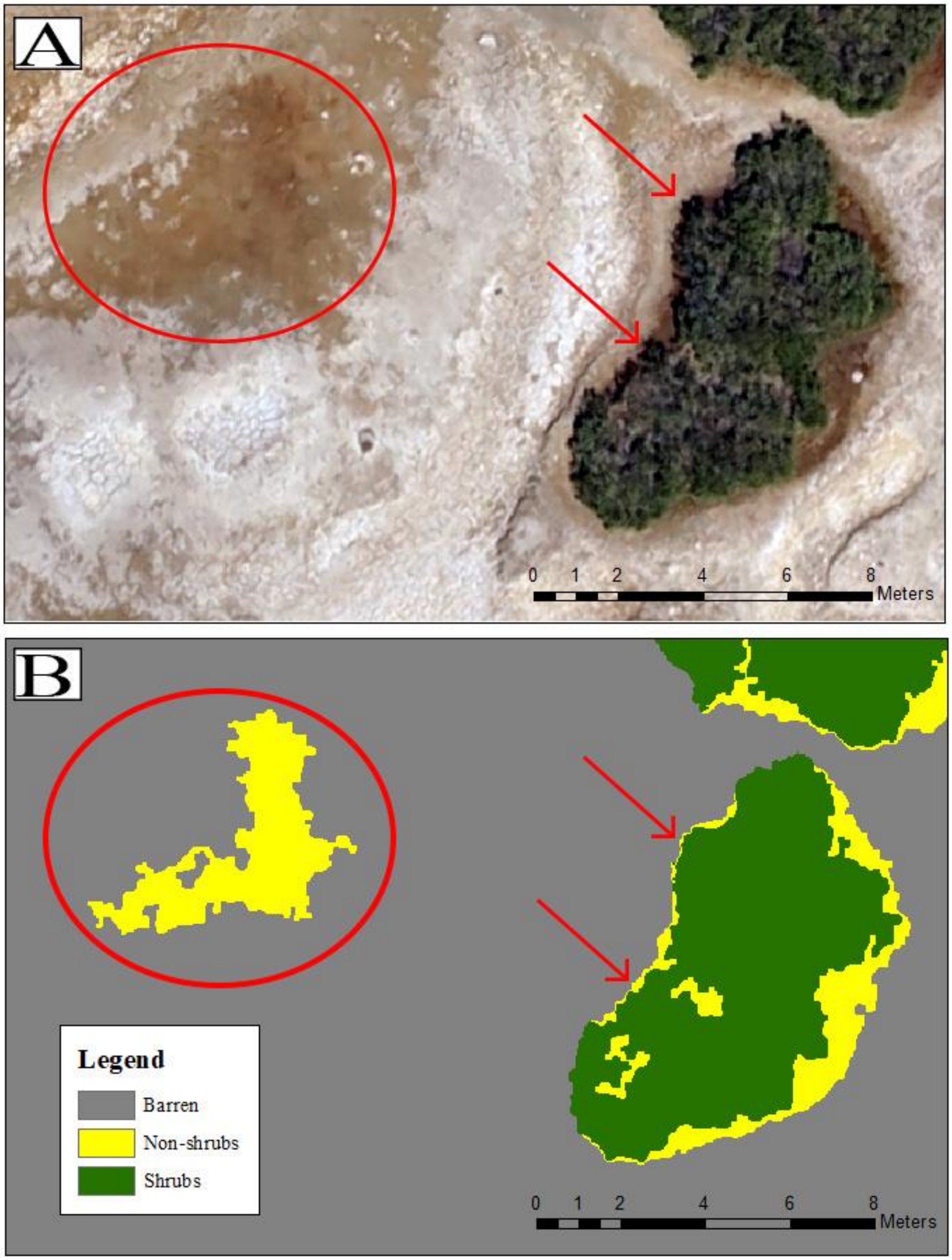

Figure 6 Comparisons between RGB drone imagery and classified product. (A) Example RGB imagery at 120 m AGL (B) final classified image. Post processing tools failed to eliminate the patch of darker barren surface and incorrectly classified the patch as non-shrub vegetation (indicated by the red circle). Shadows along the edge of the vegetation patch were improperly classified as shrubs (indicated by red arrows).

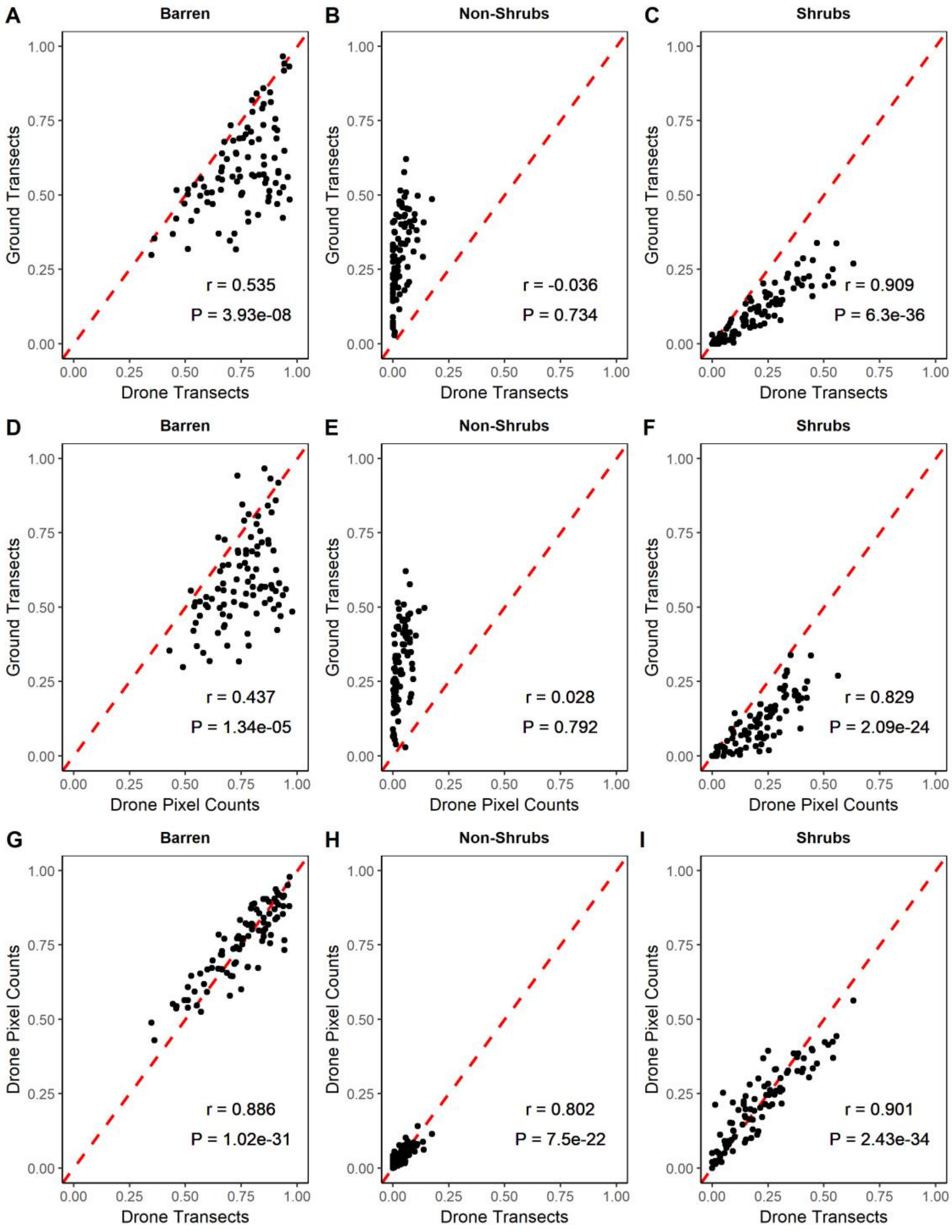

Figure 7 Plotted proportional values and Pearson's correlation coefficients between three methods of data acquisition (ground transects, drone transects and drone pixel counts). Data presented for each cover type (barren, non-shrubs, and shrubs). Each point represents proportional cover data collected within the same cell (n=92) for each method. Drone imagery collected at 75 m AGL. Red dashed line represents 1:1 relationship.

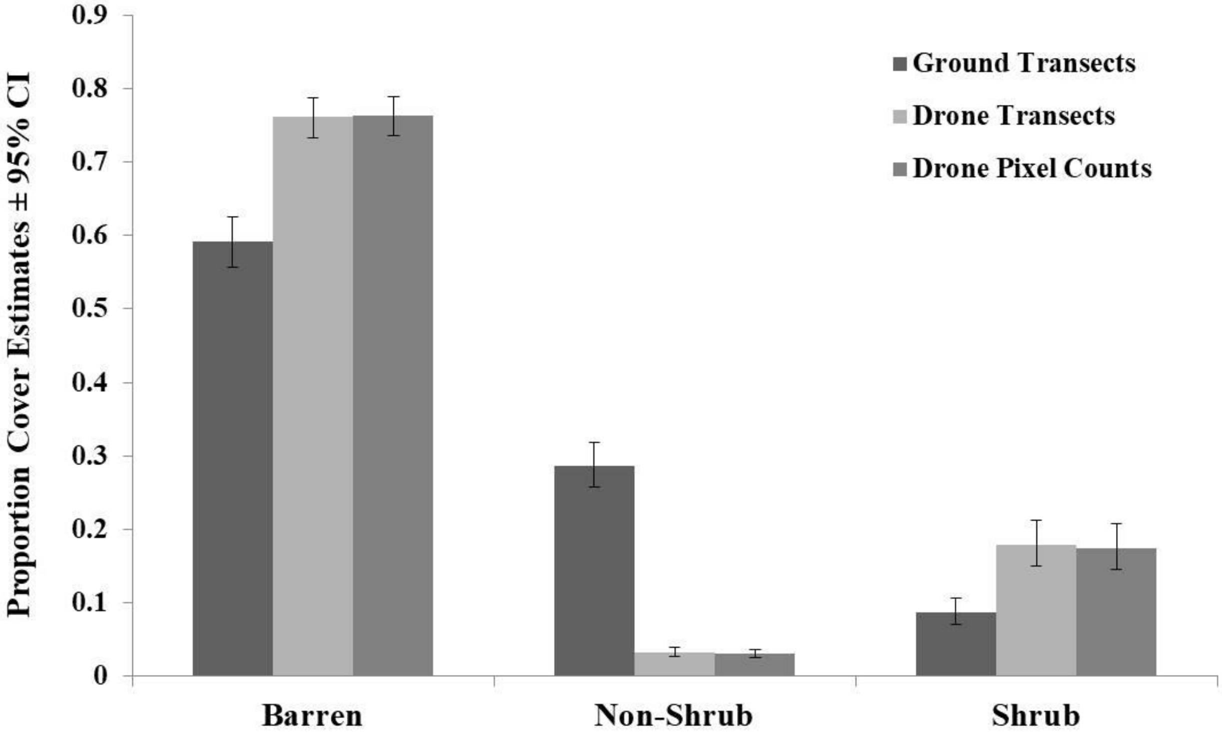

Figure 8 Mixed model estimates of proportion land cover type from three different methods of data collection. Ground transects data collected as linear transects, drone transects are the same transects overlaid on classified drone imagery (see Methods section) with land cover values were extracted every meter, and drone pixel counts based on the enumeration of pixels for each land cover type as a proportion of all pixels in each cell. Drone estimates made from imagery collected at 75 m AGL. Cover data obtained from 92 cells across 5 study plots.

Table 6 Proportion land cover type classification of drone (Trimble UX5) imagery at three altitudes. Proportion values are obtained from the enumeration of pixel types for each land cover class across all 5 plots. Accuracy and kappa statistics presented as mean ± SD, along with the range of values

	Drone Survey Altitude		
	75m	**100m**	**120m**
Proportion Barren	0.755	0.761	0.741
Proportion Non-Shrubs	0.035	0.032	0.050
Proportion Shrubs	0.210	0.207	0.208
Overall Accuracy	92.0±0.019% Range: 0.90-0.95%	90.8±0.036% Range: 0.86-0.94%	88.8±0.024% Range: 0.86-0.92%
Kappa Coefficient	0.81±0.088 Range: 0.66-0.90	0.79±0.075 Range: 0.70-0.88	0.73±0.113 Range: 0.54-0.83

Table 7 Coefficient estimates from Beta GLMM for each cover type (barren, non-shrub, and shrub) as measured by drone pixel counts at altitudes of 75, 100 and 120m AGL. Estimates obtained from 92 observations (cells) across 5 different study plots.

		Cover Type	
	Barren	**Non-Shrub**	**Shrub**
Coefficient Estimate ± SE			
Intercept	1.274 ± 0.088	-3.418 ± 0.089	-1.590 ± 0.116
100 m AGL*	0.036 ± 0.020	-0.087 ± 0.095	-0.022 ± 0.010
120 m AGL*	-0.075 ± 0.020	0.395 ± 0.086	-0.020 ± 0.010
Covariance Parameter Estimates ± SE			
Cell	0.687 ± 0.105	0.320 ± 0.070	1.232 ± 0.191
Fixed Effect Tests			
Altitude	$F_{2,182}$ = 16.24, P<0.0001	$F_{2,182}$ = 18.56, P<0.0001	$F_{2,182}$ = 3.02, P=0.051
Fit Statistics			
Generalized Chi-Square/DF	1.00	1.00	1.00

*****Baseline comparisons are to measurements made from drone pixel counts at 75 m AGL

Table 8 Coefficient estimates from Beta GLMM for each cover type (barren, non-shrub, and shrub) as measured by drone transects at altitudes of 75, 100 and 120m AGL. Estimates obtained from 92 observations (cells) across 5 different study plots.

	Cover Type		
	Barren	**Non-Shrub**	**Shrub**
Coefficient Estimate ± SE			
Intercept	1.295 ± 0.101	-3.337 ± 0.098	-1.635 ± 0.129
100 m AGL*	0.032 ± 0.033	-0.083 ± 0.113	-0.016 ± 0.025
120 m AGL*	-0.109 ± 0.033	0.355 ± 0.103	0.024 ± 0.025
Covariance Parameter Estimates ± SE			
Cell	0.873 ± 0.135	0.307 ± 0.074	1.484 ± 0.231
Fixed Effect Tests			
Altitude	$F_{2,182}$ = 10.17, P<0.0001	$F_{2,182}$ = 10.49, P<0.0001	$F_{2,182}$ = 1.30, P=0.275
Fit Statistics			
Generalized Chi-Square/DF	1.00	1.00	1.00

*****Baseline comparisons are to measurements made from drone transects at 75 m AGL

Table 9 Coefficient estimates from Beta GLMM for each cover type (barren, non-shrub, and shrub) as measured by ground based transects, drone based transects and drone pixel counts at 75 m AGL. Estimates obtained from 92 observations (cells) across 5 different study plots.

	Cover Type		
	Barren	**Non-Shrub**	**Shrub**
Coefficient Estimate ± SE			
Intercept	0.371 ± 0.072	-0.910 ± 0.074	-2.3488 ± 0.111
Drone Pixel Counts*	0.802 ± 0.066	-2.549 ± 0.082	0.798 ± 0.051
Drone Based Transects*	0.787 ± 0.066	-2.483 ± 0.080	0.825 ± 0.050
Covariance Parameter Estimates ± SE			
Cell	0.299 ± 0.056	0.406 ± 0.075	0.969 ± 0.161
Fixed Effect Tests			
Method	$F_{2,182}$ = 100.03, P<0.0001	$F_{2,182}$ = 843.77, P<0.0001	$F_{2,182}$ = 160.16, P<0.0001
Fit Statistics			
Generalized Chi-Square/DF	1.00	1.00	1.00

*****Baseline comparisons are to measurements made from ground based transects

CHAPTER V A PHENOLOGICAL COMPARISON OF GRIZZLY AND POLAR BEARS AS WATERFOWL NEST PREDATORS IN WAPUSK NATIONAL PARK

Abstract:

Grizzly bears (*Ursus arctos*) have been increasingly observed along the coast of western Hudson Bay, but relatively little is known about the ecological impact of these individuals. From 2012-2018 we monitored nests of common eiders (*Somateria mollissima sedentaria*) and lesser snow geese (*Anser caerulescens caerulescens*) using remote trail cameras, and documented grizzlies consuming eggs of both species in all years except 2013. In years where both grizzly and polar bears (*Ursus maritimus*) were detected in waterfowl colonies, grizzlies were detected earlier in the year and had greater overlap with the estimated availability window of incubating birds. As such, we hypothesize that grizzly bears in this region may have the capacity to reduce the availability of waterfowl eggs to polar bears. Grizzlies will likely have a larger impact on waterfowl populations than polar bears, as grizzly bears are a more consistent nest predator. Repeat observations of the same individual grizzly bear consuming eggs in 2015, 2016 and 2018 suggests that these resources may play an important role in facilitating grizzly persistence in the park. Future work should attempt to quantify the abundance of grizzly bears and their effects on waterfowl nest survival using formal statistical methods that account for imperfect detection.

Introduction

Observations of grizzly bears (*Ursus arctos*) along the coast of western Hudson Bay have been increasingly reported since the 1990’s (D. Clark, 2000; D. A. Clark et al., 2018; COSEWIC, 2012; Robert Rockwell, Gormezano, & Hedman, 2008). The majority of these observations have been collected within Wapusk National Park (WNP), an ecologically significant area for several charismatic species including polar bears (*Ursus maritimus*)

(Richardson, Stirling, & Hik, 2005), caribou (*Rangifer tarandus*) (COSEWIC, 2017) and many species of migratory waterfowl (R. F. Rockwell et al., 2009). The recent investigation of Clark et al. (2018) on the occurrence of grizzly bears in WNP suggests repeat annual habitat use by multiple individuals and perhaps local denning. While much attention has been focused on the spatial and temporal patterns of grizzly bear occurrence within the park (D. A. Clark et al., 2018; Robert Rockwell et al., 2008), relatively little is known about the ecological consequences of novel predation pressure introduced by grizzly bears in this region.

Diets of barren ground grizzly bears in other areas of the Arctic contain important contributions from berries and other mixed vegetation, but bears are thought to be predominately carnivorous (Gau, Case, Penner, & McLoughlin, 2002). In WNP, calves of caribou or moose (*Alces alces*) are available as prey to grizzlies (Boertje, Gasaway, Grangaard, & Kelleyhouse, 1988; Gau et al., 2002; Young Jr & McCabe, 1997); however, the pursuit of these prey may be energetically costly to bears on flat, open tundra with little cover. Alternatively, bears may exploit the seasonal abundance of nesting waterfowl, specifically their energetically rich eggs. In other parts of their range, grizzlies have not been considered regular predators of Arctic nesting birds (Barry, 1967; Johnson & Noel, 2005), but several reports suggest that just a small number of bears can have catastrophic impacts on nesting birds via egg consumption (Armstrong, 1998; Obst, Hines, Dufour, Woodard, & Bromley, 2013; Rode, Robbins, Nelson, & Amstrup, 2015). Throughout the Arctic, grizzlies have been documented consuming several species of nesting birds and their eggs including king eiders (*Somateria spectabilis*) (Obst et al., 2013), black brant (*Branta bernicla nigricans*) (Armstrong, 1998), common eiders (*Somateria mollissima*), white fronted geese (*Anser albifrons*) (Johnson & Noel, 2005), and lesser snow geese (*Anser caerulescens caerulescens*) (Barry, 1967; Obst et al., 2013). The patterns and impacts of grizzly predation on birds has not been systematically studied, but Kerbes et al. (2006) speculated that persistent predation by grizzlies was a contributing factor leading to population declines of a goose colony in the Queen Maud Gulf Migratory Bird Sanctuary from 1988-1998.

In addition to being a novel predation source in an expanded part of their range, grizzlies may also differ from other Ursids with respect to timing of nest predation events in bird colonies. Throughout the Arctic, polar bears are also well documented as nest predators of birds and can have catastrophic impacts on bird populations in some years (Dey et al., 2017; Prop, Oudman, van Spanje, & Wolters, 2013; Stempniewicz, 2006). Predation of nests by polar bears has been increasing annually throughout the Arctic due to reductions in spring sea-ice, but their arrival on land is highly dependent on sea-ice dynamics (Iverson, Gilchrist, Smith, Gaston, & Forbes, 2014; R. F. Rockwell, Gormezano, & Koons, 2011; Smith, Elliott, Gaston, & Gilchrist, 2010). Arctic grizzly bears rarely venture onto sea-ice (Taylor, 1995), and therefore could conceivably have earlier access to bird nests than polar bears, limiting the availability of eggs to polar bears in years of later sea-ice breakup.

WNP is one of the few places where grizzly and polar bears are known to overlap and could possibly share a common prey base (Clark et al. 2018; Rockwell et al. 2008, but see Miller et al. 2015). As both species have a demonstrated capacity for causing high rates of reproductive failure in waterfowl (Obst et al., 2013; RF Rockwell & Gormezano, 2009), our site provides an unprecedented opportunity to study nest predation of both bear species simultaneously. We evaluate Ursid nest predation using a multi-year camera trapping study on Hudson Bay common eiders (*Somateria mollissima sedentaria*) and lesser snow geese (hereafter “eiders” and “snow geese” respectively), allowing us to make inferences on patterns within and among years. Specifically, we investigate the rates of waterfowl nest predation for each bear species and address the questions: 1) how consistent are grizzly and polar bear occurrences among years, and 2) how does the timing of grizzly and polar bear predation compare in years when both species occur during the period of waterfowl nesting?

Methods

Study Area

We annually survey nesting effort and success in two eider and three snow goose colonies in WNP, Manitoba, Canada (Figure 9). Eider colonies are located in the coastal tributaries of the Mast River and WaWao Creek. Nests are located along the shores and on islands throughout the braided river deltas which ultimately feed into western Hudson Bay. Nests are predominately located within dense stands of dwarf birch (*Betchula glandulosa*) and willow species (*Salix sp*.). One snow goose colony is located approximately 2 km east of La Pérouse Bay, while the other two are located approximately 50 km south on the northern and southern sides of Thompson Point (Figure 9). Snow goose colonies in this study are located in freshwater marsh habitat, with nests often placed on raised hummocks with relatively little vegetation for concealment. For a detailed physiographic description of the region see Brook and Kenkel (2002); Shilts, Aylsworth, Kaszycki, and Klassen (1987).

Camera Monitoring

We installed trail cameras at waterfowl nests in late May to mid-July from 2012 – 2018 to investigate nest predators and nesting behaviours of attendant females. In 2012 only eiders were monitored, using ScoutGuard SG 550 cameras (HCO Outdoor Products, Peachtree Corners, Georgia), programmed to take a burst of 3 pictures when movement was detected and with a quiet period of 30 seconds. From 2013-2015 we monitored eiders and snow geese using both ScoutGuards and Reconyx PC-800 Hyperfire cameras (Reconyx, Holmen, Wisconsin), which were programmed to take a burst of 30 images when movement was detected, along with a single image every 2 minutes. No quiet period was used with the Reconyx models. From 2016-2018 we switched to only using Reconyx models in all colonies. Cameras were secured on wooden or steel posts, mounted approximately 0.5-1.5m off the ground. Images were stored on SD cards and downloaded during regular nest checks throughout incubation. Cameras were removed during nest checks if nests were determined to have failed or hatched.

Images were reviewed by a team of researchers for both species of bears and occurrences were tabulated for each nesting colony. Occurrences of bears were only included where clear species identification of bears was possible. We then filtered these occurrences to estimate the number of unique colony visitations represented by the data, assuming that images of bears across multiple cameras on the same day, within the same colony, likely represented the same bear. For example, a bear detected in a colony on one camera at 0900 hours and again at 1700 hours on a different camera would be considered the same colony visitation. We recorded whether bears were observed consuming eggs or hatchlings on camera, but also made inferences on nest fate based on predator sign at the nest during camera checks when images were unclear (e.g., low quality night images).

Phenology Comparisons

Since we were interested in the relative timing of bear occurrences in eider and snow goose colonies, we calculated the mean colony visitation date for each bear species using package *lubridate* in R v3.4.3 (Grolemund & Wickham, 2011; R Core Team, 2017). We then examined bear occurrences in relation to an index of availability of eider and snow goose nests each year. For both bird species we used a nest availability of 28 days based on a 24 day incubation period and average laying period of 4 days (1 egg per day, based on average clutch size of 4) (Cooke, Rockwell, & Lank, 1995; Iles et al., 2013). Initiation dates of individual nests were estimated via egg candling (Weller, 1956) and egg flotation (Westerskov, 1950), which were used to calculate the mean initiation date for each species and the resulting index of availability for 28 days thereafter.

We used a randomization approach to evaluate the probability that the phenological patterns we observed (i.e., that grizzlies arrived earlier than polar bears each year; see *Results*) were due to chance. We generated a series of 10,000 replicate datasets by assigning a random date to each bear observation from a discrete uniform distribution. For example, in a year where we observed 2 grizzlies and 3 polar bears, we would randomly draw dates for 5 bears (2 for grizzlies and 3 for polar bears). Dates were constrained between the earliest and latest detection date of bears for each year. We then calculated the proportion of randomized datasets in which grizzlies arrived earlier than the first polar bear in all years, as observed in our study. Because there was no difference in phenology between the bear species in our randomized datasets (i.e., arrival dates for both were drawn from the same uniform distribution), this approach quantifies the probability that the phenological difference we observed between grizzlies and polar bears was simply an artifact of sampling error.

Results

From 2012 to 2018 we deployed 197 cameras across 2 eider colonies and 233 across 3 snow goose colonies (Appendix D Table 1). Grizzly bears were observed in all years except 2013, while polar bears were only observed in years 2013 – 2016 (Appendix D Table 2). We identified grizzly bears on 26 cameras across all nesting waterfowl colonies, representing 16 unique colony visitation events (Table 10). On these cameras, grizzlies were either directly observed or inferred (based on sign at the nest) to have consumed eggs or nestlings from 20 out of 28 camera-monitored nests they encountered (Figure 10A, B), but in 7 cases bears arrived after nests had hatched or been preyed upon by another predator (Figure 10C). Polar bears were identified on more cameras than grizzlies in both eider and goose colonies (Table 10), and consumed 49 out of 60 available nests (Fig. 3). Although black bears (*Ursus americanus*) are known to occur in the region (Abraham, Mineau, & Cooke, 1977; D. A. Clark et al., 2018), we did not detect any individuals on cameras during our study.

We detected both grizzly and polar bears during the same season in three years (2014-2016). In all three of these years, grizzly bears were detected earlier in the year than polar bears (Figure 12). The probability this pattern would have occurred if there was no difference between grizzly and polar bear phenology was 0.096 (determined using a non-parametric randomization test; see Appendix D Figure 1). This represents moderate evidence that grizzlies arrive earlier than polar bears at our study site. Grizzlies overlapped with the estimated nesting period of snow geese in 4 out of 5 years they were detected in goose colonies, and overlapped with eider nesting in all 4 years (Figure 12). In contrast, polar bears only overlapped with snow geese in 2013 (1/3 years), but had higher overlap with eiders (3/4 years). It is important to note here that overlap with incubation is based on an estimated index of availability, and nests could be available outside these periods due to early or late nest initiation. For example, the only polar bear detected in 2016 was consuming eider eggs on Julian Day 198, well after the estimated end of incubation (Julian Day 184).

All observations of grizzlies were of lone adults and appeared to be in good health. Since individuals were not marked, it is not possible to estimate the number of grizzlies that were active in waterfowl colonies. However, one individual bear in our images possesses a unique rostral scar, allowing individual recognition with sufficiently clear images. We first identified this individual in 2015 foraging in both snow goose and eider colonies, and the same bear was again identified in an eider colony in 2016, and in a snow goose colony in 2018 (Appendix D Figure 2). Clear pictures of another grizzly without the characteristic scar in 2016 allow us to confirm that at least 2 individuals were present in WNP in 2016.

Discussion

Our study sheds important light on the ecological role of grizzly bears in an expanding part of their range, and demonstrates possible food resources for grizzlies in WNP. Here, we show that grizzlies should be considered a common nest predator of waterfowl nests. More importantly, these predation events by grizzlies are likely to be earlier than those by polar bears. Our findings also extend the time series of observations of grizzlies in the region by 2 years, adding to the growing documentation of these novel predators in the region.

Grizzly bears in the Canadian Arctic are thought to be expanding their range (COSEWIC, 2012; Doupé, England, Furze, & Paetkau, 2007), but food availability is an important limiting factor for bear populations in the Arctic (McLoughlin et al., 2002). Waterfowl eggs in WNP, specifically those of overabundant snow geese (Alisauskas et al., 2011), may therefore be facilitating the apparent increased grizzly presence in the park. Although nest consumption by grizzlies was relatively infrequent, when bears were observed on camera they tended to consume most of the available nests in the field of view of the camera. Our observations of the same individual grizzly over several years allow us to confirm hypotheses of Clark et al. (2018) that at least one individual has repeatedly used the same habitat space in WNP over multiple years. This, along with observations of grizzly bears almost every year in nesting colonies, suggests that grizzly bears have become a regular predator of waterfowl nests in the region. Grizzlies are known to have consumed goose nests here in the past (Abraham et al., 1977; D. Clark, 2000), but these events were likely of transient individuals as observations were lacking in subsequent years. If grizzlies in WNP are considered annual residents, then management efforts should be focused on determining other aspects of park use throughout the year (e.g. denning locations, seasonal habitat preferences, etc.).

Apparent differences in bear phenology within nesting colonies could play an important role in the availability of eggs for both bear species. Grizzlies were detected earlier in the year than polar bears when both species were detected in the same year. This likely reflects the fact that dates of polar bear arrival on land are dependent on spring sea-ice dynamics (Cherry, Derocher, Thiemann, & Lunn, 2013; Stirling, Lunn, & Iacozza, 1999). In years of later sea-ice breakup, polar bears may not arrive on land until well past the mean hatch date of waterfowl. Conversely, in years of early breakup polar bears would arrive much earlier and have higher overlap with nesting birds (Iverson et al., 2014; RF Rockwell & Gormezano, 2009; Smith et al., 2010), allowing increased rates of nest predation as appeared to be the case in 2013. However, the timing of grizzly bear arrival in nesting colonies is independent of sea-ice dynamics and is more likely to be predicted by environmental or physiological factors related to winter den emergence (Evans et al., 2016; Pigeon, Stenhouse, & Côté, 2016). Clark et al. (2018) reported 6 of 10 grizzly observations in the Cape Churchill region were in the spring, and 3 of these were in late May. The activity of grizzlies early in the spring before the arrival of polar bears on land suggests that grizzly bears should have early access to waterfowl eggs, thereby potentially depleting the availability of these eggs to polar bears. Indeed, in the only year of study where we did not observe grizzly bears, polar bears consumed 40 nests, but in all other years when grizzlies were also present, polar bears only consumed 9 additional nests. We caution interpretation of this finding, as polar bears arrived outside our estimated window of nest availability. Therefore, the lack of consumed nests by polar bears could simply be due to the lack of available nests at the time of polar bear arrival within the colonies.

Competition between grizzly and polar bears for terrestrial food sources may become an important consideration in the future. Polar bears will be forced ashore into terrestrial habitats earlier in the year if current rates of sea-ice loss continue (Cherry et al., 2013; Stern & Laidre, 2016; Stirling & Derocher, 2012). Waterfowl eggs have been suggested as a potential supplementary food source for polar bears spending more time on land (Gormezano & Rockwell, 2015). However, increased time on land also increases the probability of overlap with grizzly bears and potential competition for terrestrial food resources. In northern Alaska where polar and grizzly bears regularly co-occur at whale bone piles, grizzly bears are socially dominant and may permanently displace polar bears from these feeding sites (Miller, Wilder, & Wilson, 2015). Further, female polar bears with cubs were most likely to avoid feeding sites when grizzly bears were present (Miller et al., 2015). The classes of polar bears that are more likely to take advantage of terrestrial resources are females with cubs (Lunn & Stirling, 1985), and smaller individuals who would expend less energy pursuing prey (Gormezano, McWilliams, Iles, & Rockwell, 2016). However if grizzly bears can outcompete both these groups, then reliance on supplementary terrestrial resources by polar bears may not be likely in areas where the two species co-occur. While black bears are known to also occur in WNP (D. A. Clark et al., 2018), we did not observe any individuals in waterfowl colonies. Since black bears are thought to be infrequent predators of waterfowl nests (Abraham et al., 1977), they are not likely to compete with either grizzly or polar bears for these resources.

Consistency of Ursid arrival in bird colonies each year will have important consequences for the population stability of nesting waterfowl. Some waterfowl such as snow geese are able to defend nests from predation attempts by traditional predators like arctic foxes (*Vulpes lagopus*) or avian predators (Cooke et al., 1995), but are not likely to successfully defend against bears. Polar bear predation of goose nests is predicted to reduce the population size of snow geese, but periodic mismatch between polar bears and snow geese should allow goose populations to persist in the short term (R. F. Rockwell et al., 2011). However, since the arrival of grizzly bears in colonies is decoupled from sea-ice breakup, grizzlies could conceivably cause consistent years of high predation, depriving birds of their periodic respite from Ursid predation. Repeat years of high predation by grizzlies would more rapidly reduce the nesting populations of waterfowl in the area than would predation by polar bears. Apart from decreases in population size, consistent bear predation may produce indirect effects such as altered nesting distributions (Dey et al., 2017). Grizzly presence may also facilitate predation or scavenging opportunities for other predator species, further increasing predation pressure on lower trophic levels.

Future work should attempt to quantify the abundance of grizzly bears and their effects on waterfowl nest survival using formal statistical methods that account for imperfect detection. However, the large home ranges and variable habitat use of grizzlies will make this a considerable challenge due to relatively sparse data (i.e. observations) in remote regions. Additional avenues of research should explore the role of recently colonized grizzlies in relation to the native predator community. Comparisons between grizzlies and polar bears will be especially interesting due to the demonstrated differences in phenology. The continued rate of sea-ice loss will inevitably lead to higher rates of overlap between the two Ursid species during waterfowl incubation, potentially resulting in years of extremely high predation which will need to be accounted for in predicting the effects of climate change on Arctic nesting waterfowl populations.

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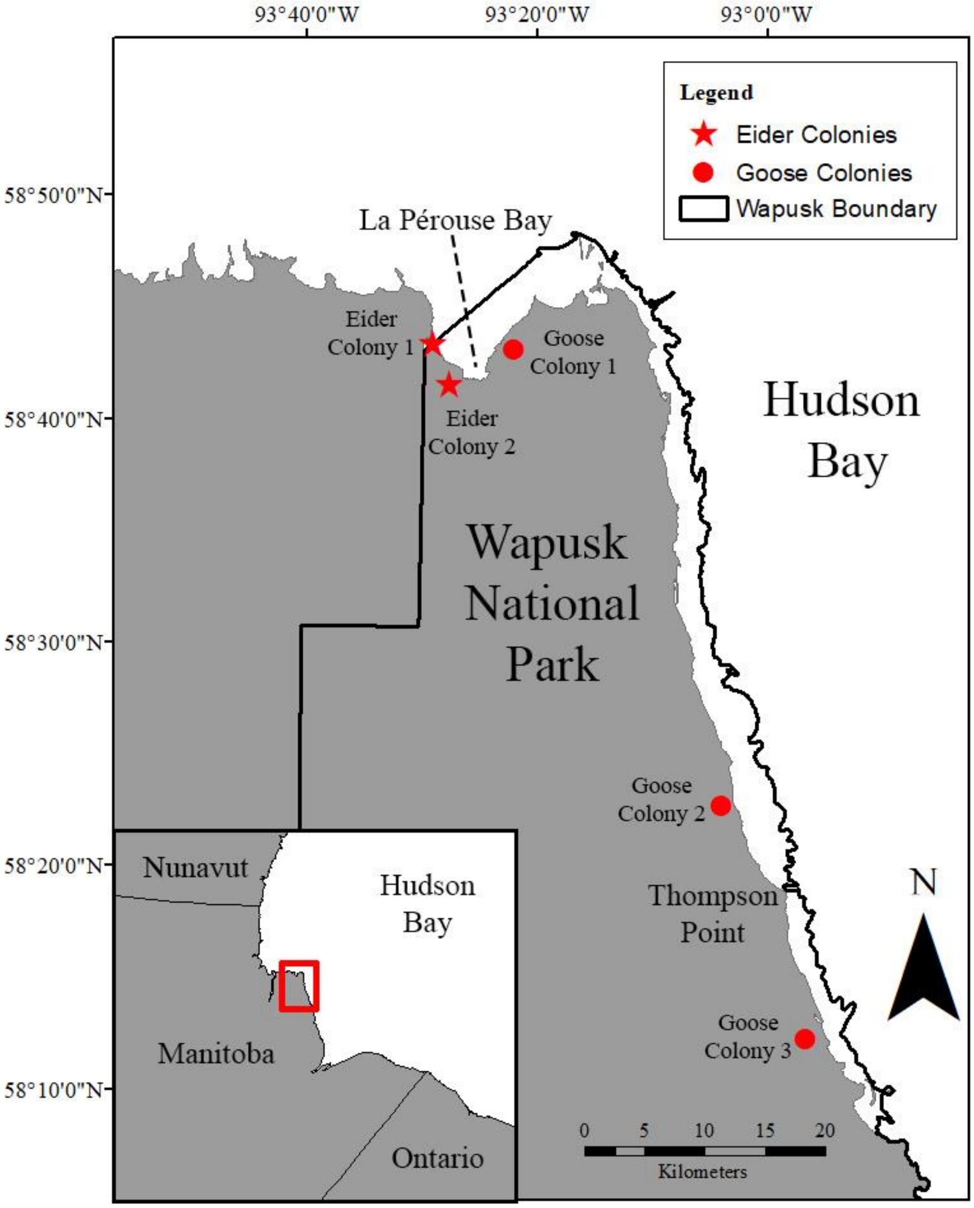

Figure 9 Sampling locations in common eider (*Somateria mollissima sedentaria*) and lesser snow goose (*Anser caerulescens caerulescens*) colonies located within Wapusk National Park, Manitoba, Canada.

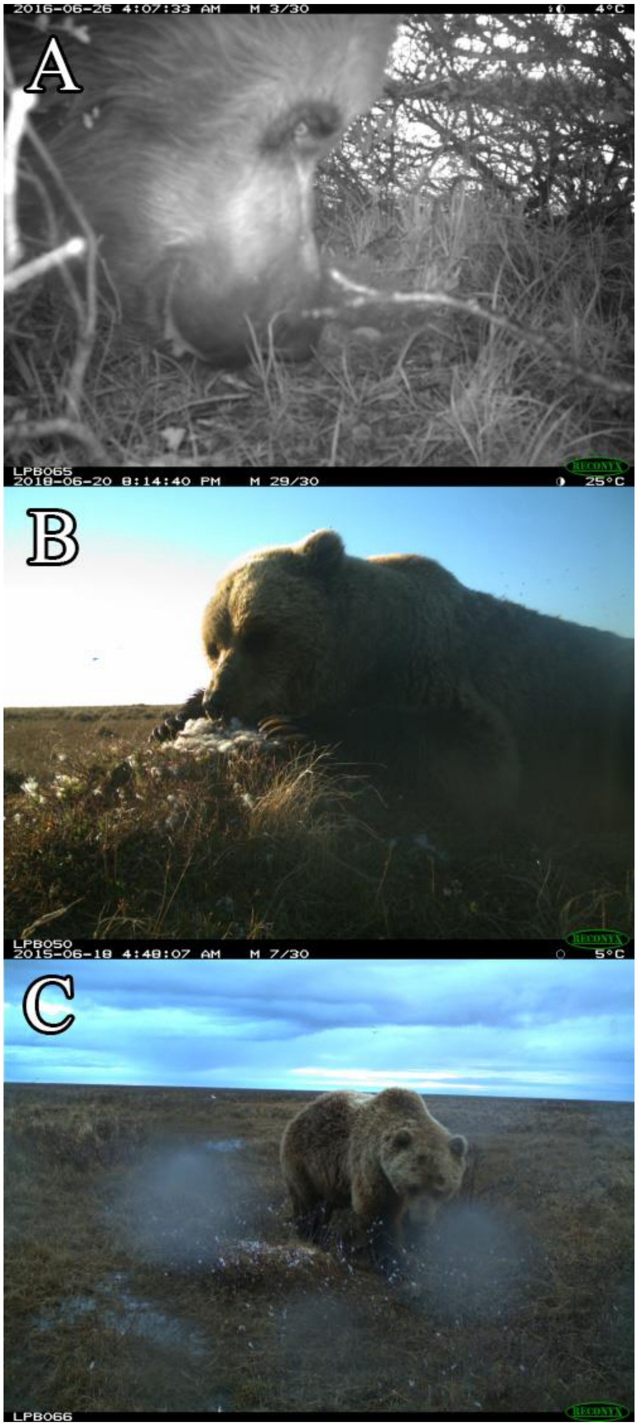

Figure 10 Trail camera images of grizzly bear (*Ursus arctos*) occurrence in nesting waterfowl colonies within Wapusk National Park, Manitoba, Canada. A) Predation of a common eider (*Somateria mollissima sedentaria*) nest. B) Predation of a lesser snow goose (*Anser caerulescens caerulescens*) nest. C) A bear examines a previously hatched snow goose nest.

Figure 11 Trail camera image of a polar bear (*Ursus maritimus*) consuming common eider (*Somateria mollissima sedentaria*) eggs in Wapusk National Park, Manitoba, Canada.

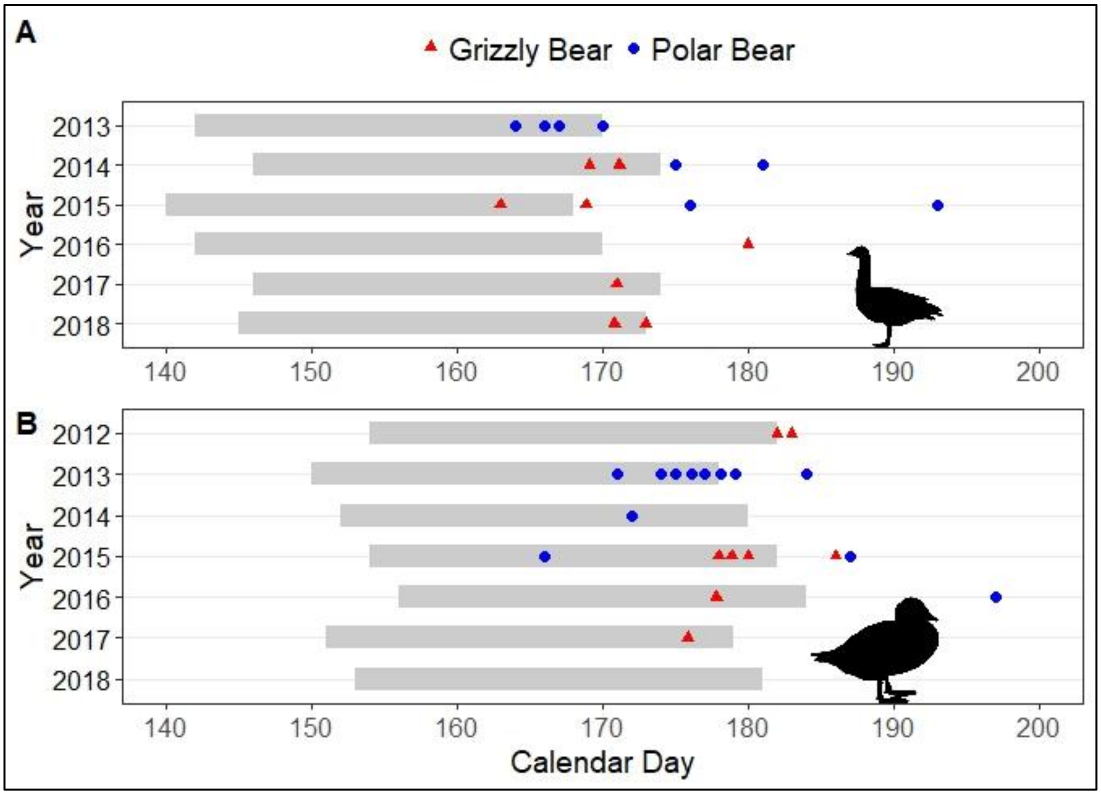

Figure 12 Bear occurrences in A) lesser snow goose (*Anser caerulescens caerulescens*) and B) common eider (*Somateria mollissima sedentaria*) colonies from 2012-2018 in Wapusk National Park, Manitoba, Canada. Gray bars represent an estimated index of nest availability (28 days), based on a 24 day incubation period and 4 day laying period (see Methods: Phenology Comparisons).

Table 10 Summary of grizzly (*Ursus arctos*) and polar bear (*Ursus maritimus*) occurrences captured on camera in two common eider (*Somateria mollissima sedentaria*)and three lesser snow goose (*Anser caerulescens caerulescens*) colonies from 2012-2018 within Wapusk National Park, Manitoba, Canada.

	Total	**Eider colonies**	**Goose colonies**
Number of cameras	430	197	233
Grizzly bears			
Number of cameras with detections	26	15	11
Number of colony events	16	8	8
Mean colony event observation date (Range)	June 24th (June 12th – July 5th)	June 28th (June 25th – July 5th)	June 19th (June 12th – June 28th)
Polar bears			
Number of cameras with detections	49	27	22
Number of colony events	21	12	9
Mean colony event observation date (Range)	June 25th (June 13th – July 15th)	June 26th (June 15th – July 15th)	June 23rd (June 13th - July 12th)

CHAPTER VI LESSER SNOW GEESE INCREASE NEST ATTENDANCE IN RESPONSE TO FORAGING BEARS AND ASSOCIATED AVIAN PREDATORS. A POSSIBLE DEFENCE AGAINST AVIAN KLEPTOPARASITISM?

Abstract

Polar bears (*Ursus maritimus*) and grizzly bears (*Ursus arctos*) are increasingly common predators of Arctic nesting birds, but most research has focused on direct impacts of bears on nest success through egg consumption. However, bears in bird colonies may have indirect effects on nesting bird behaviour and facilitate heterospecific predator foraging. We tested whether: 1) bear foraging in lesser snow goose (*Anser caerulescens caerulescens*) colonies causes geese to spend more time off-nest, and 2) avian predator species have a positive association with foraging bears to capitalize on unattended goose nests. From 2013-2018 we deployed 233 remote cameras on goose nests in Wapusk National Park, Manitoba, Canada, and reviewed images on days when bears were known to be active in the colony (bear-days) and compared them to the day before bear detections (control-days). For nests that were not consumed by bears, we recorded time spent off-nest by birds on each day, and estimated the effect of bear presence on bird behaviour using generalized linear mixed models. We recorded avian predators when bears were detected on camera (bear-days) and during the same time period on control-days, then estimated effect of bears on avian predator presence using logistic regression. Contrary to predictions, geese spent less total time off-nest on bear-days than control-days ($\beta = -0.32 \pm 0.13$, $P < 0.05$). Avian predators were observed more frequently on bear-days (13/18 days) than their paired control-days (2/18 days), and bear presence has a positive effect on avian predator occurrence ($\beta = 3.035 \pm 0.916$, $P < 0.001$). We suspect that geese spend more time on-nest in response to bears to defend nests from increased activity of avian predators. These findings provide evidence of

behavioural impacts of bears across trophic levels, indicating bears may have indirect effects on nesting geese.

Introduction

Climate induced loss of sea ice is accelerating in the Arctic (Gagnon & Gough, 2005; Stern & Laidre, 2016; Stroeve, Holland, Meier, Scambos, & Serreze, 2007), forcing polar bears (*Ursus maritimus*) to spend increasing amounts of time on land (Cherry, Derocher, Thiemann, & Lunn, 2013; Rode, Wilson, et al., 2015). One consequence of earlier sea ice breakup is the increasing temporal overlap and intrusion of polar bears into breeding bird colonies (Smith, Elliott, Gaston, & Gilchrist, 2010). Polar bears have been documented predating eggs and/or individuals in nesting colonies of Glaucous gulls (*Larus hyperboreus*) (Stempniewicz, 2006), Little auk (*Alle alle*) (Stempniewicz, 1993), Arctic Terns (*Sterna paradisaea*) (Gormezano, Ellis-Felege, Iles, Barnas, & Rockwell, 2017), Thick-billed murres (*Uria lomvia*) (Gaston & Elliott, 2013), Common eiders (*Somateria mollissima*) (Iverson, Gilchrist, Smith, Gaston, & Forbes, 2014), Black guillemot (*Cepphus grylle*) (Stempniewicz, Kidawa, Barcikowski, & Iliszko, 2014), Lesser snow geese (*Anser caerulescens caerulescens*) (Abraham, Mineau, & Cooke, 1977; Iles, Peterson, Gormezano, Koons, & Rockwell, 2013), Pink-footed geese (*Anser brachyrhynchus*) (Prop, Oudman, van Spanje, & Wolters, 2013), and Barnacle geese (*Branta leucopsis*) (Prop et al., 2015). Although these birds and their eggs are thought by some to serve as an important energetic supplement for individual bears (Gormezano & Rockwell, 2013; RF Rockwell & Gormezano, 2009), terrestrial based food resources are not likely to support large populations of bears in the future (Dey et al., 2017; Molnár, Derocher, Thiemann, & Lewis, 2010; Pilfold et al., 2016; Rode, Robbins, Nelson, & Amstrup, 2015). Furthermore, since forays of bears into nesting bird colonies have been shown to cause near total reproductive failure, the availability of these energetic resources is not likely to be sustainable even for small numbers of bears (Iverson et al., 2014; Rode, Robbins, et al., 2015).

Concurrent to the increasing time spent in terrestrial habitats by polar bears, Arctic grizzly bear (*Ursus arctos*) populations are thought to be undergoing a geographic expansion (Clark et al., 2018). This expansion of grizzlies into novel habitats introduces increased predation pressure in areas where grizzlies have been historically absent (Clark et al., 2018; Robert Rockwell, Gormezano, & Hedman, 2008). In other areas of the Arctic, grizzlies are well documented to consume several species of nesting waterfowl and their eggs (Armstrong, 1998; Barry, 1967; Johnson & Noel, 2005; Obst, Hines, Dufour, Woodard, & Bromley, 2013). Therefore waterfowl nesting areas where polar and grizzly bears overlap (or have the potential to overlap in the future) could face combined pressure by two novel apex predators with a high capacity for causing reproductive failure.

Until recently the phenomenon of bear foraging in bird colonies has been discussed predominately in the context of energetic resource availability for bears and their capacity for causing reproductive failure, with little attention paid to the broader ecological consequences of the bears' activities. Predation events directly impact a single focal prey individual, but predator presence has the potential to indirectly affect multiple non-targeted prey individuals through introduced risk effects (Schmitz, Beckerman, & O'Brien, 1997; Schmitz & Suttle, 2001). As such, the increasing presence of foraging bears in nesting colonies has potential to influence nesting behaviours of birds, which ultimately could have impacts on community dynamics and prey population distributions. Indeed, agent-based simulations of polar bear foraging in a Common eider colony predict that over time birds will respond by shifting nesting locations closer to mainland habitats, and that nests will become increasingly dispersed over time (Dey et al., 2017).

One interesting consequence of bear foraging in bird colonies is the potential interaction between avian predators and bears. Avian predators are known to follow and kleptoparasitise large mammals to access food resources that would otherwise be unavailable to them (Ridoux, 1987; Sakamoto, Takahashi, Iwata, & Trathan, 2009; Stahler, Heinrich, & Smith, 2002). While preying on colonial nesting birds, avian predators are also thought to take advantage of disturbance events (i.e. conspecific predator presence, human disturbance) that force attendant parents off their nests, thereby making eggs and chicks available for avian predator consumption (Åhlund & Götmark, 1989; Verbeek, 1982). Remains from polar bear kills are frequently located and scavenged by avian predators on sea ice (Derocher, 2012; Gjertz & Lydersen, 1986), and this behaviour could be generalized to take advantage of bears foraging in terrestrial environments.

Direct observations of grizzly and polar bear foraging on land often lack specific details, but a few reports provide indications of such interactions between terrestrial bears and avian predators. Rode, Robbins, et al. (2015) attributed the mass 2013 reproductive failure of a Black Brant colony on the southern Beaufort Sea coast to brown bears and associated avian predators. In the Anderson River Delta, grizzly bears have previously been estimated to destroy approximately 37% of goose nests in a colony, but 5-10% of these nest losses were attributed to avian predators taking advantage of absent parent geese while bears were foraging (Barry, 1967). Similar associations have been described for polar bears and gulls (*Larus sp.*) in the Hudson Strait-Northern Hudson Bay Narrows region of the Canadian Arctic (Iverson et al., 2014). Gaston and Elliott (2013) reported that glaucous gulls actively followed foraging polar bears in a thick-billed murre colony, and when bear activity caused mass colony panic the gulls flew in to consume unattended eggs and chicks (Gaston & Elliott, 2013). On the Cape Churchill Peninsula, scavenging by herring gulls (*Larus argentatus*) on lesser snow geese killed by polar bears was also reported by Iles et al. (2013). Clearly there is a capacity for avian predators to take advantage of a novel source of colony disturbance and subsequent prey availability, but to date this has only been anecdotally reported and not rigorously quantified.

Here, we propose a cascading behavioural mechanism whereby the presence of foraging bears in nesting bird colonies facilitates foraging by avian predators. We hypothesize that the presence of bears in a nesting colony will result in reduced nest attendance by female birds due to introduced risk effects (e.g. incubating birds will leave their nest in response to the presence of bears). Next, we hypothesize that when bears are active in the colony, avian predators will be closely associated with bears to take advantage of nests lacking attendant parents. In combination, we suspect that nest predation by avian predators could be a substantial cause of nest failure on days when bears are actively foraging in bird colonies. In the following, we specifically test whether 1) goose nest attendance patterns are altered by the presence of bears in the colony, and 2) if there is a higher probability of observing avian predators on days when bears are in the colony.

Methods

Study Area

We collected data in three sub-colonies of a large nesting Lesser snow goose (hereafter “snow geese”) population along the western Hudson Bay coast in Wapusk National Park, Manitoba, Canada (Figure 13). This region is predominately low-lying with the exception of sand bars and glacial beach ridges, and the vegetation structure within sub-colonies offers little overhead concealment against avian predators. For a detailed physiographic description of the region see Brook and Kenkel (2002); Shilts et al. (1987).

Trail camera set up and image review

We set up a series of Reconyx PC-800 Hyperfire trail cameras throughout three sub-colonies of snow geese from 2013-2018. Cameras were deployed as a part of annual snow goose monitoring protocols, and we placed cameras opportunistically at active nests (at least one viable egg present). Cameras were mounted on steel poles or wooden stakes, approximately 0.5-1.5m off the ground. Angle of cameras were optimized to include a single focal nest directly in the field of view, but often multiple nests were able to be included in the background of images. Cameras were programmed to take a single picture every two minutes (time-lapse), but also to take a burst of 30 pictures (trigger) if movement was detected by the infrared sensor. Trigger sensitivity was set to high, timing settings were set to rapidfire (approximately 2 frames per second), and no quiet period was used between triggers. Annual timing of placement and retrieval of cameras was dictated by logistic and environmental conditions. Placement occurred between 30-May and 14-June, and retrieval was done between 24-June and 25-July. We placed 10-70 cameras each year, see Appendix E Table 1 for further details on camera numbers, timing, and placement. Images were reviewed for presence of polar and grizzly bears in goose colonies by the authors and trained technicians.

Effects of bears on goose nest attendance

We focused our analysis of nest attendance on nests that were not visited (and thus not consumed) by bears within the same colony, thereby allowing us to investigate the indirect impacts of bears on goose behaviour. To estimate the effect of bear presence on goose behaviour, we examined nest attendance of geese on days with bears (hereafter denoted “Bear Days”) and on the day before the bear was detected (hereafter denoted "Control Days"). We excluded background nests that were not visible for the full 24 hours on each day (e.g. obscured by poor visibility due to inclement weather or distance from camera), and any nests where goslings were observed, since geese leave the nest shortly after hatch (Cooke, Rockwell, and Lank (1995), *A.Barnas pers. obs*.).

For each nest, we measured nest attendance as the length of on-nest and off-nest behaviours (mins), and the number of these behaviour events on each day using package *lubridate* (Grolemund & Wickham, 2011). To determine the effects of bear presence on daily nest attendance behaviours of geese, we used generalized linear mixed models examining three different measures of nest attendance. We constructed separate models examining: 1) the total time spent off-nest by birds in a day (Gaussian), 2) the number of nest recess events in a day (Poisson), and 3) the length of individual recess events (Gaussian). To facilitate the use of Gaussian models for total time off-nest and recess length models, we log transformed response data and back-transformed model predictions. To accommodate log transformations in Gaussian models, we artificially increased 0 value observations to 0.0001.

All models contained only the fixed effect of Day (categorical with two levels: Control Day and Bear Day), and the random effect of Nest ID. Models were constructed in packages *lme4* (Bates, Sarkar, Bates, & Matrix, 2007), and parameter significance terms were calculated using package *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017). We calculated 95% confidence intervals around the back-transformed mean responses using a parametric bootstrapping approach with 1000 simulations in package *merTools* (Knowles & Frederick, 2016). Models were fit via maximum likelihood and model fit was assessed with a likelihood ratio test, which compares the deviance of the candidate model to an intercept-only (null) model.

Avian predator association with bears

To estimate the association between bears and avian predators we examined specific time periods surrounding individual detections of bears on camera. We defined “Bear Events” as the period of bear activity beginning 10 minutes prior to the first image of a bear, lasting until 10 minutes after the last picture of a bear by a camera. We chose this relatively short time window so as to capture any close association between bears and avian predators, rather than incidental observations of avian predators during a longer time window. We reviewed images during Bear Events for the presence of avian predators on days with bears (Bear Days) and during the same time period, from the same camera, on the day before the bear (Control Days). During these equivalent time periods on both days (Bear and Control Days), we recorded the presence or absence of any avian predators, the minimum number of avian predators and their species (if identifiable). Detection of avian predator on each day is a binary outcome, so we modeled avian presence with logistic regression models examining the fixed effect of Day (categorical with two levels: Bear Day and Control Day) and bear species (categorical with two levels: Grizzly and Polar). To account for the possibility that environmental conditions may have played a role in the similar activity of bears and avian predators, we also examined the fixed effects of temperature (°C) and wind speed (km h^{-1}). Hourly weather data was obtained from a weather station near Churchill Manitoba (Churchill A: 58°44'21.000" N, 94°03'59.000" W), and we chose the measurement nearest to the start of each bear event. Candidate models were constructed for varying combinations of fixed effects (along with an intercept only model), and evaluated using Akaike Information Criterion (AICc) for small sample sizes in package *MuMIn* (Akaike, 1998; Barton, 2009; Burnham & Anderson, 2002). We then used the top model to predict the probability of observing an avian predator for each day. Model fit was assessed via likelihood ratio test.

Observations of avian predators on Bear Days may be positively skewed due to larger numbers of camera images on Bear Days vs Control Days (i.e. bear activity triggers cameras resulting in more images, therefore more opportunities for observing avian predators by chance). After removing images from each bear event which could not be used for evaluating detection (e.g. completely blacked out images due to camera malfunction or extremely close up pictures of bears), we tested the hypothesis that Bear Days would have more camera images than their paired Control Days using a one-tailed paired t-test. We then used a randomization approach to evaluate the probability of increased observations of avian predators on Bear Days were due to chance associated with sampling error (i.e. more camera images). Images on Bear Days with avian predator detections were assigned 0's or 1's for whether or not they contained avian predators. We generated a series of 10,000 replicated datasets by randomly subsetting images from each Bear Event's Bear Day, based on the number of images for that Bear Event's paired Control Day. For example, if a Control Day had 20 images and the paired Bear Day had 50 images, we would randomly select 20 images (without replacement) from the Bear Day images, and determine if avian predator(s) would have been observed using this image set. For each simulated dataset, this process was repeated for each Bear Day with a positive detection of avian predators (i.e. we estimated detection bias for days when avian predators were detected). We then calculated the proportion of randomized datasets in which avian predators were detected on all Bear Days (compared to the number of Bear Days with original detections using all images, see *Results*), which quantifies the probability that any increased observations of avian predators on Bear Days was simply an artifact of sampling error. All analyses were conducted in R v3.4.3 (R Core Team, 2017).

Results

From 2013-2018 we placed and reviewed 233 cameras across three sampling locations (Appendix El Table 1). Image review from these cameras revealed 33 detections of bears on 18 days in separate goose colonies during the study years.

Effects of bears on goose nest attendance

We were unable to collect nest attendance behaviour from 4 Bear Days due to late arrival of bears in goose colonies (i.e. all monitored nests had hatched), and chose not to review 2 other days due to researcher presence in the field during the paired Control Days which would likely have impacted goose nest attendance. In a single instance, a bear was present in a colony for two days in a row. In this case we only used data from the first day of the bear being active in the colony, to accommodate a single Bear Day and paired Control Day (the day before the bear initially entered the colony). Ultimately, we were able to collect nest attendance on 11 paired days across 85 nests.

The effect of Bear Days on total time spent off nest by geese was negative ($\beta = -0.32 \pm 0.13$, $P=0.01$, Table 11), and this model fit better than an intercept only model ($\chi^2(1) = 6.4098$, $P=0.01$). The effects of Bear Days on recess length and number of recesses was negative, but not significant ($\beta = -0.04 \pm 0.04$, $P=0.32$, and $\beta = -0.05 \pm 0.05$, $P=0.38$ respectively, see Table 11). Neither of these two models fit better than an intercept-only model; recess length $\chi^2(1) = 1.01$, $P=0.31$, recess number: $\chi^2(1)=0.75$, $P=0.39$. Contrary to expectations, model predictions indicate geese spend less time off-nest on Bear Days (Figure 14A). Similarly, the number of recesses and individual recess lengths tended to be lower on Bear Days than Control Days (Figure 14B, C); however we caution interpretation of these results due to overlapping 95% confidence intervals.

Avian predator association with bears

From the original 33 individual detections of bears, we excluded 7 Bear Events that took place between the hours of 18:30:00 and 04:30:00, which had poor quality images due to lighting conditions or inclement weather. We also merged 11 Bear Events that overlapped in time, as a result of the same bear being captured on multiple cameras on the same day (within the same colony). For example, an event ranging from 12:30:00 to 12:50:00 and another ranging from 12:45:00 to 13:15:00 would become a single event ranging from 12:30:00 to 13:15:00. Similar to the nest attendance analyses, for the single instance that a bear was present within a colony for two days in a row, we only used data from the first day of the bear being active in the colony. These filtering steps resulted in 18 Bear Events that were used for analyses (Table 12).

Avian predators were observed more frequently on Bear Days than in their paired Control Day (Figure 15), but on average there were more images collected on Bear Days ($t_{0.05(1), 12}$, P = 0.0054). A randomization test indicated a small bias in probability of detecting avian predators on Bear Days due to the increased number of images, but this bias was small and likely not substantial enough to explain the greater trend of increased avian predator observations on Bear Days (Appendix E Figure 1).The most common species of avian predator present was Common Ravens (12/18 bear days), followed by Herring Gulls (5/18 bear days), and Bald Eagles (3/18 bear days). When avian predators were observed in images with bears predating goose nests, they were often found to inspect nest remains, likely searching for any remaining materials such as unconsumed eggs or yolk (Figure 16).

The candidate model for avian predator occurrence that included only the single fixed effect of Day received the most support, but noteably models also including the additional parameters of either wind speed, temperature, or bear species all received higher support based on ΔAICc and Akaike weights (Table 13). However, given that Day is nested within these top 4 models, and the similar log likelihood values, the single additional parameters of wind speed, temperature, or bear species are not likely to be informative for predicting avian predator occurrence (Arnold, 2010). We made predictions of avian predator occurrence from the top model, which estimated that bear presence in bird colonies has a large, positive effect on avian predator occurrence (β = 3.035, P =0.0009, Table 14). Predicted probabilities of avian predator occurrence are much higher on days with bears (0.72, 95% CI[0.48, 0.88]) than the day before (0.11, 95% CI[0.03, 0.35]). Overall this model as a whole fit significantly better than an intercept-only model ($\chi^2(1) = 15.1$, $P < 0.001$).

Discussion

Polar and Grizzly bear foraging in nesting bird colonies is an increasingly common phenomenon in the Arctic, which is well demonstrated to cause mass reproductive failure (Iverson et al., 2014; Rode, Robbins, et al., 2015; Smith et al., 2010). However, the relationship between bears and their bird prey species is more complex than commonly depicted, and bear activities may have more subtle, indirect effects on bird communities. We observed close associations between avian predators and bears in nesting snow goose colonies, and suggest that this association is likely an attempt to capitalize on colony disturbance as a result of bear presence. We demonstrate that incubating snow geese increase their nest attendance on days when bears are active within colonies, but whether geese are responding to bears or avian predators (or both) remains unclear.

Avian predators are a significant cause of egg loss in Arctic nesting geese but are generally unable to access goose eggs while female geese are incubating (J. M. Harvey, 1971; Inglis, 1977; Prop, Eerden, & Drent, 1985). Larger raptors in these regions such as Bald or Golden eagles (*Aquila chrysaetos*) may occasionally kill females on nests (Cooke et al. (1995), *A.Barnas personal observation*), but most avian predators require the absence of attendant parents to take eggs (J. M. Harvey, 1971; Inglis, 1977; Prop et al., 1985). Therefore any disturbance to geese which causes parents to vacate the nest presents a foraging opportunity for highly mobile avian predator species (Bêty & Gauthier, 2001; Götmark & Åhlund, 1984; J. Harvey, Lieff, MacInnes, & Prevett, 1968). Tight associations between bears and avian predators were clear in this study, but we did not observe the predicted higher rates of predation by these birds acting as kleptoparasites of bears. Instead, we found some evidence of avian predators acting as scavengers, quickly arriving to nests shortly after the departure of bears. This is in contrast to previously published accounts which describe avian predators as the proximate cause of nest failures in association with foraging bears (Barry, 1967; Rode, Robbins, et al., 2015), but these lack detailed descriptions of methods for evaluating any such associations or causes of nest failures. Gaston and Elliott (2013) reports a combination of apparent kleptoparasitism by glaucous gulls taking advantage of unattended thick-billed murre nests, but also scavenging on unconsumed adults and chicks killed by polar bears. This suggests a possible important supplementary food source for opportunistic scavenger species in Arctic environments. Although the specific nature of bear foraging at bird nests is often lacking, the complete consumption of eggs without any spillage of egg contents (yolk, albumen, partially developed embryos, etc.) is unlikely. Any leftover contents could provide a potentially low-cost, high-reward energetic resource for scavengers, especially if this resource is compounded across hundreds of nests.

Scavenging in association with bears may be a more effective strategy than kleptoparasitism, but this is likely dependent on the characteristics of the bird colonies invaded by bears. Cliff nesting thick-billed murres nest on difficult to reach cliffs as a possible deterrent to predation, but also invoke predator mobbing of avian predators (Gilchrist & Gaston, 1997). However, the naivety to- and inability to defend against novel bear predators may be a causal factor in the "…mass panic of adult murre [in response to polar bears]" described by Gaston and Elliott (2013): pg 47. Further, the number of nests lacking attendant parents during any disturbance event (and thus opportunity for avian predation) depends on the local nest density in the immediate vicinity of a disturbance source. Bêty and Gauthier (2001) hypothesized that investigator disturbance in a greater snow goose colony had a greater impact on avian predator activity in years with higher nesting density, due to the increased opportunities for predators near the disturbance epicenter. Larger numbers of unattended nests should better facilitate kleptoparasitism rather than scavenging (but importantly both may occur), facilitating avian predators as the proximate cause of nest failure. Therefore, naive bird colonies with higher nest densities may be more vulnerable to the additive pressure of bear and avian nest predation.

The lack of goose nest failure resulting from avian predators on Bear Days in our study was likely mitigated due to increased nest attendance by geese on these days. We originally hypothesized that geese would leave their nest in response to bear presence, but we found that birds instead increased their total time spent on nest. This corroborates experimental evidence that nesting birds will reduce activity at their nests in scenarios of higher perceived predation risk (Kovařík & Pavel, 2011). Reductions in activity at the nest by incubating birds are thought to decrease the chances of revealing the nest location to visually acute predators (Martin, Martin, Olson, Heidinger, & Fontaine, 2000), which may be a more relevant strategy in predator-prey relationships where prey species are unable to defend against larger predators (Montgomerie & Weatherhead, 1988). For geese nesting in open landscapes, unattended nests are attacked less frequently by Arctic foxes than expected by chance, which is attributed to the reduced visibility of these nests from a low vantage point compared to those with an attendant female (Samelius & Alisauskas, 2001). Therefore, vacating nests far in advance of approaching terrestrial predators may be a viable strategy against the perceived predation risk of foraging bears, in the hopes that bears simply will not happen upon nests by chance in the absence of visual cues (parent geese). However, geese must also account for other predators with varying foraging patterns, and this strategy would put nests at greater risk to avian predators with an aerial vantage point who can quickly cue in on unguarded nests (Opermanis, 2004). Therefore, we suggest that the increased nest attendance observed by geese in the presence of bears is predominately a strategy to reduce predation by associated avian predators. Future work should be aimed at understanding the behavioural decision making by geese in such multi-predator environments, and how tradeoffs between remaining on nests versus flushing off nests are influenced by factors such as local nest density, future reproductive opportunities, predator search efficiencies, etc.

Regardless of the ultimate cause of increased nest attendance by geese, alterations in nest attendance rates may have important consequences for females' ability to successfully hatch nests. Arctic geese generally have very high nest attendance rates throughout incubation, thought in part to be due to the colder Arctic environments (Ankney & MacInnes, 1978; Thompson & Raveling, 1987). During incubation, energy reserves of female geese are rapidly depleted and individuals may be forced to take short recess breaks to feed, or else they risk starvation on the nest (Ankney & MacInnes, 1978; Cooke et al., 1995). Years of high bear and avian predator activity could indirectly impact goose nest success then by reducing the number of feeding breaks for female birds to replenish nutrient reserves. Although we did not detect significant effects of bears on the smaller individual components of nest attendance (recess numbers or recess length), this may be attributed to the fact that geese typically have high overall nest attendance and take very few recess breaks throughout incubation anyways. Any such effect of bears and avian predators on nest attendance may be exacerbated in years of particularly cold or inclement weather, further increasing the metabolic costs of thermoregulating eggs and nutritional stress on females. Predation of adult geese and goslings by bears and avian predators does occur after hatch during brood rearing (Gormezano et al., 2017; Gormezano, McWilliams, Iles, & Rockwell, 2016; Iles et al., 2013), and similar behavioural impacts of bear presence leading to reductions in feeding opportunities may also impact gosling survival and population recruitment.

Although we observed overall increased nest attendance, there was considerable variation in behavioural responses by individual geese, which could have been due to differences in age classes of geese in our sample. Younger, less experienced females are less attentive to their nests, and may more readily leave their nests due to perceived predation risks (Cooke, Bousfield, & Sadura, 1981; Cooke et al., 1995), possibly in favour of future breeding opportunities (Curio, 1983; Montgomerie & Weatherhead, 1988). Bears foraging in goose colonies are not likely to discriminate among age classes of nests they are preying upon (given that they have located them), instead they probably consume whichever nests are in their paths (but see Prop et al. (2013), Gormezano et al. (2017)). However the younger, less attentive female geese may be disproportionately at risk to any secondary predators associated with foraging bears, which presents a pathway for downstream demographic consequences of bear foraging in goose colonies. This also represents an important bias in our study, in that the bulk of predation on snow goose nests is thought to occur during the egg-laying stage and early incubation, likely on these younger, inexperienced birds (Cooke et al., 1995; RF Rockwell, Cooch, Thompson, & Cooke, 1993). In this case, the nests that would have been most susceptible to avian predation in this study (through decreased nest attentiveness) may have already been removed from the population sample before observations began. Further, this could have led to an overestimation of overall nest attentiveness, since it is possible our sample was dominated by older, more attentive birds. However, our focus here remains on the differences in nest attendance between treatments, rather than the absolute time spent on nest each day. Future experiments of responses by birds of known-ages would be extremely beneficial in understanding the relationship between nest attendance and bear presence.

Future avenues of research should also examine the indirect effects of bear presence on incubating birds beyond behavioural patterns such as physiological responses, indirect effects on gosling growth during brood rearing, or changes in future nest site selection. It may be especially helpful or interesting to consider these responses in the context of a “landscape of fear” approach to understanding prey responses to novel predator communities. Comparisons of responses of birds with differing life history characteristics will be especially interesting in considering the various factors involved in decision making to Ursid and avian predation risk. Ultimately, future work examining the impacts of bears on colonial nesting Arctic birds should account for interactions with traditional predator communities rather than examining impacts on prey in isolation.

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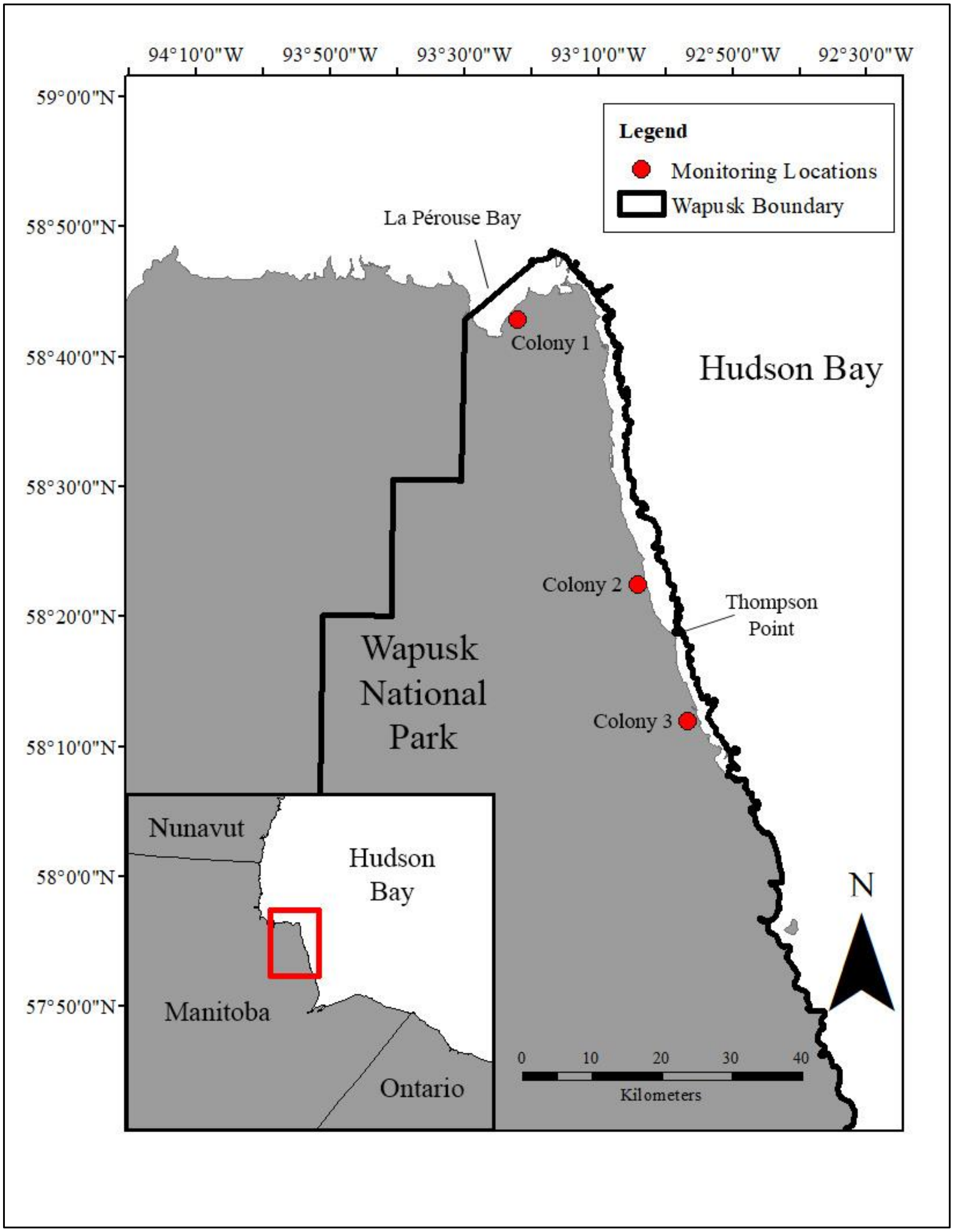

Figure 13 Trail camera monitoring locations in sub-colonies of Lesser snow geese (*Anser caerulescens caerulescens*) within Wapusk National Park, Manitoba, Canada.

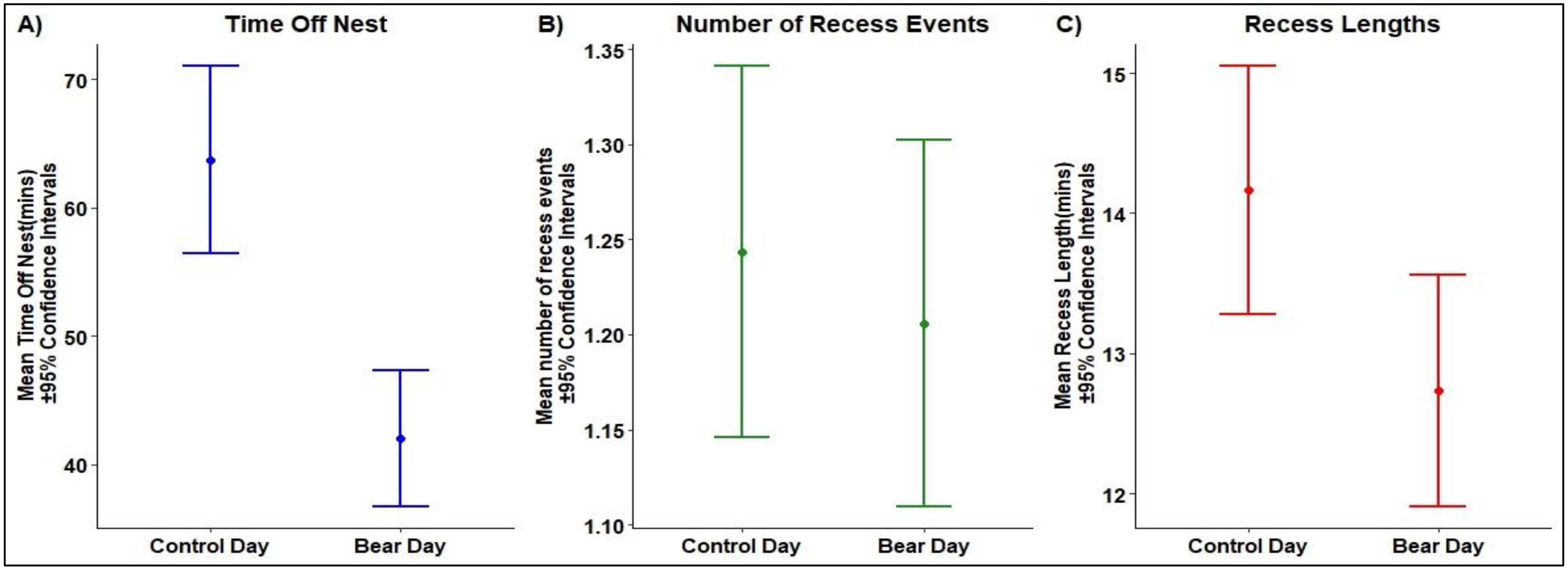

Figure 14 Data scale mean model predictions and bootstrapped 95% confidence intervals for measures of Lesser snow goose (*Anser caerulescens caerulescens*) nest attendance on Bear Days and paired Control Days. Nesting behaviour collected from 11 paired Bear Day/Control Days across 85 nests. A) Total time spent off nest (mins), B) Number of recess events, C) Recess event lengths (mins).

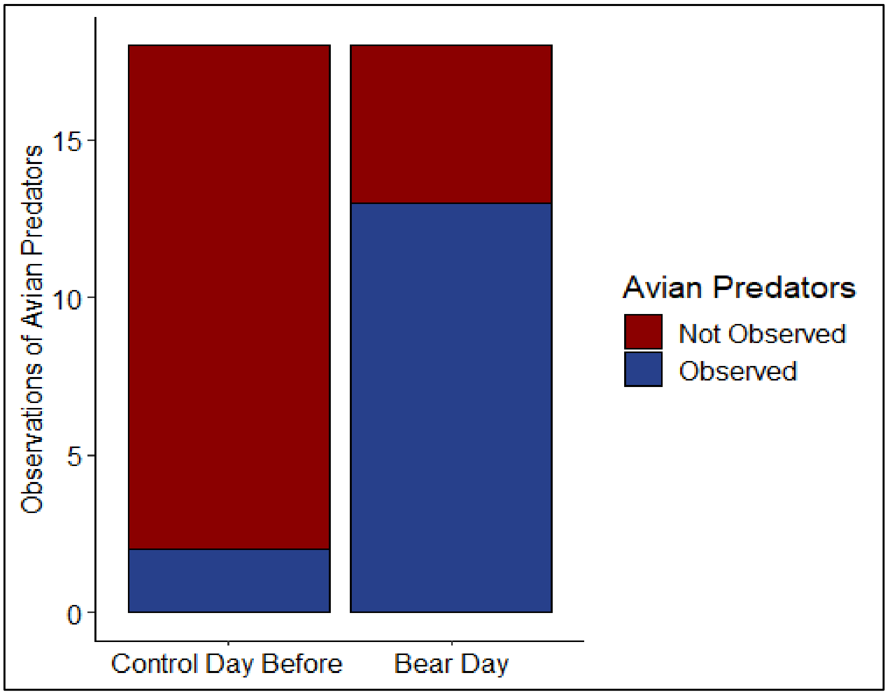

Figure 15 Number of observations of avian predators during bear events on the day a bear was observed and the paired control day before (n=18 bear events).

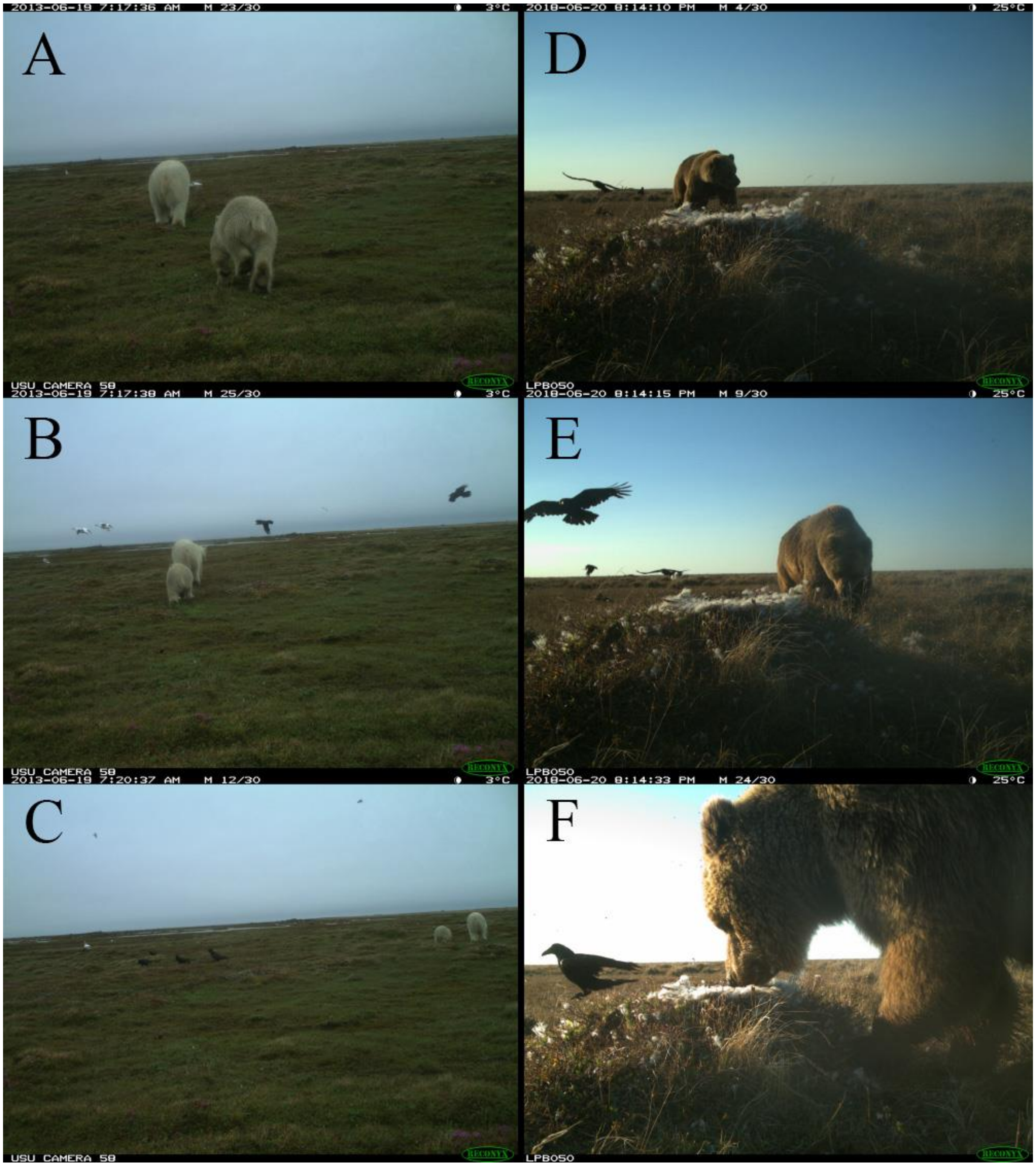

Figure 16 Observations of avian predators following bears foraging in a nesting snow goose colony. A-C) A female polar bear (*Ursus maritimus*) and cub cause a female lesser snow goose (*Anser caerulescens caerulescens)* to abandon its nest. Following predation of the nest, four common ravens (*Corvus corax*) inspect the nest for any unconsumed materials. D-F) A lone grizzly bear (*Ursus arctos*) approaches and consumes a lesser snow goose nest and is closely followed by at least three common ravens.

Table 11 Results of generalized linear mixed models examining measures of nest attendance in lesser snow geese (*Anser caerulescens caerulescens)* on Bear Days (days bears were present in nesting colonies). Nesting behaviour collected from 11 paired Bear Day/Control Days across 85 nests.

Response	**Family**	**Fixed Effect Estimates ± SE**		**Random Effect (Nest) Variance ± SD**	
		Intercept	Bear Day*	Intercept	Residual
Log Total time off nest (mins)	Gaussian	3.71±0.14[†]	-0.32±0.13[†]	0.904±0.951	1.12±1.06
Number of Recess Events	Poisson	1.27±0.06[†]	-0.05±0.06	0.17±0.41	NA
Log Recess lengths (mins)	Gaussian	2.46±0.04[†]	-0.04±0.04	0.07±0.27	0.43±0.66

*Reference category = Control Day (day before bear was detected in colony)

[†] Denotes statistical significance at $\alpha=0.05$

Table 12 Summary statistics of the number of avian predators (mean ± SD) observed during Bear Event time periods, on Bear Days and paired Control Days at or around lesser snow goose nests.

	Any Ursid	**Polar bears**	**Grizzly bears**
Number of events	18	9	9
Number of birds on bear days (mean ± SD)	3.33 ± 3.48	4.89 ± 4.17	1.78 ± 1.72
Number of birds on control days	0.11 ± 0.32	0.22 ± 0.44	0 ± 0

Table 13 Candidate logistic regression models for avian predator presence during Bear Events, with corresponding Model Rank, Log Likelihoods, AICc, ΔAICc, and Akaike Weights.

Model	**Model Rank**	**Log Likelihood**	**AICc**	**ΔAICc**	**Akaike Weight**
Day	1	-16.9141	38.19191	0	0.458749
Day + Wind	2	-16.7087	40.16744	1.97553	0.170842
Day + Bear	3	-16.8211	40.39217	2.200261	0.152684
Day + Temp	4	-16.9	40.54992	2.35801	0.141104
Day + Temp + Wind	5	-16.4996	42.28957	4.097657	0.059126
Day + Temp+ Wind+ Bear	6	-16.4957	44.99145	6.799536	0.015313
Null	7	-24.451	51.01956	12.82765	0.000752
Wind	8	-23.45	51.2637	13.07178	0.000665
Temp + Wind	9	-23.1984	53.14681	14.9549	0.00026
Bear	10	-24.3938	53.1512	14.95929	0.000259
Temp	11	-24.4447	53.25294	15.06103	0.000246

Table 14 Logistic regression model results of avian predator occurrence during Bear Events. Estimates made from the top model which included only the fixed effect of Day.

Response	Parameter	β	SE	P
Avian predator occurrence (1 vs 0)	Intercept	-2.079	0.750	0.00556
	Bear Day*	3.035	0.916	0.00092

*Reference category = Control Day (day before bear was detected in colony)

CHAPTER VII NESTING BEHAVIOURS OF LESSER SNOW GEESE IN A MIXED PREDATOR ENVIRONMENT: AN AGENT BASED MODEL APPROACH

Abstract

The behaviour of nesting birds is strongly driven by predators, and the defence strategies employed by nesting birds are often predator-specific. However, in mixed predator environments, nesting birds may have to make compromises between predator-specific strategies, as the strategy against one predator may be ineffective or even detrimental against another predator species. Lesser snow geese (*Anser caerulescens caerulescens*) nesting in the sub-Arctic must contend with a diverse suite of predators, including terrestrial polar bears (*Ursus maritimus*) and avian predators. In scenarios featuring both bears and avian predators, geese likely experience a behavioural tradeoff where they can leave their nest to reduce detection by terrestrial bears, but this leaves nest contents vulnerable to highly mobile avian predators. We constructed agent-based simulation models to examine nesting behaviour decisions by lesser snow geese in a mixed predator environment. Models were populated with virtual entities (i.e. “agents”) representing nesting snow geese, along with foraging polar bears and avian predators. Geese were allowed to make decisions on when to leave their nest in response to foraging bears, and nest success was analyzed as a function of the distance at which birds left their nest using generalized additive models. We found that parent geese leaving their nest far in advance to approaching bears was a successful strategy in “bear-only” predator landscapes, as bears had difficulty locating snow goose nests without attendant parents. However, in a mixed predator

environment this strategy is not successful as unattended nests (off-nest) were quickly consumed by avian predators. We originally hypothesized increased nest attendance by geese would increase probability of nest failure by bears, but we did not find evidence to support this in our models. The direct impacts of polar bears on nesting birds can be catastrophic and are likely to continue with the projected decrease in spring sea-ice cover; however, that is not a driver for grizzly bears. Future estimates of the impacts of bears on breeding birds should consider the effects on bird behaviour and physiology, and also take the annual variability in presence of specific bear species into account.

Introduction

Nest predators are thought to be the primary cause of reproductive failure in birds; thus, predators exhibit strong selective pressure on avian nesting strategies (Martin, 1995; Montgomerie & Weatherhead, 1988; Ricklefs, 1969). Generally, selection should favour nesting birds who either decrease the overall probability of predators locating their nest, or the increase the ability of birds to actively defend their nest against predator attacks (Martin, Martin, Olson, Heidinger, & Fontaine, 2000; Montgomerie & Weatherhead, 1988). However, the strategies employed by nesting birds is largely dependent on the type of predator in question. For example, it may be more successful to employ a cryptic nesting strategy against large, relatively well-armed predators rather than attempt to physically defend the nest at risk to parental survival (Caro, 2005). Conversely, if nesting birds are relatively well-armed against predators, a more successful strategy may be to simply remain with the nest and actively defend against attacks. In either scenario, selection should favour the ability of nesting birds to assess the relative risk from predators and adjust their nesting strategies in response (Curio, 1975). Anecdotal observations and experimental manipulation of predation risk in nesting birds provides evidence for this in several species (Armstrong, 1954; Fontaine & Martin, 2006; Gochfeld, 1984; Maziarz, Piggott, & Burgess, 2018).

Unfortunately, evolutionarily selected predator-specific nesting strategies may be rendered maladaptive due to climate change-induced alterations in biotic communities (Walther et al., 2002). This may take the form of range expansions introducing novel predators to which native birds are naïve (Wynn, Josey, Martin, Johns, & Yésou, 2007), the temporal overlap of predator species with prey due to changes in phenology (Rockwell & Gormezano, 2009), or simply increased native predator populations. However, changes in individual predator populations should not be considered in isolation, as the interaction between different predator species may result in complex biological phenomenon such as interspecific foraging associations. Such associations occur when two (or more) predator species forage in association together, and are thought to form via increases in foraging efficiencies for one (or more) of the predators involved in the association (Sridhar, Beauchamp, & Shanker, 2009; Stensland, Angerbjörn, & Berggren, 2003). These associations may have a disproportionately negative impact on prey species when the respective defensive strategies against each focal predator species are ineffective against the respective partner predator species. For example, in response to coyotes (*Canis latrans*), ground squirrels (*Spermophilus armatus*) flee into underground burrows, but will exit their burrows in response to subterranean American badgers (*Taxidea taxus*) (Minta, Minta, & Lott, 1992). Thus when hunting associations form between coyotes and badgers, ground squirrels are left without refugia and are overall more susceptible to predation (Thornton et al., 2018).

Changing predator communities are rapidly becoming problematic for Arctic nesting birds, as climate change is thought to be occurring more rapidly in these regions than in other parts of the world and impacting distributions of predators (Stroeve, Holland, Meier, Scambos, & Serreze, 2007). One widely cited “novel” predator for Arctic nesting birds are polar bears (*Ursus maritimus*), which are increasingly present in the terrestrial habitats of nesting bird colonies due to reductions in spring sea ice (Iverson, Gilchrist, Smith, Gaston, & Forbes, 2014; Rode et al., 2015; Smith, Elliott, Gaston, & Gilchrist, 2010). The intrusion of polar bears into terrestrial ecosystem clearly has direct negative impacts on prey species (Prop et al., 2015), but interactions between polar bears and native predator communities should be considered when understanding the full effects of climate change on nesting birds. Lesser snow geese (*Anser caerulescens caerulescens*) are well documented prey species of polar bears (Gormezano & Rockwell, 2013a, 2013b; Iles, Peterson, Gormezano, Koons, & Rockwell, 2013), but already have a complex predator community involving Arctic foxes (*Vulpes lagopus*), wolves (*Canis lupus*), and a suite of avian predators including herring gulls (*Larus argentatus*), parasitic jaegers (*Stercorarius parasiticus*), and common ravens (*Corvus corax*) (Cooke, Rockwell, & Lank, 1995). These avian predators are of particular concern to nesting geese due to their high mobility, visual acuity, and relatively ubiquitous presence throughout the nesting period of geese. However, parent geese are relatively well-armed against avian predators and can often fend-off attacks (Cooke et al., 1995). As such, it is thought that when parent geese are present, avian predators are generally unable to access goose eggs or goslings (Harvey, 1971; Inglis, 1977; Prop, Eerden, & Drent, 1985).

In the previous chapter, evidence was provided for an interspecific foraging association between avian predators and bears in lesser snow goose colonies, and it was suggested that snow geese increase their nest attendance on days when bears were known to be foraging in the colony. However, in response to bears this seems to be maladaptive strategy in a flat, relatively featureless landscape, as a conspicuous attendant female goose would provide visual cues for bears on nest location. It has been suggested that Arctic foxes rely on the presence of nesting female geese to provide reliable nest location information (Samelius & Alisauskas, 2001), and in principle this could present a limitation on the ability of polar bears to locate individual nests while foraging in goose colonies. However, the observation that geese increase overall nest attendance when bears are present suggests that geese may be responding to stimuli beyond the presence of polar bears, such as the presence of avian predators in interspecific foraging associations with polar bears. Therefore, geese are likely faced with the following tradeoff in response to the intraspecific foraging association between bears and avian predators: 1) leave the nest to decrease the probability of detection by bears, but increase risk to avian predators searching for unattended nests, or 2) remain with the nest to protect eggs from avian predators, but increase the probability of being detected by bears (Figure 17).

The objectives of this chapter are to examine these tradeoffs by modeling snow goose nesting behaviours in response to interspecific foraging associations between polar bears and avian predators. To do this, I make use of Agent Based Models (ABMs), a technique whereby a system of 'agents' are programed to follow pre-set behavioural rules, and simulations are run allowing interactions between agents and their environment (McLane, Semeniuk, McDermid, & Marceau, 2011; Uri Wilensky & Rand, 2015). Specifically, I ask: 1) Is decreased nest attendance by snow geese a good strategy against foraging polar bears *in isolation*?, 2) Is decreased nest attendance by snow geese a good strategy against an interspecific foraging association of polar bears and avian predators?, 3) Does the ability of snow geese to weigh the relative risk of predation by polar bears or avian predators result in increased nest attendance?

Methods

Agent Based Model

ABMs were constructed in Netlogo v6.0.1 (Uri Wilensky, 1999). Documentation and justification of model processes are provided in the following sections according to the ODD (Overview, Design concepts, and Details) protocol for ABMs (Grimm et al., 2006; Grimm et al., 2010).

1. Purpose

The purpose of these agent-based simulations is to examine the behavioural tradeoffs that nesting geese experience in a mixed predator environment. These behavioural tradeoffs are examined in the context of predator-specific nest defense strategies, and how parent geese might adjust strategies against interspecific foraging associations between bears and avian predators.

2. Entities, state variables, and scales

Models are primarily composed of prey (snow goose nests) and predator (bears and avian predators) agents. Simulations are structured to examine the impact of predators on snow goose behaviour (and ultimately, nest success), given that predators are foraging within the colony. Thus, all simulations involve nesting geese and at least one predator species. Note that although here we are simulating the failure/success of snow goose nests, behavioural decision making is in the context of the female parent attending each nest. The individual bird is not explicitly represented as an agent within simulations, but they are ultimately the entity making the decisions that change the state of their nest.

Snow goose nest agents are represented as a stationary nest on the landscape and can exist in three states: 1) nests are active and are attended by a female parent: “on-nest”, 2) nests are active, but are not attended by a female parent: “off-nest”, 3) nests are not active (female parent no longer relevant) and are considered “failed”. The default state for nests are “on-nest” as Arctic nesting geese have extremely high rates of nest attendance, see Thompson & Raveling

(1987). Snow goose nests can change their state between on-nest and off-nest depending if the parent goose is forced to make a decision on whether to remain on their nest or not in the presence of a foraging bear. Snow goose nests also record this as a state-variable *saw-bear?* (“True” if geese saw a bear, “False” if geese did not see a bear”, based on each nest’s *bear-sensing-distance,* see section 4.7 *Sensing*), and if snow goose nests fail, they record the predator agent that caused them to fail. The geographic location of goose nests do not change within simulations.

Each simulation is populated with a single bear agent that is actively foraging within the goose colony. Bears walk relatively slowly through the colony searching for goose nests to consume. Bears are better at detecting nests with attendant parents (on-nest) versus those without parents (off-nest); however if an unattended nest is relatively close to the bear then the bear is able to detect it and will move towards the nest. If the bear cannot detect any snow goose nests nearby, it will move forward in a correlated random direction. There is no limit to the number of nests which can be consumed by an individual bear. If the bear reaches the edge of the world (e.g. leaves), the simulation ends.

Avian predators are represented in models as highly mobile predators which sense snow goose nests in a similar fashion to bears, although avian predators have a much wider sensing radius due to their acute vision and aerial perspective (Opermanis, 2004). The number of avian predators in each simulation is constant at 10, although individual avian predator agents can leave the system, in which case they are immediately replaced by a new avian predator agent randomly at the edge of the world. We chose to populate simulations with 10 avian predators to represent approximate “worst-case” scenarios of avian predation, based on anecdotal observations in the field. Avian predators can only attack unattended snow goose nests, and do not bother trying to attack snow goose nests in the on-nest state (i.e. with a parent goose incubating eggs). There is no limit on the number of nests which can be consumed by an individual avian predator. See section 4.7 *Sensing* for further details on the bear and avian predator sensing abilities.

The landscape is represented as a 200m by 100m rectangle (0.5km^2), composed of individual 25m^2 patches. Patches in this model hold no state variables and only serve as a surface for the interaction of snow goose nests, bear, and avian predator agents (Figure 18). World wrapping is not used in these models (i.e. the world is not torus shaped, and the patches at one end of the world are not immediate neighbours of patches on the other end of the world). Therefore, if a predator reaches the edge of the world, it leaves the system.

Simulations proceed in one-second time steps. Thus, parameters on predator movement given as meters$^{-\text{second}}$ in section 6. *Input Data* are scaled to discrete one-second time step values. The model records the number of seconds since the model begins, and resets to zero at the start of each new model run (e.g. when each simulation ends).

3. Process overview and scheduling

Individual simulations begin with the distribution of snow goose nests and a single bear on the landscape. Briefly, 150 snow goose nests are given random locations, while a single bear is placed in the center of the colony. If model scenarios call for avian predators, then 10 avian predator agents are generated with random locations at the start of simulations. For further details on the initial distribution of agents, see 5. *Initialization*.

Models proceed in discrete, one-second time steps. First, any snow goose nests that are active (e.g. have not failed due to predation) evaluate their current predator environment. If there are no predators around, the nests remain attended by a parent goose (on-nest). However, if bears are within a snow goose nest’s given *bear-sensing-distance,* parent geese may choose to get off their nest or not (thereby changing the state of their nest from on-nest to off-nest, or vice-versa).

Next, bears sense their environment for available snow goose nests. If they locate a snow goose nest, they face the direction of the nearest snow goose nest agent and move one step towards the nest. Note that at the next step, if a bear is already heading towards a nest they will continue to move towards this target nest (unless they happen to come across a different individual snow goose nest that is closer). If no snow goose nests are located, bears move forward in a random correlated direction. Finally, avian predators sense their environment (similar to bears), and face the closest snow goose nest they locate. If no snow goose nests are located, avian predators move forward in a random correlated direction.

4. Design concepts

4.1 Basic principles

Basic principles (context and justification) of this model are provided in the manuscript Introduction (see Figure 17).

4.2 Emergence

The primary data output of this model is whether or not individual snow goose nests are successful or not, but the emergent patterns from this model are the relationship between snow goose nest’s *bear-sensing-distance,* and the specific predator agent responsible for causing each nest to fail.

4.3 Adaptation

Individual simulations only occur for a single bear foraging event within the colony, as such there is no information carried over in subsequent model runs (i.e. individual snow goose nests are not modeled on an annual basis). Within model runs, snow goose nests can adapt (the parents of each nest make decisions) based on their current local predator environment (see 7.3 *Relative Predator Risk*). Predators adapt to their local prey environment by sensing snow goose nests and altering their movement direction towards available prey (if located).

4.4 Objectives

The main objectives of predators (bears and avian predators) are to locate and consume as many snow goose nests as possible. On the contrary, the main goal of snow goose nests are to not be destroyed by predators, but also have their parent goose remain on-nest long as possible. Note that snow goose nests may compromise on the latter in favour of reducing the probability of being detected by bears.

4.5 Learning

Learning is not incorporated in these models. Predator foraging efficiency and snow goose perception of predators (*bear-sensing-distance*) does not change within individual model runs.

4.6 Prediction

Prediction is only considered with snow goose agents, who may be said to “predict” which predator may arrive to their location first and adjust their nesting strategies (e.g. if the parent goose remains on-nest or not, see 7.3 *Relative Predator Risk*).

4.7 Sensing

Predator agents sense snow goose nests based solely on whether a snow goose nest is attended (on-nest) or unattended (off-nest) by a parent goose. Note we do not consider the ability of bears to detect nests via olfaction here. Bear agents are able to detect any snow goose nests located within a restricted-vision-cone with a radius of 50m and viewing angle of 90°. In contrast, within a larger wide-vision-cone with a radius of 100 and viewing angle of 90°, bears can only detect attended snow goose nests (on-nest) (Figure 19A). Avian predators have a much wider vision cone (radius 100m, viewing angle of 260°), but can only detect and attack snow goose nests lacking attendant female parents (off-nest) (Figure 19B).

Snow goose nests sense predators differently depending on the model scenario. In the first scenario, snow goose nests only sense approaching bears, and if a bear comes within a snow goose nests's *bear-sensing-distance* (the distance in meters that bears can be deteced), the female goose gets off their nest (or gets back on if the bear becomes farther away). In the second scenario, if a bear comes within a snow goose nest's *bear-sensing-distance*, the both bears and avian predators are detected and snow goose nests calculate the relative risk posed by each (see 7.3 *Relative Predator Risk*). Note here we are describing the actions taken by snow goose nest agents, but in the biological context it is the attendant parent goose that would sense predators and make decisions on whether to remain on-nest or not.

4.8 Interaction

The only direct interaction between agents is the interactions between predators and prey. If predators locate and arrive at an available snow goose nests, predators cause the nest to fail (switching the snow goose nest state to "failure"). Predators can also cause snow goose nests to alter their nest attendance behaviour, switching between on-nest and off-nest states (but still remaining "active"). Note that predators can indirectly interact with each other by consuming potential snow goose nests, thus rendering those snow goose nests unavailable for other predators to consume. Snow goose nests cannot change any predator state variables.

4.9 Stochasticity

Stochasticity is only considered during the initial positioning of snow goose nest agents (but density/number of snow goose nests is parameterized based on field-derived estimates, see

5. *Initialization*). Stochasticity is also considered for the initial positioning of avian predators, and the position of new avian predators entering at the edge of the world.

4.10 Collectives

Collectives (i.e. groups of individual agents) are not used in these models. Rather, all decision making is made at the level of the individual entity, rather than being made for groups of individuals.

4.11 Observation

At the end of each simulation (e.g. if the bear leaves or if all snow goose nests are "failures"), snow goose agents output data on whether they survived or not, and which predator agent caused them to lose their nest if they did not survive. During model runs, plot monitors record the number of snow goose nests that were "failures" as caused by either bears and avian predators respectively, as well as the identity of any individual snow goose nests being targeted by bears (for book keeping purposes within individual model runs).

5. Initialization

Each model run is initialized with a new landscape of predators and snow goose nests agents. Patches do not have any state variables and thus remain the same in all models. A single bear agent is positioned at the landscape origin (center), facing a random direction in a 360° circle. If avian predators are included in simulations, then 10 avian predators are positioned randomly throughout the landscape facing a random direction in a 360° circle.

Snow goose nest density in models was informed by nest density data collected during the summer of 2016 from a portion of historically monitored snow goose population in Wapusk National Park, Manitoba Canada. Nesting density data was collected via drone (Chapman, 2014) imagery flown at 100m above ground level (AGL). For further detail on drone aircraft and flight specifications, see Chapter II. Briefly, RGB imagery was collected using a fixed wing drone flown approximately 1.5 weeks into snow goose nest incubation. Imagery was mosaicked together and reviewed by a trained technician (E. Woods), who manually identified goose nests via a grid-assisted search pattern (i.e. individually searching 50 x 50m grid cells). We estimated snow goose nest density as the number of counted nests per 0.5km^2 in each mosaic, and used the mean value across all mosaics to inform the number of nest agents to populate our 0.5km^2 model landscape. We found a mean nesting density of 146 nests per 0.5km^2 , but we rounded up to 150 nests for simplicity in model runs (Table 15).

Snow goose nest locations from each drone mosaic were then loaded into ArcGIS 10.6 (ESRI, Redlands, California). We estimated the dispersal pattern using ArcGIS' Average Nearest Neighbour tool, based on the spatial extent of the RGB imagery. This was done separately for non-overlapping mosaics (i.e. we did not use areas of mosaics which overlapped spatially). Nearest neighbour analyses indicated a mix of random and dispersed nesting locations (Table 15). To accommodate a more dispersed nesting pattern in our models, we estimated the minimum distance between nearest neighbours for each mosaic. We used the mean minimum distance of 30.6m (*neighbour-min*) between neighbouring nests as a minimum threshold when populating landscapes (Table 16).

Finally, during model initialization 150 snow goose nest agents were generated and randomly positioned throughout the landscape. If a nest was generated within *neighbour-min* of another snow goose nest agent, it relocated to a new random position on the landscape (repeating until no nests were located within *neighbour-min*). All geese began the simulation in the default state of on-nest (active, with a parent goose incubating eggs). All snow goose nests were assigned the same *bear-sensing-distance* based on the chosen value for the current model run.

6. Input Data

Input data on the number and characteristics of snow goose nests were based on drone imagery estimates reported in *5. Initialization*. The only other input data used were literature derived estimates of polar bear walking speed, and anecdotal estimates of avian predator flight speed (while hunting). Polar bears were simulated to walk at $2\text{km}^{-\text{Hour}}$ based on Amstrup, Durner, Stirling, Lunn, and Messier (2000), and following the convention of an ABM presented by Dey et al. (2017). Avian predators were simulated to fly at $10\text{km}^{-\text{Hour}}$, based anecdotal estimates of avian predator flight speeds in the field (*A.Barnas, personal observations*), but also to simulate a highly mobile predator agent (distinctly different from the relatively slow bear agents). Note these values were scaled to accommodate 1-second time steps within models.

7. Submodels

7.1 Bear Movement

At the start of each time step, bears detect any active snow goose nests (in on-nest or off-nest states) that are within their restricted-vision-cone. If no active snow goose nests are detected within the restricted-vision-cone, bears try to detect snow goose nests in the on-nest state within their wide-vision-cone (see *4.7 Sensing*). If any potential prey snow goose nests are located in either one of these steps, the bear faces the nearest active snow goose nest and moves forward 0.55m towards the target nest (polar bear walking speed ~$2\text{km}^{-\text{Hour}}$). If the target nest is within 0.55m, the bear simply moves to the exact snow goose nest location and causes the snow goose nest to fail. If no snow goose nests are located in either vision cone, bears face a random direction within 10° to the left or right of the bear’s current heading, and moves forward 0.55m.

7.2 Avian Predator Movement

At the start of each time step, avian predators detect any unattended nests within their wide-vision-cone (note this is much larger than bears and avian predators due not require a restricted-vision-cone, see 4.7 *Sensing*). If any potential prey snow goose nests are located within the vision cone, avian predators face the nearest active snow goose nest and moves forward 2.87m (avian predator travel speed ~10km^{-Hour}). If the target snow goose nest is within 2.87m, the avian predator simply moves to the exact nest location and causes the nest to fail. If no snow goose nests are located within the vision cone, avian predators face a random direction within 10° degrees to the left or right of the avian predator's current heading, and move forward 2.78m.

7.3 Relative Predator Risk

In scenarios featuring both predator species, separate model scenarios were constructed where snow goose nests would either 1) only react to approaching bears and have parents leave the nest (off-nest) once the bear was within the snow goose nest's *bear-sensing-distance*, or 2) snow goose nests would calculate a Relative Predator Risk score and choose whether to have parents leave their nest or not. Relative Predator Risk scores represent the relative risk that each predator species poses to an individual snow goose nest, and is calculated based on the distance between the snow goose nest and the predator in meteres, and the speed at which the predator is moving in meters$^{-second}$. This represents an estimate of which predator would arrive to the snow goose nest's location first if travelling in straight line towards the nest.

$$Relative\ Predator\ Risk\ = \frac{\left(\frac{Bear\ travel\ speed}{Distance\ to\ Bear}\right)}{\left(\frac{Avian\ Predator\ travel\ speed}{Distance\ to\ Nearest\ Avian\ Predator}\right)}$$

Where:

Relative Predator Risk ≥ 1 → Bear poses greater risk to the snow goose nest, parent goose leaves nest (off-nest state)

Relative Predator Risk < 1 → Avian predators pose greater risk to the snow goose nest, parent goose is on the nest (on-nest state)

Note that snow goose nests only calculate Relative Predator Risk if a bear is within a snow goose nest's *bear-sensing-distance*. Therefore, parent geese may remain in an on-nest state even if a bear is within the *bear-sensing-distance*, but since both types or predator agents are sensed, parent geese remain on-nest. If snow goose nests are not calculating Relative Predator Risk, then parents simply leave their nest when bears are within the *bear-sensing-distance*, and get back on the nest if bears are farther than that distance (provided the snow goose nest has not been attacked by a predator). Again, recall here that while calculations and sensing are done from the snow goose nest agent, in the biological context the attendant female goose for each nest would be the entity making behavioural decisions to leave the nest or not.

Data Analysis

To examine the relationship between *bear-sensing-distance* and the probability of snow goose nest failure, we ran model batches in Netlogo's *BehaviorSpace* function (U Wilensky & Shargel, 2002), which systematically increased the *bear-sensing-distance* of snow goose nests from 5m to 150m (by 5m increments, 10 replicates each) in separate model runs. ABMs were run in three predator landscape scenarios: 1) Bears Only, 2) Bears and Avian predators together (without Relative Predator Risk calculation by snow goose nests), and 3) Bears and Avian predators together (with Relative Predator Risk calculations by snow goose nests). This resulted in a total of 1200 model runs (400 of each scenario). At the end of each model run, we recorded whether or not a snow goose nest was successful or a failure, and which predator caused failures to occur. For analyses, we only considered snow goose nests which had had a bear come within their given *bear-sensing-distance* for that model run, since the majority of snow goose nests within any given model run did not come into contact with bears. Further, this allowed us to restrict our analyses to snow goose nests which were forced to make a decision based on bear presence.

Estimates for probability of snow goose nest failure were made by fitting generalized additive models (GAMs) (Hastie & Tibshirani, 1990; S. N. Wood, 2006). GAMs provide a flexible framework to fit complex relationships (non-linearity) and produce readily interpretable outputs from which we can make inferences on ecological relationships. Models were constructed separately for different predator landscape scenarios (e.g. bears only vs bears and avian predators together), and fit for different responses within each scenario; 1) overall probability of nest failure, and 2) probability of nest failure by specific predators (e.g. bears vs avian predators if present). GAMs were fit with a binomial distribution (1- nest failure, 0- nest success), a logit link function, and *bear-sensing-threshold* as the sole predictor with a thin plate regression spline. Models were fit with the *mgcv* package (S. Wood & Wood, 2015) which iteratively optimizes model wiggliness by choosing smoothing parameters based on restricted maximum likelihood. The number of basis functions (the individual functions used to construct the overall smooth function) used in each model was allowed to vary based on iterative model fitting. If too few basis functions were used by default, we manually added basis functions until residuals of smooth terms were randomly distributed ($P \geq \alpha$, note that this is an approximate significance test).We employed a Bonferroni Correction and chose an adjusted α of 0.007 to account for inflated type-I errors with the multiple approximate significance tests for non-parametric smooth terms and basis function checking. Probability scale model predictions and 95% confidence intervals were plotted in *ggplot2* (Wickham, 2016).

Results

From 1200 Netlogo model runs, we ultimately recorded data from 33,967 snow goose nest agents that had to make a nesting behaviour decision in response to a bear. We constructed seven separate GAMs (each representing a separate model response for a given predator landscape scenario), which all indicated a non-linear relationship between bear sensing distance and probability of nest failure (all EDF > 7.08, P<0.0001, Table 17). The only exception was the model examining probability of failure by avian predators where snow goose nests could calculate Relative Predator Risk, indicating a non-significant, linear relationship (EDF = 1.57, P=0.69).

We found that snow goose nests with parent geese leaving their nest far in advance to approaching bears was a successful strategy in "bear-only" predator landscapes, as bears had difficulty locating snow goose nests without attendant parents (Figure 20A). However, in a mixed predator environment this strategy is not successful as unattended nests (off-nest) were quickly consumed by avian predators (Figure 20A). Model predictions examining the probability of nest failure by specific predators were qualitatively similar to the hypothesized relationship between bears, avian predators and geese presented in Figure 17. For the given overarching model parameters (e.g. predator numbers, sensing abilities, nesting density), it appears an optimal *bear-sensing-distance* in a mixed predator environment exists around approximately 75m.

However, when snow goose nests were given the ability to calculate Relative Predator Risk presented by each predator species, snow goose nest's parent geese chose to remain on their nest and significantly reduced nest predation by avian predators (Table 17, Figure 21). Interestingly, predation by bears remained similar in these scenarios and overall probability of nest failure did not qualitatively differ from the original "bears-only" predator landscape (Figure 22).

For all scenarios involving avian predators, the shape of the relationship between probability of snow goose nest failure and *bear-sensing-distance* became more wiggly beyond approximately 50m (Figures 20-22). The proximate cause of this changing relationship is unclear, and future models could explore ecological processes occurring beyond 50m distances in the simulation steps, or potentially alternative smooths in the analysis step (e.g. adaptive smooths).

Discussion

Here we have demonstrated that lesser snow geese can successfully employ different nesting strategies against different predators. However, when presented with a mixed predator environment, it is beneficial for geese to weigh the relative risk posed by each predator and make an informed decision on nest attendance strategies (Ellis-Felege, Burnam, Palmer, Sisson, & Carroll, 2013; Xu, Ellis-Felege, & Carroll, 2017). By remaining on nest in the presence of avian predators, geese can almost entirely reduce nest loss by these predators, which results in little increased risk by foraging bears.

The interspecific foraging association between polar bears and avian predators demonstrates that the relationship between bears and nesting birds is more complex than originally thought. While we originally hypothesized increased nest attendance by geese would increase probability of nest failure by bears, we did not find evidence to support this. It is possible that inside of some distance threshold, the risk of predation by bear is relatively constant since bears are likely to locate these nests anyways (regardless if geese are on- or off-nest). It may be more interesting to examine nest attendance of geese at greater distances (e.g. > 150m), as this is where the consequences of nest attendance decisions may be empirically realized, rather than "local" birds whose risk levels are relatively constant. If it can be demonstrated that geese at a distance (who remain on their nest in response to avian predators), ultimately attract bears to their area, then this would provide evidence that avian predators actually benefit foraging bears through facilitating the discovery of nests. Whereas the opposite relationship would occur inside a “local” distance threshold, where avian predators benefit from the presence of bears. Further investigation into this phenomenon is required.

We only considered predator foraging based on visual cues, but additional stimuli such as olfactory cues may be important to consider, especially for Ursids (Togunov, Derocher, & Lunn, 2017). There are few detailed accounts of bear foraging in bird colonies, but there is some evidence to support the notion that bears visually scan their environment for available prey (or relevant indicator cues) (Gormezano, Ellis-Felege, Iles, Barnas, & Rockwell, 2017; Prop, Oudman, van Spanje, & Wolters, 2013). On the other hand, avian predators are highly visually acute and can quickly locate available prey from a high vantage point (Opermanis, 2004). This may be the reason for the disproportionately high number of reports on interspecific foraging associations between avian predators and other terrestrial species (Booth-Binczik, Binczik, & Labisky, 2004; Sakamoto, Takahashi, Iwata, & Trathan, 2009; Silveira, Jácomo, Rodrigues, & Crawshaw Jr, 1997; Stahler, Heinrich, & Smith, 2002; Stempniewicz & Iliszko, 2010).

There are several important caveats to the simulation models presented here. First, the distance at which geese made decisions was constant across all individuals within each simulation. However, younger geese are much less attentive to their nests than older individuals (Cooke, Bousfield, & Sadura, 1981; Cooke et al., 1995). This may be due in part to the lack of experience in younger birds, but life history theory predicts younger birds should be more risk-averse in favour of future breeding opportunities (Curio, 1983; Montgomerie & Weatherhead, 1988). Therefore in the presence of bears, young geese may simply abandon their nests, while older birds would be more likely to remain on-nest. This provides a possible avenue for the indirect interaction between birds with differing levels of nest attentiveness. If an individual bird chooses to leave their nest in response to a bear, but a neighboring individual chooses to remain on their nest, bears could be drawn into the area of both birds by the actions of the second bird, thus increasing probability of predation of the first bird (who initially made the "correct" decision). Such interactions would be heavily influenced by the nesting density of birds in a given year, which leads to the second major caveat. In all models, we considered snow goose nesting density to be constant, instead examining patterns of predation independent of nesting patterns. However, nesting density is annually variable and may be influenced by factors such as nest site availability and years of high nest failure (Cooke et al., 1995; Lank, Cooch, Rockwell, & Cooke, 1989). Future models should examine variation in nesting density, and incorporate the ability of individuals to make decisions based on the strategies of neighbouring birds.

The direct impacts of polar bears on nesting bird populations can be catastrophic and are likely to continue with the projected decrease in spring sea-ice cover (Prop et al., 2015). However, the indirect impacts of bears on breeding birds should warrant special attention, as these impacts demonstrate the more subtle, yet equally important effects of climate change on Arctic species (Bartley et al., 2019). Ultimately, breeding birds may be forced to alter breeding strategies by either phenological adjustments to nesting periods, or changes in nesting behaviour. Such behavioural changes may include changes in geographic distribution (Dey et al., 2017) or potential alterations in incubation strategies as discussed here. In any case, the effects of foraging bears on breeding birds are not likely to be straightforward and should continue to be investigated.

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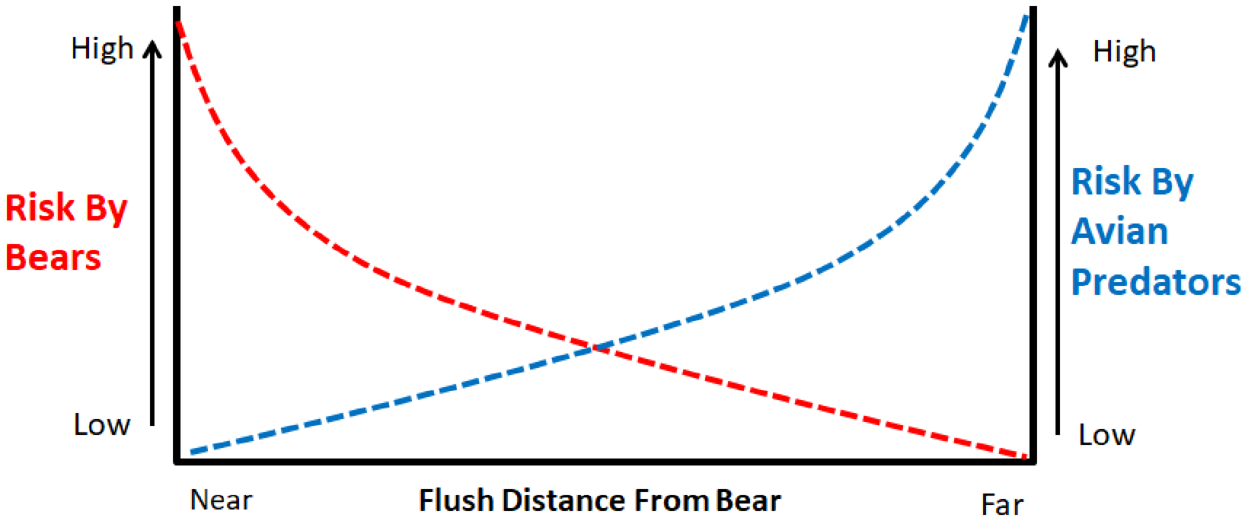


Figure 17 Hypothetical relationship between lesser snow goose flush distance from a bear and the probability of nest failure caused by either bears or avian predators. Birds that flush far in advance of approaching bears reduce the probability of bears locating nests, but this leaves nests open to attack by highly mobile avian predators. Remaining on the nest is a good strategy against avian predators, but this provides nest location information to bears and increases the probability of predation by bears.

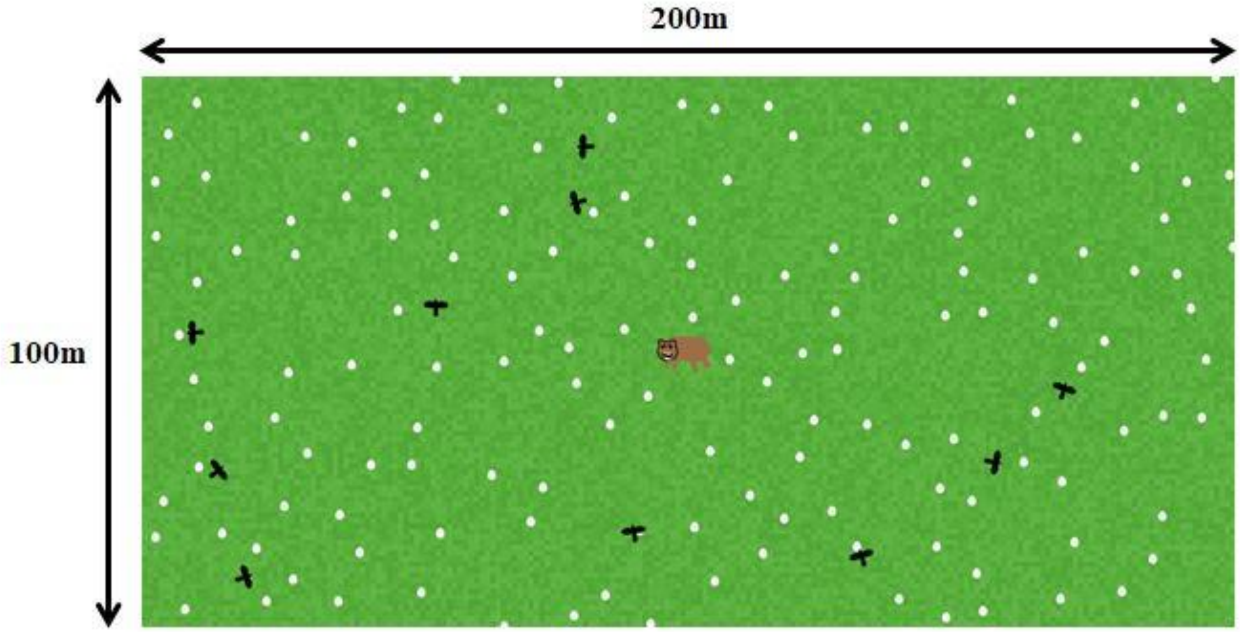


Figure 18 Example initialized landscape used in simulations. Snow goose agents depicted as white “eggs”, avian predators as black “hawks”, and bears as a brown custom “bear” shape. Note agent shape is artificially large here for demonstration purposes. Variation in patch color used to assist visual distinction between adjacent cells, patches hold no state variables of their own. Each patch represents a 5m x 5m area ($25m^2$).

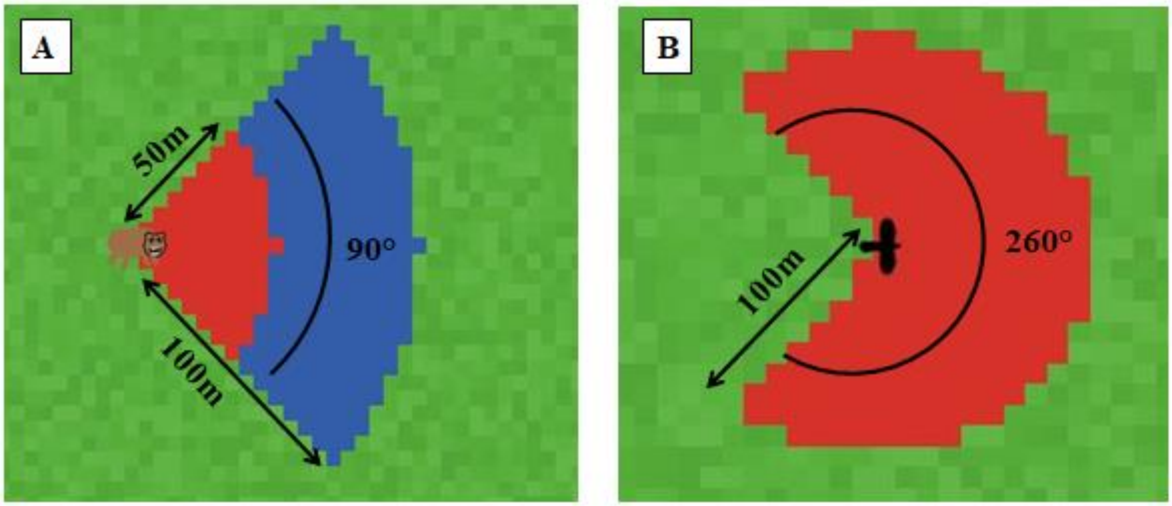


Figure 19 Vision cones of predator agents. A) Bear agents are able to detect any nest located within a restricted-vision-cone with a radius of 50m and viewing angle of 90°, but can only detect attended nests within a wide-vision-cone with a radius of 100 and viewing angle of 90°. B) Avian predators have a much wider vision cone (radius 100m, viewing angle of 260°), but can only detect and attack nests lacking attendant parents.

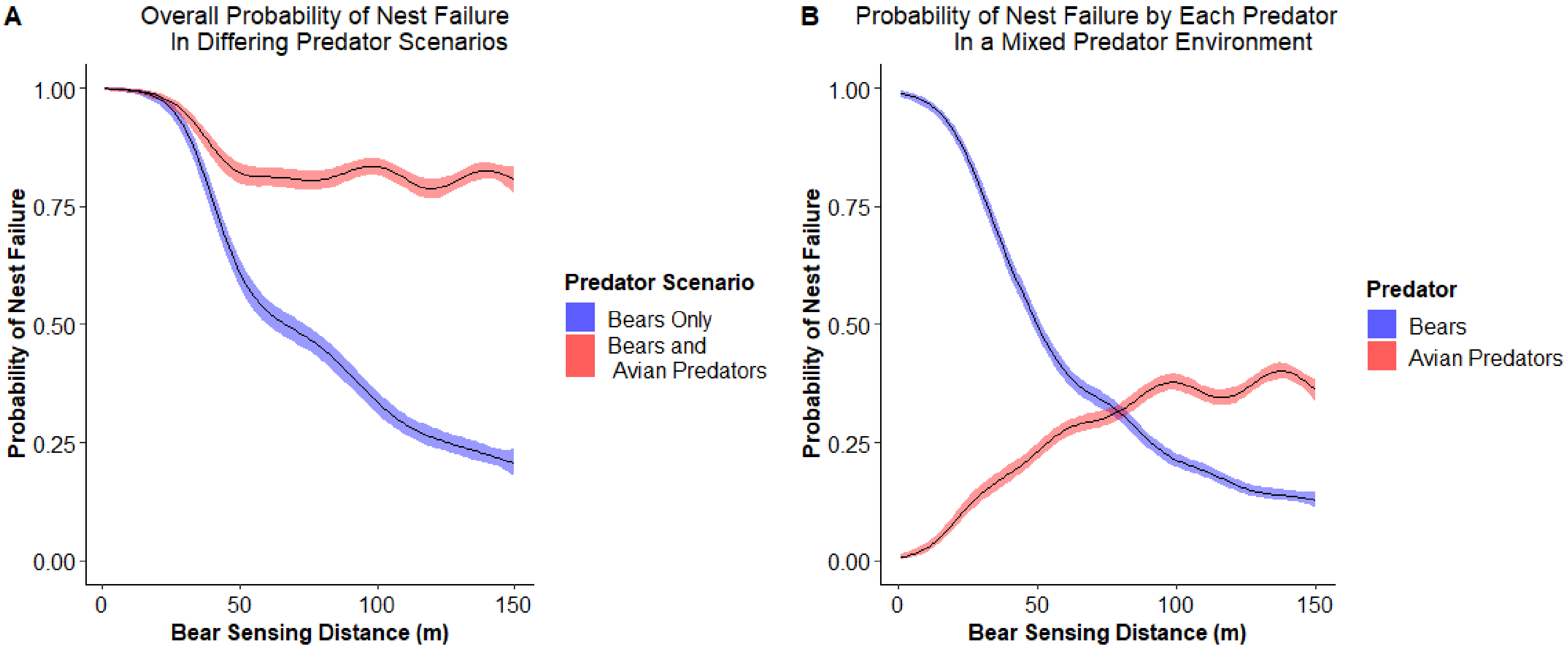


Figure 20 GAM results for probability of snow goose nest failure vs bear sensing distances (m). Solid lines represent mean model predictions, shaded areas represent 95% confidence intervals A) Overall probability of nest failure in differing predator environments: bears only, and environments featuring bears and avian predators together. B) Probability of nest failure caused by bears or avian predators within a mixed predator environment.

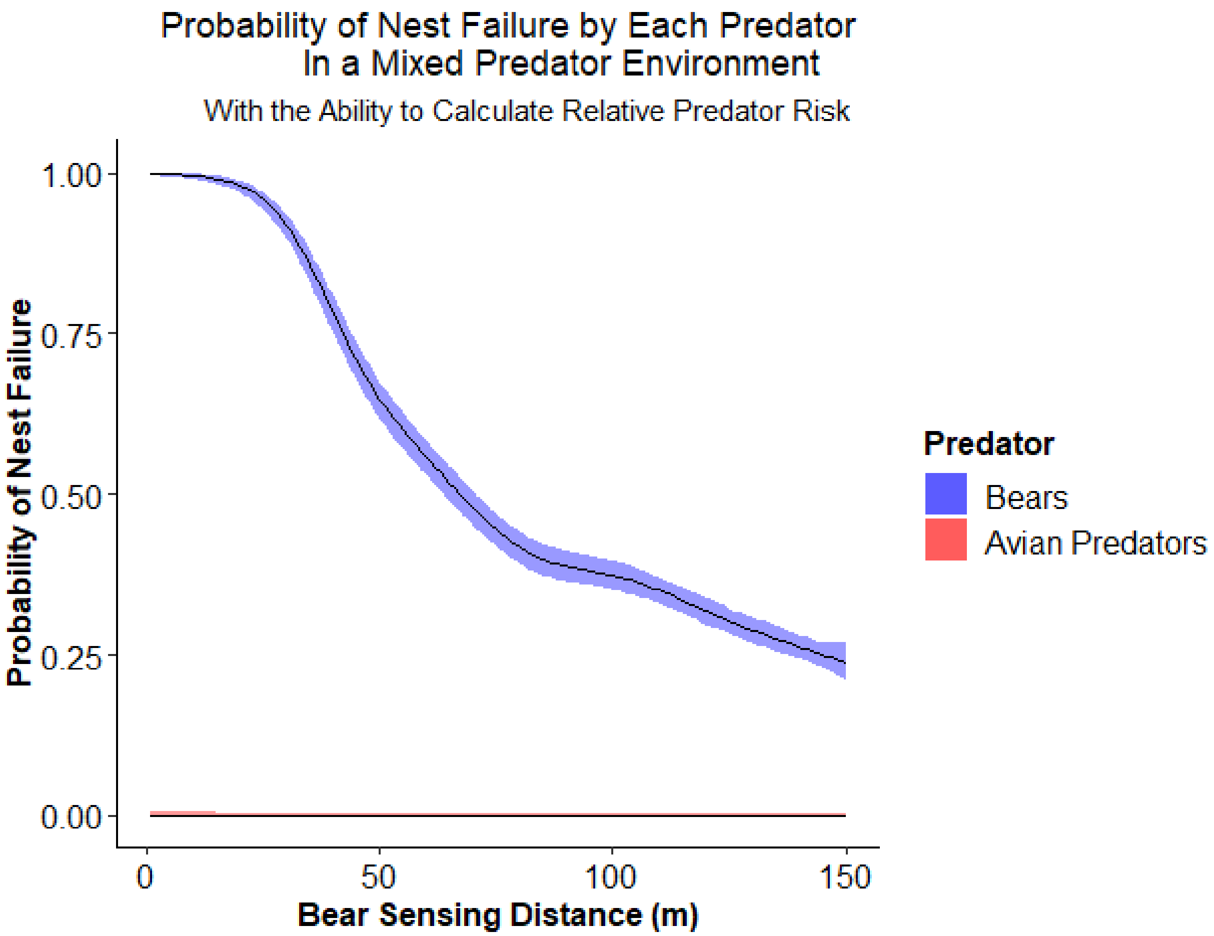


Figure 21 GAM results for probability of snow goose nest failure caused by specific predators in a mixed predator environment. Here, geese have the ability to calculate the Relative Predator Risk posed to them by bears and avian predators, and choose whether to remain on the nest or stay off (See *7.3 Relative Predator Risk*). Solid lines represent mean model predictions, shaded areas represent 95% confidence intervals.

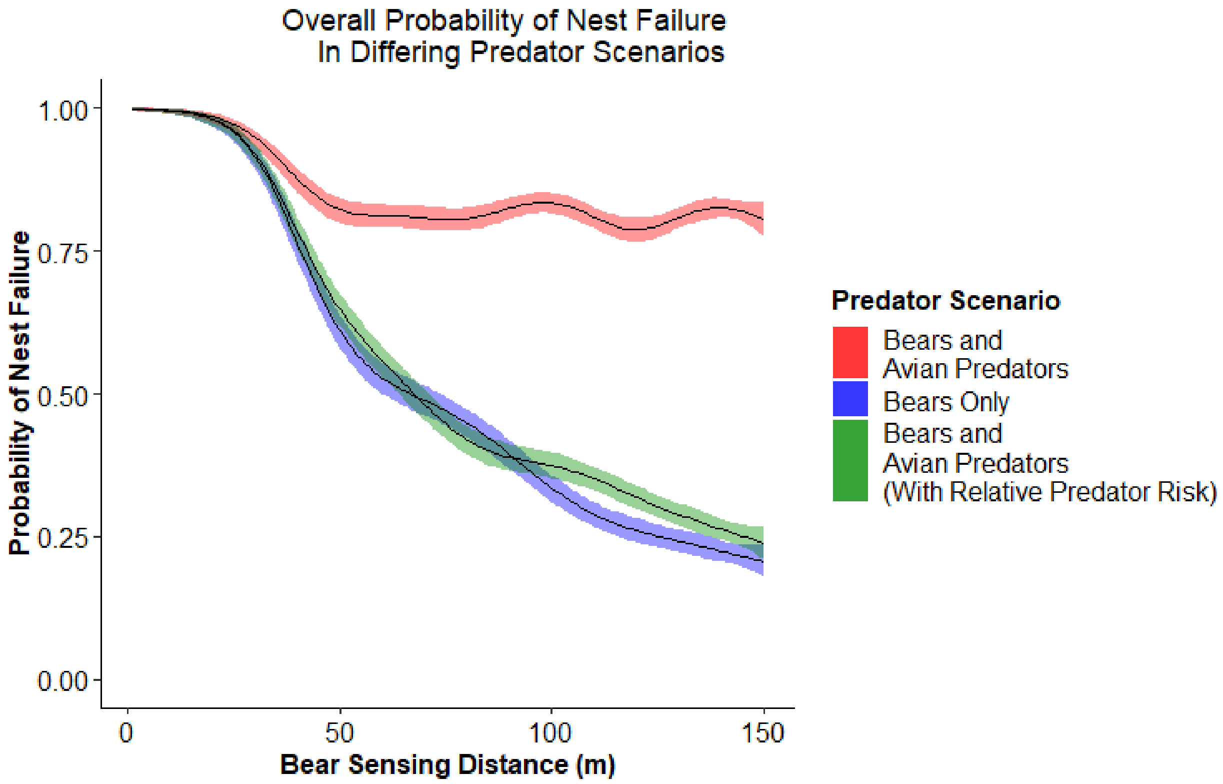


Figure 22 GAM results for overall probability of snow goose nest failure vs bear sensing distances (m). Solid lines represent mean model predictions, shaded areas represent 95% confidence intervals. Note the overall probability of nest failure including relative predator risk is simply overlain on top of the smooths from Figure 20A (which did not include Relative Predator Risk calculations).

Table 15 Nearest neighbour analysis of lesser snow goose nest locations from 100m AGL drone imagery. Data collected in 2016 within Wapusk National Park, Manitoba, Canada.

Mosaic ID	Mean nest density (nests/0.5km^2)	R*	Z-Score	P	Nesting Pattern
20160603_pr_cp_02_100m	69.23	0.99	-0.13	0.894	Random
20160603_pr_cp_03_100m	171.43	1.10	2.68	0.007	Dispersed
20160607_pr_bh_01_100m	154.76	1.13	3.41	>0.001	Dispersed
20160607_pr_cp_03_100m	227.94	1.11	3.72	>0.001	Dispersed
20160612_pr_cp_03_100m	152.63	1.16	2.38	0.017	Dispersed
20160612_pr_cp_05_100m	102.13	0.97	-0.62	0.532	Random

*Where R is the ratio of the observed average distance between nearest neighbours and the expected average distance between neighbours given a random distribution. Values above 1 suggest a dispersed point pattern, values less than 1 suggest a clustered point pattern, and values of 1 suggest a random point pattern.

Table 16 Minimum distances measurements between neighbouring lesser snow goose nests from 100m AGL drone imagery. Data collected in 2016 within Wapusk National Park, Manitoba, Canada.

Mosaic ID	Spatial Extent (km^2)	Number of nests counted	Mean Minimum Neighbour Distance ± SD (m)	Minimum Observed Nearest Neighbour Distance (m)	Maximum Observed Nearest Neighbour Distance (m)
20160603_pr_cp_02_100m	0.57	79	42.2 ± 29.9	9.4	161.0
20160603_pr_cp_03_100m	0.63	216	29.6±14.2	6.7	98.7
20160607_pr_bh_01_100m	0.63	195	32.3±20.3	7.2	155.0
20160607_pr_cp_03_100m	0.68	310	25.9±11.8	6.9	117.0
20160612_pr_cp_03_100m	0.19	58	33.2±14.3	14.6	88.7
20160612_pr_cp_05_100m	0.47	96	33.7±16.7	14.2	116.0
All Mosaics	**3.17**	**953**	**30.6±17.5**	**6.7**	**161.0**

Table 17. Summary statistics from generalized additive models for each predator scenario and model response. Note that P-values are based on an approximate test of significance of smooth terms. A significant smooth term suggests a wiggly relationship with the model response variable.

Predator Scenario	**Model Response**	**Parametric Terms**		**Non-Parametric Smooth Terms**		
		Intercept ± SE	*P*	*Effective Degrees of Freedom*	*Reference Degrees of Freedom*	P*
1. Bears Only (No RPRǂ)	Overall Failure	-0.116 ± 0.03	<0.001	7.10	7.9	<0.001
2. Bears and Avian Predators (No RPRǂ)	Overall Failure	1.802 ± 0.03	<0.001	7.25	8.08	<0.001
3. Bears and Avian Predators (No RPRǂ)	Bear Caused Failure	-0.765 ± 0.02	<0.001	7.86	9.12	<0.001
	Avian Predator Cause Failure	-0.910 ± 0.02	<0.001	8.11	8.72	<0.001
4. Bears and Avian Predators (With RPRǂ)	Bear Caused Failure	-0.052 ± 0.03	0.089	7.10	7.94	<0.001
	Avian Predator Caused Failure	-7.301±0.36	<0.001	1.57	1.94	0.69
	Overall Failure	-0.048±0.03	0.112	7.08	7.93	<0.001

*Statistical significance at P<0.007 based on Bonferroni correction for multiple tests

ǂ RPR- Relative Predator Risk calculations (see section 7.3)

APPENDIX A

(Chapter II)

Appendix A Figure 1 The Trimble UX5 on the elastic catapult launcher. Photo credit Dr. Susan Ellis-Felege (June 2015).

Appendix A Table 1. Candidate models with their corresponding AICc scores, weights (w), and deviances for each behaviour response (Resting, Nest Maintenance, Low Scan, High Scan, Head Cock and Off Nest) of LSGO on days before and during UAS surveys. "*day*"= flight vs no flight, "*group*"= flown over vs control birds, "null" = intercept and random effects only.

Model	**AICc**	**ΔAICc**	**w**	**Deviance**
Resting				
Day*Group	328.71	0	0.721	322.31
Day Group	330.78	2.07	0.256	324.38
Group	336.5	7.79	0.015	330.11
Day	337.93	9.22	0.007	331.54
Null	342.89	14.18	0.001	336.5
Nest Maintenance				
Day*Group	212.62	0	0.798	208.42
Day Group	216.48	3.86	0.116	212.28
Day	217.14	4.52	0.083	212.94
Group	225.61	12.99	0.001	221.42
Null	225.7	13.08	0.001	221.51
Low Scan				
Day*Group	306.57	0	0.651	300.16
Day Group	309.02	2.45	0.191	302.62
Group	309.65	3.08	0.139	303.26
Day	314.76	8.19	0.011	308.36
Null	315.37	8.8	0.008	308.98
High Scan				
Day*Group	328.2	0	0.683	321.79
Day Group	330.72	2.52	0.194	324.32
Day	332.89	4.69	0.065	326.5
Group	333.74	5.54	0.043	327.34
Null	335.75	7.55	0.016	329.36
Head Cock				
Day*Group	290.59	0	0.854	286.39
Day Group	294.42	3.83	0.126	290.22
Day	298.1	7.51	0.020	293.9
Group	321.54	30.95	0.000	317.34
Null	323.47	32.88	0.000	319.28
Off Nest				
Day*Group	347.61	0	0.786	341.2
Day Group	350.85	3.24	0.156	344.45
Day	352.9	5.29	0.056	346.51
Group	359.88	12.27	0.002	353.48
Null	362.67	15.06	0	356.28

Appendix A Table 2 Candidate models with their corresponding AICc scores, weights (w), and deviances for each behaviour response type (Resting, Nest Maintenance, Low Scan, High Scan, Head Cock and Off Nest) of LSGO during UAS surveys. "*group"*= flown over vs control birds, "*altitude*"= altitude of survey 75m, 100m, 120m or control (no flight overhead), "*launch distance*"= distance from aircraft launch to nest observed, "*period*"= period of flight (PRE, AIR, POST), "*global*" = *group + altitude + launch distance + period*, "*null*"= intercept and random effects only.

Model	AICc	ΔAICc	w	Deviance
Resting				
Altitude + Period	682.45	0	0.537	676.22
Group x Period	682.85	0.4	0.440	676.61
Alt	689.43	6.98	0.016	683.2
Global	692	9.55	0.005	685.76
Period	694.72	12.27	0.001	688.5
Group	696.7	14.25	0	690.48
Null	701.66	19.21	0	695.44
Launch distance + Period	703.26	20.81	0	697.04
Launch distance	710.21	27.76	0	703.99
Nest Maintenance				
Group x Period	580.31	0	0.852	574.08
Altitude + Period	583.94	3.63	0.139	577.71
Period	590.02	9.71	0.007	585.91
Global	592.85	12.54	0.002	588.74
Alt	594.05	13.74	0.001	589.94
Group	597.91	17.6	0	593.8
Launch distance + Period	598.26	17.95	0	594.15
Null	602.14	21.83	0	598.03
Launch distance	610.6	30.29	0	606.49
Low Scan				
Group x Period	588.93	0	0.500	582.7
Altitude + Period	588.94	0.01	0.497	582.71
Global	599.89	10.96	0.002	593.66
Period	601.51	12.58	0.001	595.29
Alt	608.23	19.3	0	602.21
Launch distance + Period	612.57	23.64	0	606.34
Group	614.36	25.43	0	608.14
Null	619.74	30.81	0	613.52
Launch distance	630.9	41.97	0	624.68
High Scan				
Group x Period	560.57	0	0.753	554.34
Altitude + Period	562.91	2.34	0.234	556.68
Alt	569.93	9.36	0.007	563.71
Period	571.01	10.44	0.004	564.78
Global	573.15	12.58	0.001	566.92
Group	575.75	15.18	0	569.53
Null	578.08	17.51	0	571.86
Launch distance + Period	582.34	21.77	0	576.12
Launch distance	589.42	28.85	0	583.19

Appendix A Table 2 Continued.

Model	AICc	ΔAICc	w	Deviance
Head Cock				
Group x Period	536.88	0	0.924	532.77
Altitude + Period	542.12	5.24	0.067	535.89
Period	546.39	9.51	0.008	542.28
Global	553.3	16.42	0	547.06
Launch distance + Period	558.15	21.27	0	554.04
Alt	564.29	27.41	0	560.18
Group	567.38	30.5	0	563.27
Null	569.02	32.14	0	564.91
Launch distance	580.78	43.9	0	576.67
Off Nest				
Altitude + Period	636.96	0	0.453	630.73
Group x Period	637.06	0.1	0.431	630.83
Global	639.83	2.87	0.108	633.6
Alt	646.57	9.61	0.004	640.34
Period	646.83	9.87	0.003	640.6
Launch distance + Period	653.03	16.07	0	646.8
Group	653.69	16.73	0	647.47
Null	656.32	19.36	0	650.1
Launch distance	662.48	25.52	0	656.25

APPENDIX B

(Chapter III)

Appendix B Table 1 Descriptive statistics of adult male polar bears (n=3 individuals) behaviour during individual UAS flights in July 2016.

UAS Flight of day	Bear ID	UAS Flight Altitude (m)	Number of Passes in UAS Flight*	UAS Flight Time (mins)	Number of Head-ups	Head-ups per Hour	Vigilance Bout Length ± SD (Range)	Between Bout Interval ± SD (Range)
1	PB01	120	24	26	15	34.6	32.0 ± 36.6 (9-141)	67.2 ± 69.6 (5-262)
2	PB01	75	25	28	10	21.4	25.2 ± 17.1 (2-52)	128.2 ± 231.4 (12-813)
3	PB02	120	26	29	7	14.4	7.6 ± 3.9 (3-12)	208.0 ± 201.0 (6-572)
4	PB02	75	28	30	8	16.0	11.6 ± 7.7 (3-23)	191.8 ± 233.8 (30-675)
5	PB03	75	23	29	27	55.9	13.9 ± 10.5 (4-40)	49.9 ± 56.5 (6-232)

* Note that the number of passes in UAS flight indicates the number of transects required to cover the total flight area, not the number of passes directly overhead of an individual bear.

APPENDIX C

(Chapter IV)

Appendix C Table 1 Further details on rectangular study plots dimensions and number of cells.

Plot Number	**Area (ha)**	**Number of Cells**	**Year Originally Established**
1	7	28	1979*
2	3	12	1999+
3	3	12	1999+
4	5	20	1999+
5	5	20	1999+

* See Weatherhead, P.J. 1979. Ecological correlates of monogamy in tundra-breeding savannah sparrows. *Auk*. 96: 391-401

\+ See Rockwell, R.F., Witte, C.R., Jefferies, R.L., and Weatherhead, P.J. 2003. Response of nesting savannah sparrows to 25 years of habitat change in a snow goose colony. *Ecoscience*. 10: 33-37

Appendix C Table 2 Landcover and vegetation classifications used in ground based linear transects. Cover was collapsed into three categories: Bare, Non-Shrub, and Shrub.

Cover Type	**Common Name**	**Code**	**Classification Type**	
Mud/bare ground	Mud/bare ground	A	Barren	0
Algal mat	Algal mat	A1	Barren	0
Pond with water	Pond with water	B1+	Barren	0
Pond with no water	Pond with no water	B1-	Barren	0
Stream with water	Stream with water	B2+	Barren	0
Stream with no water	Stream with no water	B2-	Barren	0
Moss	Moss	C3	Non-Shrub	1
Atriplex sp.	Saltbush	H	Non-Shrub	1
Carex subspathacea	Hoppner’s sedge	C1	Non-Shrub	1
Puccinnelia phyrganodes	Alkali grass	C1	Non-Shrub	1
Calamagrostis deschampiodes	Reedgrass	C2	Non-Shrub	1
Festuca rubra	Fescue	C2	Non-Shrub	1
Empetrum nigrum	Black crowberry	C4	Non-Shrub	1
Unidentified flowering plant	Flowers	C5	Non-Shrub	1
Carex aquatilis	Watersedge	D	Non-Shrub	1
Eriophorum sp.	Cottongrass	D	Non-Shrub	1
Elymus sp.	Wildrye	E	Non-Shrub	1
Salicornia sp.	Pickleweed	F	Non-Shrub	1
Spergularia sp.	Sandspurry	F*	Non-Shrub	1
Senecio sp.	Ragwort	G	Non-Shrub	1
Ranunculus sp.	Crowfoot	I	Non-Shrub	1
Hippuris vulgaris	Common mare tail	Hv	Non-Shrub	1
Petasites sagittatus	Arrowleaf	Ps	Non-Shrub	1
Triglochin maritima	Seaside arrowgrass	Tm	Non-Shrub	1
Triglochin palustris	Marsh arrowgrass	Tp	Non-Shrub	1
Rumex occidentalis	Western Dock	Ro	Non-Shrub	1
Matricia amigua	Mayweed	Ma	Non-Shrub	1
Salix sp.	Willow	S	Shrub	2
Salix brachycarpa	Shortfruit willow	Sb	Shrub	2
Salix candida	Sageleaf willow	Sc	Shrub	2
Salix planifolia	Diamondleaf willow	Sp	Shrub	2
Salix lanata	Wolly willow	Sl	Shrub	2
Salix reticulata	Netleaf willow	Sr	Shrub	2
Myrica gale	Sweetgale	Mg	Shrub	2
Betula glandulosa	Dwarf birch	Bg	Shrub	2

Appendix C Table 3 Confusion matrices of unsupervised classification results from drone imagery at 75, 100, and 120 meters above ground level for Plots 1-5. Individual accuracy results based on 100 equally stratified random points. Numbers on the diagonal of each matrix represent correct classifications.

75m Plot 1					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	65	4	0	69	0.94
Non-Shrub	1	8	0	9	0.89
Shrub	0	0	22	22	1
Total Points Assigned	66	12	22	100	-
Producer's Accuracy	0.98	0.67	1	-	-
Overall Accuracy	95.0%				
Kappa Coefficient	0.897				
75m Plot 2					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	58	0	1	59	0.98
Non-Shrub	5	5	0	10	0.5
Shrub	2	0	29	31	0.94
Total Points Assigned	65	5	30	100	-
Producer's Accuracy	0.89	1	0.97	-	-
Overall Accuracy	92.0%				
Kappa Coefficient	0.846				
75m Plot 3					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	64	2	1	67	0.96
Non-Shrub	5	4	0	9	0.44
Shrub	0	1	23	24	0.96
Total Points Assigned	69	7	24	100	-
Producer's Accuracy	0.93	0.57	0.96	-	-
Overall Accuracy	91.0%				
Kappa Coefficient	0.81				
75m Plot 4					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	64	0	0	64	1
Non-Shrub	3	6	0	9	0.67
Shrub	2	3	22	27	0.81
Total Points Assigned	69	9	22	100	-
Producer's Accuracy	0.93	0.67	1	-	-
Overall Accuracy	92.0%				
Kappa Coefficient	0.837				

Appendix C Table 3 Continued

75m Plot 5					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	79	1	0	80	0.99
Non-Shrub	6	2	2	10	0.2
Shrub	1	0	9	10	0.9
Total Points Assigned	86	3	11	100	-
Producer's Accuracy	0.92	0.67	0.82	-	-
Overall Accuracy	90.0%				
Kappa Coefficient	0.664				
100m Plot 1					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	66	2	0	68	0.97
Non-Shrub	3	7	0	10	0.7
Shrub	0	3	19	22	0.86
Total Points Assigned	69	12	19	100	-
Producer's Accuracy	0.97	0.58	1	-	-
Overall Accuracy	92.0%				
Kappa Coefficient	0.832				
100m Plot 2					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	60	0	0	60	1
Non-Shrub	5	5	0	10	0.5
Shrub	1	0	29	30	0.97
Total Points Assigned	66	5	29	100	-
Producer's Accuracy	0.91	1	1	-	-
Overall Accuracy	94.0%				
Kappa Coefficient	0.883				
100m Plot 3					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	65	1	1	67	0.97
Non-Shrub	7	2	1	10	0.2
Shrub	2	0	21	23	0.91
Total Points Assigned	74	3	23	100	-
Producer's Accuracy	0.87	0.67	0.91	-	-
Overall Accuracy	88.0%				
Kappa Coefficient	0.723				

Appendix C Table 3 Continued

100m Plot 4

	Barren	Non-Shrub	Shrub	Total Points Allocated	User’s Accuracy
Barren	64	1	2	67	0.96
Non-Shrub	5	4	0	9	0.44
Shrub	3	3	18	24	0.75
Total Points Assigned	72	8	20	100	-
Producer’s Accuracy	0.89	0.5	0.9	-	-
Overall Accuracy	86.0%				
Kappa Coefficient	0.697				

100m Plot 5

	Barren	Non-Shrub	Shrub	Total Points Allocated	User’s Accuracy
Barren	79	2	0	81	0.97
Non-Shrub	4	6	0	10	0.6
Shrub	0	0	9	9	1
Total Points Assigned	83	8	9	100	-
Producer’s Accuracy	0.95	0.75	1	-	-
Overall Accuracy	94.0%				
Kappa Coefficient	0.807				

120m Plot 1

	Barren	Non-Shrub	Shrub	Total Points Allocated	User’s Accuracy
Barren	65	2	0	67	0.97
Non-Shrub	5	5	0	10	0.5
Shrub	0	1	22	23	0.96
Total Points Assigned	70	8	22	100	-
Producer’s Accuracy	0.93	0.63	1	-	-
Overall Accuracy	92.0%				
Kappa Coefficient	0.831				

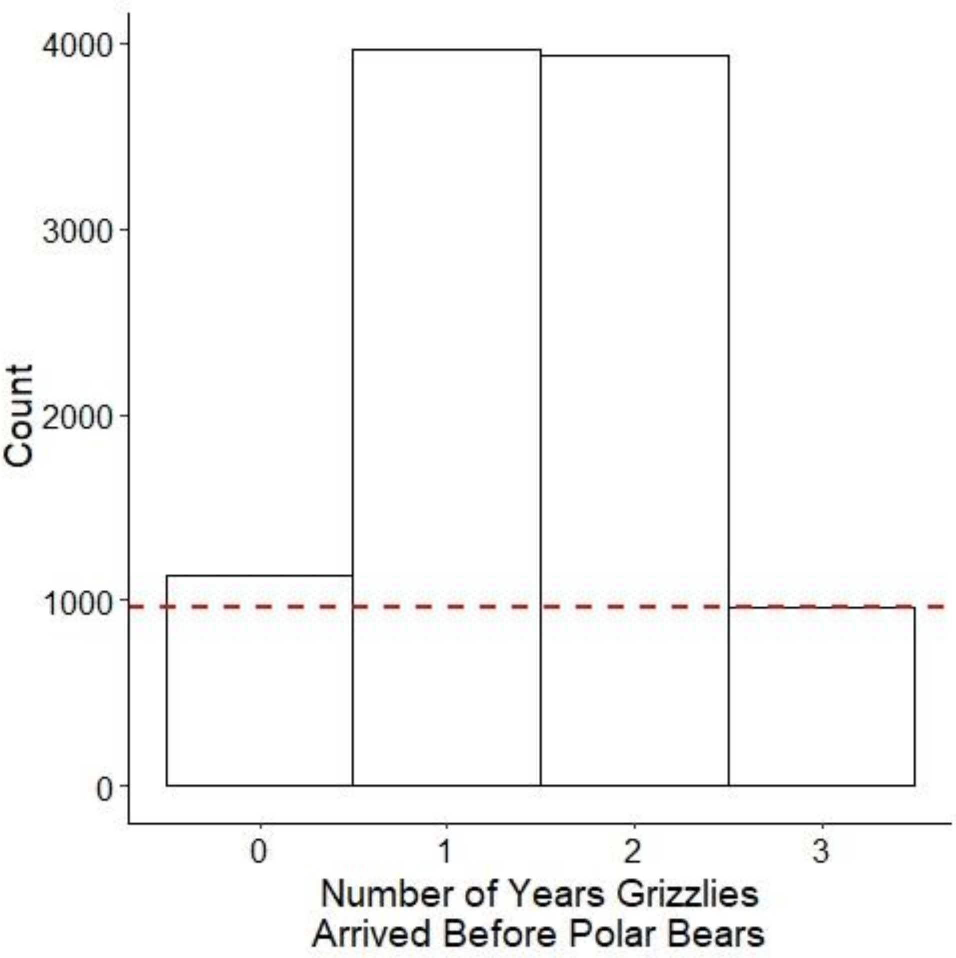
120m Plot 2

	Barren	Non-Shrub	Shrub	Total Points Allocated	User’s Accuracy
Barren	56	3	0	59	0.95
Non-Shrub	7	3	0	10	0.3
Shrub	2	2	27	31	0.87
Total Points Assigned	65	8	27	100	-
Producer’s Accuracy	0.86	0.38	1	-	-
Overall Accuracy	86.0%				
Kappa Coefficient	0.733				

Appendix C Table 3 Continued

120m Plot 3					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	67	1	0	68	0.99
Non-Shrub	5	4	0	9	0.44
Shrub	2	2	19	23	0.83
Total Points Assigned	74	7	19	100	-
Producer's Accuracy	0.91	0.57	1	-	-
Overall Accuracy	90.0%				
Kappa Coefficient	0.776				
120m Plot 4					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	62	4	0	66	0.94
Non-Shrub	5	5	0	10	0.5
Shrub	0	2	22	24	0.92
Total Points Assigned	67	11	22	100	-
Producer's Accuracy	0.93	0.45	1	-	-
Overall Accuracy	89.0%				
Kappa Coefficient	0.777				
120m Plot 5					
	Barren	Non-Shrub	Shrub	Total Points Allocated	User's Accuracy
Barren	79	2	0	81	0.98
Non-Shrub	8	2	0	10	0.2
Shrub	0	3	6	9	0.67
Total Points Assigned	87	7	6	100	-
Producer's Accuracy	0.91	0.29	1	-	-
Overall Accuracy	87.0%				
Kappa Coefficient	0.540				

APPENDIX D
(Chapter V)



Appendix D Figure 1 Simulated random dates of occurrence for grizzly (*Ursus arctos*) and polar bears (*Ursus maritimus*). Column categories represent the number of year that grizzly bears were assigned an earlier date than polar bears, based on 10,000 iterations of random draws from a uniform distribution for each year (see Methods: Phenology Comparisons). Red dashed line represents the number of datasets where grizzly bears arrived before polar bears in all three years based on random date assignments.

Appendix D Figure 2 Images of the same individual grizzly bear (*Ursus arctos*) bear with a characteristic rostral scar in the shape of an inverted “V”. A) Consuming a common eider nest (*Somateria mollissima sedentaria*) in 2015. B) Inspecting a camera in a lesser snow goose (*Anser caerulescens caerulescens*) colony in 2015. C) Consuming an eider nest in 2016. D) Inspecting a camera after consuming a goose nest in 2018

Appendix D Table 1 Number and timing for placement of trail cameras placed in common eider (*Somateria mollissima sedentaria*) and lesser snow goose (*Anser caerulescens caerulescens*) colonies each year. Nesting colonies located within Wapusk National Park, Manitoba, Canada.

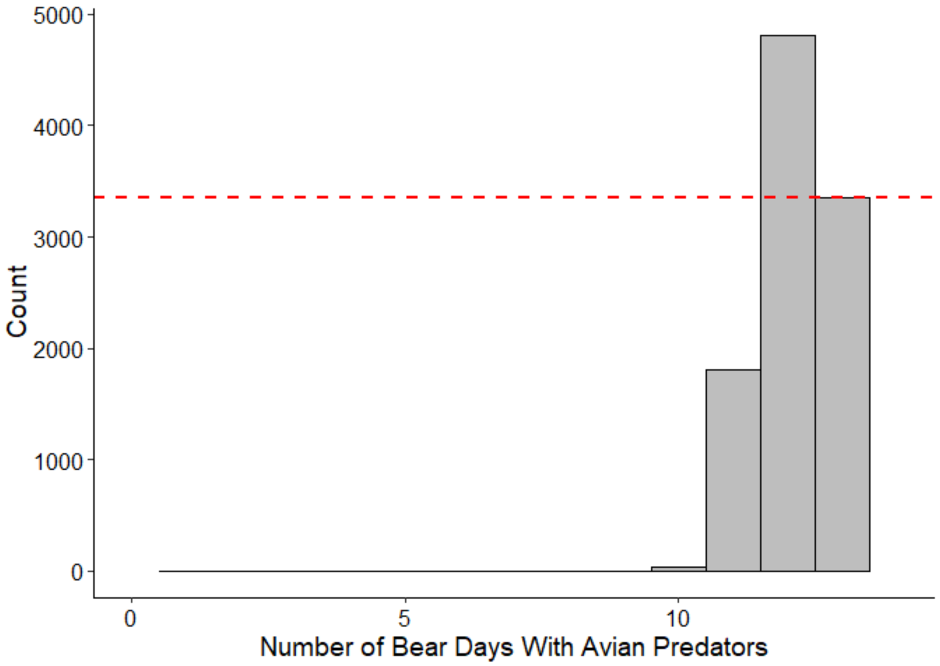
Year	**Total**	**Eider Colonies**	**Goose Colonies (Julian Date Range)**
2012	10	10 (162-176)	0
2013	69	24 (153-195)	45 (151-212)
2014	105	35 (158-207)	70 (153-195)
2015	95	38 (156-193)	57 (152-194)
2016	64	44 (158-207)	20 (152-207)
2017	67	35 (156-193)	31 (156-205)
2018	21	11 (158-187)	10 (165-175)
Total (2012-2018)	430	197	233

Appendix D Table 2 Number of bear occurrences in common eider (*Somateria mollissima sedentaria*) and lesser snow goose (*Anser caerulescens caerulescens*) colonies from 2012-2018. Nesting colonies located within Wapusk National Park, Manitoba, Canada. NA indicates colony was not monitored in that year.

Year	**Species**	**Eider Colony 1-Mast River**	**Eider Colony 2-WaWao Creek**	**Goose Colony 1-East La Pérouse Bay**	**Goose Colony 2-North of Thompson Point**	**Goose Colony 3-South of Thompson Point**	**Total**
2012	Grizzly	2	NA	NA	NA	NA	2
	Polar	0	NA	NA	NA	NA	0
2013	Grizzly	0	NA	0	0	0	0
	Polar	8	NA	2	2	0	12
2014	Grizzly	0	NA	2	0	0	2
	Polar	1	NA	2	1	0	4
2015	Grizzly	4	NA	1	0	1	6
	Polar	2	NA	0	1	1	4
2016	Grizzly	0	1	0	1	0	2
	Polar	1	0	0	0	0	1
2017	Grizzly	1	0	0	1	NA	2
	Polar	0	0	0	0	NA	0
2018	Grizzly	0	NA	2	NA	NA	2
	Polar	0	NA	0	NA	NA	0
						Total Grizzly	**16**
						Total Polar	**21**
						Total Bears	**37**

APPENDIX E

(Chapter VI)



Appendix E Figure 1 Simulated datasets with number of Bear Days where avian predators were detected. Columns represent the number of datasets where avian predators were observed on 'X' days, based on 10,000 iterations of subsetted images from Bear Days (see Methods: Avian predator association with bears). Red dashed line indicates the number of simulated datasets which matched our empirical observations of avian predators on 13 Bear Days (out of 18 total).

Appendix E Table 1 Details of Reconyx camera placement for each colony from 2013 to 2018.

Location	**Number of Cameras**	**Placement Dates**	**Retrieval Dates**
2013			
Colony 1	25	June 2nd, 6th	June 27th
Colony 2	10	May 30th	July 24th
Colony 3	10	May 30th	July 24th
2014			
Colony 1	43	June 2nd,9th	July 1st
Colony 2	15	June 3rd	July 14th
Colony 3	12	June 3rd	July 14th
2015			
Colony 1	35	June 1st, 4th, 8th	June 27th
Colony 2	11	June 5th	July 13th
Colony 3	11	June 5th	July 13th
2016			
Colony 1	10	May 31st , June 9th	June 24th, June 27th
Colony 2	10	June 4th	July 25th
Colony 3	0	NA	NA
2017			
Colony 1	21	June 5th	June 27th , July 10th
Colony 2	10	June 8th	July 24th
Colony 3	0	NA	NA
2018			
Colony 1	10	June 14th	June 29th
Colony 2	0	NA	NA
Colony 3	0	NA	NA

APPENDIX F
(Chapter VII)

Appendix F Table 1. Generalized additive model diagnostics for each predator scenario and model responses. Note that basis dimension checking results provide an approximate test of significance for residual distribution (e.g. a low P-value suggests model residuals are not randomly distributed and that additional basis functions may be required).

Predator Scenario	**Model Response**	**Number of Basis Functions**	**Effective Degrees of Freedom**	**K-index**	**P-Value***
1. Bears Only (No RPRǂ)	Overall Failure	9	7.1	0.99	0.11
2. Bears + Avian Predators (No RPRǂ)	Overall Failure	9	7.25	0.97	0.71
3. Bears + Avian Predators (No RPRǂ)	Bear Caused Failure	11	7.86	1.01	0.83
	Avian Predator Cause Failure	9	8.11	0.98	0.24
4. Bears + Avian Predators (With RPRǂ)	Bear Caused Failure	9	7.09	0.99	0.34
	Avian Predator Caused Failure	9	1.57	0.91	0.5
	Overall Failure	9	7.08	1	0.47

*Statistical significance at P<0.007 based on Bonferroni correction for multiple tests

ǂ RPR- Relative Predator Risk calculations (see section 7.3)