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## Article

### Bear presence attracts avian predators but does not impact lesser snow goose daily nest attendance

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The presence of foraging bears in Arctic breeding bird colonies has been increasingly reported in the literature, and these may constitute disturbance events which cause incubating birds to leave their nest. Avian predators may associate with bears during such events, likely to capitalize on unattended nests in the presence of bears. Here, we estimated changes in daily nest attendance of lesser snow geese *Anser caerulescens caerulescens* in the presence of foraging bears, and estimated the association between foraging bears and avian predators. We predicted decreased nest attendance by geese on days with bears, and close associations between avian predators and bears. We monitored snow goose nests with cameras from 2013 to 2018 to assess nest attendance behaviours on days when bears were in the colony compared to control days without bears. When bears were present in colonies, we estimated the probability of avian predator occurrence compared to control periods. When controlling for day of incubation and camera placement types, we found no significant effects of bears on daily nest attendance behaviours of snow geese ( $n = 85$ ). We found a significantly higher probability of observing avian predators when bears were present (0.72) compared to control periods without bears (0.11). We show that snow geese do not alter daily nest attendance in the presence of foraging bears, and suggest this is due to the presence of avian predators.

Keywords: *Anser caerulescens caerulescens*, interspecific foraging association, nesting behaviour, predation, *Ursus arctos*, *Ursus maritimus*

#### Introduction

The strongest effects of climate change are predicted to emerge from changes in biotic interactions, and this may be particularly evident through changes in predator-prey dynamics (Parmesan 2006). As predators drive the evolution of avian nesting behaviour



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(Ricklefs 1969, Montgomerie and Weatherhead 1988, Martin 1995, Schmidt 1999), climate-induced changes in predator communities (Wilmers et al. 2007, Harley 2011) may prove disadvantageous for bird populations that have evolved anti-predator behaviours for given predatory environments (Curio 1975, 1983, Martin et al. 2000, Tvardíková and Fuchs 2011, Congdon et al. 2020). Individual variation in anti-predator incubation behaviours plays a strong role in nest success (Murphy 1983, Montgomerie and Weatherhead 1988, Smith et al. 2007), which ultimately contributes to population growth/decline (Pieron and Rohwer 2010, Palmer et al. 2019). As such, investigations into behavioural responses of nesting birds to changing predator regimes should be informative to predicting population responses (Blumstein et al. 2019, Bro-Jørgensen et al. 2019).

One changing predator regime that has gained much attention is that of Arctic nesting birds and the increasing predation (Hanson 2006) of nests by polar bears *Ursus maritimus* (Donaldson et al. 1995, Rockwell and Gormezano 2009, Prop et al. 2013, 2015, Iverson et al. 2014, Gormezano et al. 2017, Madsen et al. 2019, Barnas et al. 2020, Dey et al. 2020, Jagielski et al. 2021a, b). While consumption of bird eggs by bears has been reported in the past (Canadian Wildlife Service 1992, Cooke et al. 1995, Derocher 2012), climate-induced loss of spring sea-ice is increasing the amount of time bears spend on land in recent years resulting in more frequent overlap with the incubation period of Arctic nesting birds than has likely occurred in the past (Smith et al. 2010, Iverson et al. 2014). Polar bears are not efficient predators of bird eggs as they are likely to incur energetic losses searching for eggs (Jagielski et al. 2021a, b), but even so, a relatively small number of bears can cause mass colony failure in a short amount of time (Rode et al. 2015, Gormezano et al. 2017, Jagielski et al. 2021b). Mechanisms by which birds can reduce nest loss to foraging bears has garnered little attention and should be relevant for understanding how populations will respond to increasing bear presence. For example, recent simulations of common eider *Somateria mollissima* populations predict that individuals may increase nest survival in the face of bear predation by selecting nest sites closer to mainland habitats and nesting in lower density aggregations (Dey et al. 2017, 2018) (although this has not yet been demonstrated empirically, Dey et al. 2020). For eiders, this response would incur a tradeoff whereby nesting close to the mainland increases predation risk by Arctic foxes *Vulpes lagopus* (Laurila 1989). Any behavioural responses of birds to foraging bears should therefore be considered in the context of changes in predation risk by other predators in the system.

Avian predator species have been reported to follow foraging bears in Arctic bird colonies (Barry 1967, Gaston and Elliott 2013, Iles et al. 2013, Iverson et al. 2014, Rode et al. 2015, Madsen et al. 2019), and one site where this interaction is likely to occur is in lesser snow goose *Anser caerulescens caerulescens* colonies within Wapusk National Park (Manitoba, Canada). Snow geese in this region are experiencing increasing predation by polar bears that are being forced on shore earlier due to reduced spring sea-ice extent (Rockwell and

Gormezano 2009, Rockwell et al. 2011), and grizzly bears *Ursus arctos* that are undergoing a geographic expansion into the region (Clark et al. 2019). Female geese have extremely high nest attendance rates (Thompson and Raveling 1987, Cooke et al. 1995) and will aggressively defend nests against smaller predators such as Arctic foxes and avian predators (e.g. *Larus* spp. parasitic jaegers *Stercorarius parasiticus*, common ravens *Corvus corax*) (Harvey 1971, Samelius and Alisauskas 2001, Bêty et al. 2002). Conversely, geese are more likely to leave their nest in response to large mammals such as black bears *Ursus americanus*, wolves *Canis lupus* or caribou *Rangifer tarandus* (Abraham et al. 1977, Cooke et al. 1995, Wiebe et al. 2009). The presence of large mammals likely constitute disturbance events, and in waterfowl colonies similar disturbance events from human researchers lead to increased numbers of unattended nests (Verbeek 1982, Åhlund and Götmark 1989, Bêty and Gauthier 2001) which are vulnerable to visually acute avian predators in the absence of protective parents (Harvey 1971, Inglis 1977, Prop et al. 1985, Åhlund and Götmark 1989, Götmark 1992, Opermanis 2004). If the presence of foraging bears in nesting bird colonies results in decreased nest attendance by incubating individuals, this will create additional foraging opportunities for avian predators and potentially lead to underestimates of total nest losses ultimately due to bears. As these types of interactions between foraging bears, avian predators and nesting prey species have been reported in multiple different Arctic regions (Barry 1967, Gaston and Elliott 2013, Iles et al. 2013, Iverson et al. 2014, Rode et al. 2015, Madsen et al. 2019), formal investigation into this interspecific foraging association and prey behavioural responses are warranted.

The objectives of this research are to investigate the behavioural interactions between foraging bears, avian predators and nesting lesser snow geese. Specifically, we examine whether 1) snow goose nest attendance patterns are altered by the presence of foraging bears in the colony, and 2) if there is a higher probability of observing avian predators on days when bears are in the colony. We hypothesize that the presence of bears in a nesting colony will result in reduced daily nest attendance by female snow geese due to introduced risk effects (e.g. incubating birds will leave their nest in response to the presence of bears). We also 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.

## Material and methods

### Study area

We collected data in three sub-colonies of a large nesting snow goose population along the western Hudson Bay coast in Wapusk National Park, Manitoba, Canada (Fig. 1). These colonies were located in freshwater marsh habitats. This region is predominately low-lying with the exception of sand bars

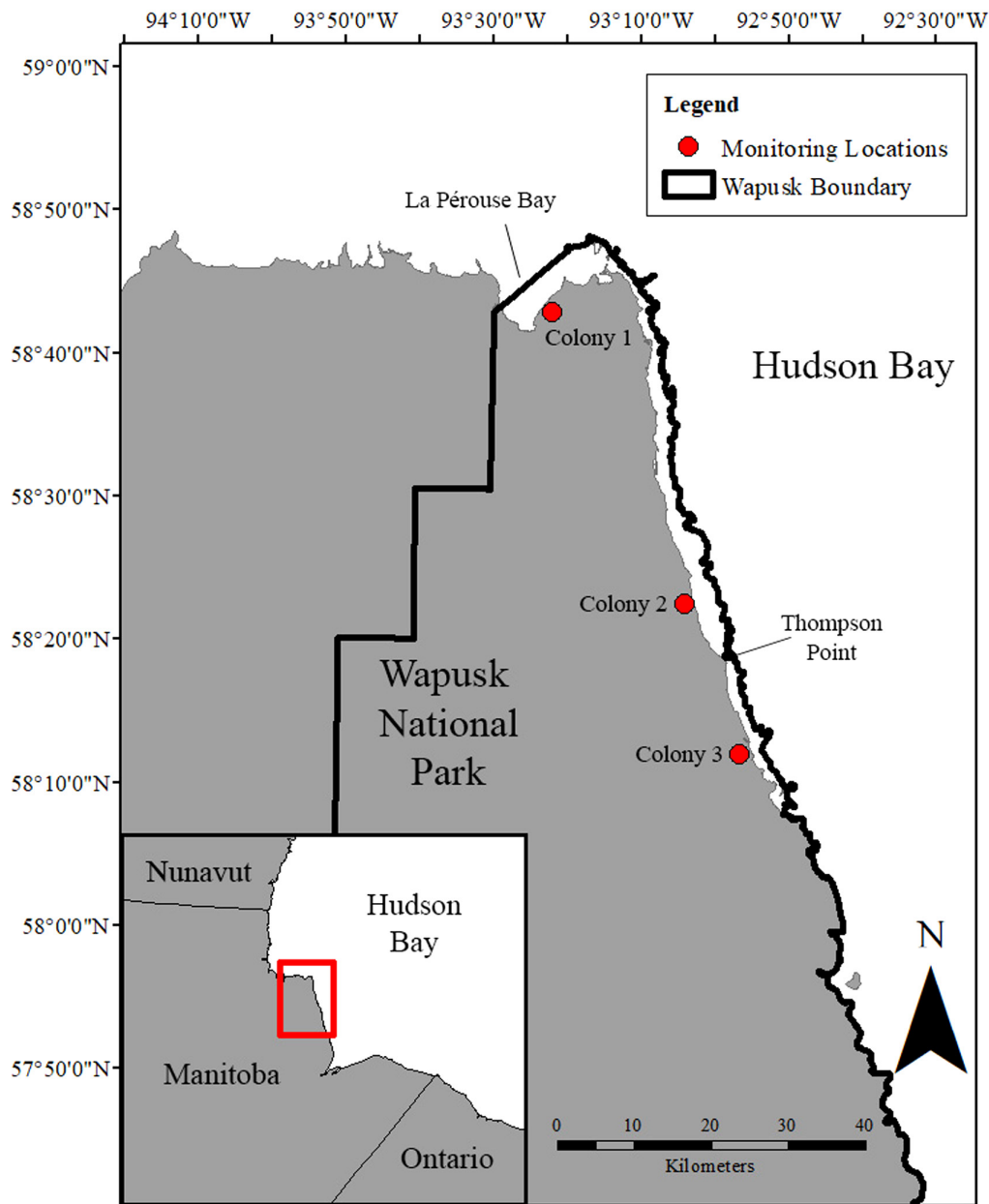


Figure 1. Trail camera monitoring locations in sub-colonies of lesser snow geese *Anser caerulescens caerulescens* within Wapusk National Park, Manitoba, Canada.

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 Shilts et al. (1987) and Brook and Kenkel (2002).

### Trail camera set up and image review

We set up a series of Reconyx PC-800 Hyperfire trail cameras throughout the three sub-colony locations from 2013 to 2018. Deployment occurred between 30 May and 14 June, and retrieval was done between 24 June and 25 July. Cameras were deployed as a part of annual snow goose monitoring protocols to document nest predation and evaluate

attendance behaviours. We placed cameras opportunistically at active nests (at least one viable egg present) across the sub-colonies. Cameras were mounted on steel poles or wooden stakes, approximately 0.5–1.5 m off the ground. Angle of cameras was 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. We placed 10–70 cameras each year, see the Supporting information 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. Note that it is possible that we missed bears that were present in the colony but did not pass through the detection zone of cameras.

### Effects of bears on snow goose nest attendance

As we were interested in the indirect impacts of bears on snow goose nest attendance behaviour, we focused our analysis of daily nest attendance on nests that were not visited by bears (and thus not consumed) within the same colony (i.e. non-target individuals within the same colony). Specifically, we examined daily nest attendance of individuals on days with bears (hereafter denoted ‘bear days’) and on the day before the bear was detected (hereafter denoted ‘control days’). We excluded nests that were not visible for the full 24 h on each day (e.g. obscured by poor visibility due to inclement weather or distance from camera), and any nests where goslings were observed on these days, since snow geese leave the nest shortly after hatch (Cooke et al. 1995). We estimated incubation date for nests within each sub-colony using an index of peak hatch date estimated by egg flotation each year (Westerskov 1950).

For each nest, we measured nest attendance as the length of on-nest (attending) and off-nest (recess) periods (mins) and the number of these behavioural events on each day using R package *lubridate* (Grolemund and Wickham 2011). To determine the effects of bear presence on daily nest attendance behaviours of snow 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 (Gamma distribution), 2) the number of nest recess events in a day (Poisson distribution) and 3) the length of individual recess events (Gamma distribution). To facilitate the use of Gamma models for total time off-nest and recess length models, we artificially increased 0 value observations to 0.001 (as Gamma distributions are not defined at values of 0 or less).

All models contained fixed effects for Day (categorical with two levels: control day and bear day), day of incubation (DOI, continuous, range: 18–31), as well as an interaction term between day and DOI. As camera angle was variable with respect to focal nests with some nests occurring close to cameras and other relatively further in the background, we included an additional fixed effect for camera placement (categorical with two levels: near and far) to estimate differences in behavioural data collected between different camera placements. All models included a random effect for snow goose nest ID, and we tested for significant improvement of model fit with this random effect structure using likelihood ratio tests. Measures of dispersion ( $\hat{c}$ ) were calculated by dividing the sum of Pearson residuals by the residual degrees of freedom (McCullagh and Nelder 1989). All nest attendance

behaviour models used a log link function and were estimated via Laplace approximation in PROC GLIMMIX (SAS Studio ver. 3.8).

### 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 ‘events’ as the time period of bear activity beginning 10 min prior to the first image of a bear in the field of view, lasting until 10 min after the last picture of a bear by a camera. We chose this short time window to capture any close association between bears and avian predators, rather than incidental observations of avian predators during a longer time window. As with the goose attendance analysis, a single person reviewed images during 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 (i.e. detection), the minimum number of avian predators and their species (if identifiable). During events on bear days, if avian predators were found to visit a snow goose nest, we evaluated if avian predators were acting as kleptoparasites or scavengers of bears. We classified kleptoparasitic behaviour as avian predators visiting unattended snow goose nests prior to bear visitation, or as visiting a nest that the bear was not observed to ever visit (as these nests would only be available to avian predators due to disturbance by a nearby bear). Scavenging behaviour was classified as avian predators visiting nests during the same time as bears, or after the bear had left.

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). 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 effect of wind speed ( $\text{km h}^{-1}$ , continuous). Hourly wind data were obtained from a weather station near Churchill Manitoba (Churchill A: 58°44′21.000″N, 94°03′59.000″W, approximately 40, 70 and 90 km west/northwest of colony 1, 2 and 3 respectively, Fig. 1), and we chose the measurement nearest to the start time of each bear event. As in the snow goose nest attendance models, we also included a fixed effect for camera placement (categorical with two levels: near and far). Candidate models were constructed for varying combinations of fixed effects (along with an intercept only model, and a fully saturated global model), and evaluated using Akaike information criterion (AICc) for small sample sizes (Akaike 1998, Burnham and Anderson 2002). All models here used a logit link function and were estimated via maximum likelihood approach in PROC GLIMMIX (SAS Studio ver. 3.8).

Observations of avian predators on bear days may be positively skewed due to larger numbers of camera images on bear



days versus 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). For bear days with avian predators, we took the entire image set for the event and assigned individual images 0s or 1s for whether or not they contained avian predators. We generated a series of 10 000 replicated datasets by randomly subsetting images from each event's bear day, based on the number of images for that 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 image set, 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 only 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, Results), which quantifies the probability that any increased observations of avian predators on bear days were an artifact of sampling error. All data management and manipulation was done using packages dplyr (Wickham et al. 2015) and data visualization was done in ggplot2 in R Studio ver. 3.4.3 (<www.r-project.org>). Statistical significance for snow goose nest attendance behaviour and avian predator occurrence was determined using  $\alpha = 0.05$ .

## Results

From 2013 to 2018 we deployed and reviewed 233 cameras across three sampling locations (Supporting information). We had 33 detections of bears, representing 17 unique days in separate goose colonies during the study years (9 polar bear, 8 grizzly bear). Polar bears were detected in 2013, 2014 and 2015, whereas grizzly bears were detected in all years except 2013.

## Effects of bears on snow goose nest attendance

We were unable to collect nest attendance behaviour from four bear days due to late arrival of bears in goose colonies (i.e. all monitored nests had hatched), and chose not to review two other days due to researcher presence in the field during the paired control days which would likely have impacted goose nest attendance behaviours. 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). We were able to collect nest attendance data on 11 paired days across 85 nests (15 in 2013, 51 in 2014, 2 in 2015, 9 in 2017 and 8 in 2018; Supporting information), resulting in 292 camera observation days. We did not observe any consumption of nests used for estimates of nest attendance.

Contrary to predictions, we failed to detect statistically significant effects of bear presence in any models of snow goose nest attendance behaviour (Table 1), and the estimated effects of bear days had large associated standard errors (Table 2). We did find significant negative effects of increasing DOI on the total time off nest ( $F_{1,204} = 5.95$ ,  $p < 0.02$ ) and recess length models ( $F_{1,1030} = 22.05$ ,  $p < 0.001$ ). We also found significant negative effects of far camera placements in the total time off nest ( $F_{1,204} = 4.22$ ,  $p < 0.05$ ) and the recess number models ( $F_{1,204} = 5.36$ ,  $p < 0.03$ ), indicating a sampling bias whereby we likely failed to observe time spent off nest by snow geese further from cameras. Our random effect structure of snow goose ID significantly improved model fit based on likelihood ratio tests for total time off nest ( $\chi^2(1) = 19.34$ ,  $p < 0.0001$ ), recess number ( $\chi^2(1) = 136.30$ ,  $p < 0.0001$ ) and recess length ( $\chi^2(1) = 156.20$ ,  $p < 0.001$ ). Inspection of conditional Pearson and Studentized residuals revealed no obvious violations of model assumptions, however for all three measures of behaviour the data were underdispersed relative to the models ( $\hat{c} = 0.29$ , 0.47 and 0.20, respectively). Concordantly data scale model estimates for all three measures of nest attendance have relatively large confidence intervals, which increase in size as DOI increases (likely reflecting the reduction in the number of nests available in the colony following peak hatch dates, Supporting information). Retrospective power analyses were performed through Monte-Carlo-style resampling schemes based on the actual experimental design and observed treatment effects (Supporting information). It was determined that over 3000

Table 1. 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.

Model	Day	DOI <sup>†</sup>	Day × DOI <sup>†</sup>	Camera angle
Total time off (mins)	$F_{1,204} = 0.42$ , $p = 0.52$	<b><math>F_{1,204} = 5.95</math>, <math>p &lt; 0.02</math></b>	$F_{1,204} = 0.53$ , $p = 0.47$	<b><math>F_{1,204} = 4.22</math>, <math>p &lt; 0.05</math></b>
Number of recesses	$F_{1,204} = 0.59$ , $p = 0.44$	$F_{1,204} = 0.18$ , $p = 0.68$	$F_{1,204} = 0.72$ , $p = 0.40$	<b><math>F_{1,204} = 5.36</math>, <math>p &lt; 0.03</math></b>
Recess length (mins)	$F_{1,1030} = 0.23$ , $p = 0.63$	<b><math>F_{1,1030} = 22.05</math>, <math>p &lt; 0.001</math></b>	$F_{1,1030} = 0.30$ , $p = 0.58$	$F_{1,1030} = 0.43$ , $p = 0.51$

\*Bold indicates statistical significance at  $\alpha = 0.05$ .

<sup>†</sup>Date of incubation.

Table 2. Fixed and random effects estimates (mean  $\pm$  standard error) 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.

Model	Family	Fixed effects estimates $\pm$ SE					Random effects estimates $\pm$ SE	
		Intercept	Bear day*	DOI	Bear day* $\times$ DOI	Far camera <sup>†</sup>	Intercept (nest ID)	Residual
Total time off (mins)	Gamma	5.12 $\pm$ 0.76	0.62 $\pm$ 0.95	-0.05 $\pm$ 0.04	-0.03 $\pm$ 0.05	-0.31 $\pm$ 0.15	0.18 $\pm$ 0.06	0.82 $\pm$ 0.07
Number of recesses	Poisson	1.32 $\pm$ 0.45	0.43 $\pm$ 0.56	0.004 $\pm$ 0.02	-0.02 $\pm$ 0.03	-0.26 $\pm$ 0.11	0.17 $\pm$ 0.04	-
Recess length (mins)	Gamma	3.47 $\pm$ 0.25	0.14 $\pm$ 0.30	-0.04 $\pm$ 0.01	-0.008 $\pm$ 0.01	-0.05 $\pm$ 0.07	0.07 $\pm$ 0.02	0.28 $\pm$ 0.01

\*Reference category = control day (day before bear was detected in the colony).

<sup>†</sup>Reference category = near cameras (focal nests that were closer to the camera than 'far cameras').

camera observation days were needed to achieve 90% power at detecting a differential number of recess events between bear days and control days, while over 8000 camera observation days were needed to achieve 90% power at detecting a differential number of recess events due to DOI.

### Avian predator association with bears

From the original 33 individual detections of bears, we excluded 7 events that took place between the hours of 18:30 and 04:30, which had poor quality images due to lighting conditions or inclement weather. We also merged 11 events that overlapped in time, because 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 to 12:50 and another ranging from 12:45 to 13:15 would become a single event ranging from 12:30 to 13:15. Events that did not overlap in time were considered separate, allowing for multiple events to occur within the same day. 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 events that were used for analyses (note that these events still represent 17 unique bear days in goose colonies).

There were more observations of avian predators being present during events on bear days than in their paired control day (Fig. 2), and more individual predator birds were detected on bear days (Table 3), but on average there were more images collected on bear days ( $t_{0.05(1),12}$ ,  $p < 0.05$ ). A randomization test indicated a small bias in the 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 (Supporting information). The most common species of avian predator present was common ravens (12/18 events), followed by herring gulls (5/18 events) and bald eagles *Haliaeetus leucocephalus* (3/18 events). We observed scavenging events by avian predators in 5/18 events compared to kleptoparasitic events in 2/18 events, and anecdotally note that avian predators appeared to flock behind bears as they moved throughout the colony rather than swooping in front of bears to attack abandoned nests before bears reached them (Fig. 3).

The candidate model for avian predator occurrence that included only the single fixed effect of day received the most support (Table 4). Other models that included additional fixed effects, beyond day, contained uninformative parameters and were not considered further (Burnham and Anderson 2002, Arnold 2010). We made predictions of avian predator occurrence from the top model, which estimated that bear presence in bird colonies has a positive effect on avian predator occurrence ( $\beta = 3.035 \pm 0.916$ ,  $F_{1,34} = 10.97$ ,  $p < 0.005$ ). Predicted probabilities of avian predator occurrence are higher on days with bears (0.72, 95% CI [0.47, 0.88]) than the day before (0.11, 95% CI [0.03, 0.37]). Examination of studentized and Pearson residual plots revealed no obvious violations of model assumptions, and we did not detect any evidence of over- or underdispersion ( $\hat{c} = 1.06$ ). A retrospective power analysis determined that over 20 camera observation events were needed to achieve 90% power at detecting a differential presence of avian predators between bear days and control (Supporting information).

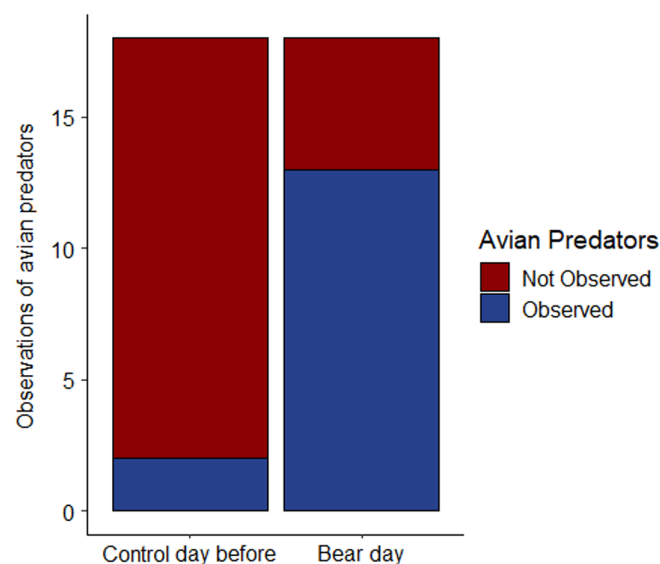


Figure 2. Number of observations of avian predators during events on the day a bear was observed and the paired control day before ( $n = 18$  bear events).

Table 3. Summary statistics of the number of avian predators (mean  $\pm$  standard deviation) observed during event time periods on bear days and paired control days.

	Any bear	Polar bears	Grizzly bears
Number of events	18	9	9
Number of birds on bear days	3.33 $\pm$ 3.48	4.89 $\pm$ 4.17	1.78 $\pm$ 1.72
Number of birds on control days	0.11 $\pm$ 0.32	0.22 $\pm$ 0.44	0 $\pm$ 0
Number of observed kleptoparasitic events	2	1	1
Number of observed scavenging events	5	2	3

## Discussion

Bear presence and foraging in nesting bird colonies is an increasingly reported phenomenon in the Arctic (Smith et al. 2010, Iverson et al. 2014, Rode et al. 2015, Clark et al. 2019,

Barnas et al. 2020). We observed close associations between avian predators and bears in nesting snow goose colonies, and suggest that this association is likely an attempt by avian predators to capitalize on colony disturbance as a result of bear presence. We failed to detect differences in snow goose



Figure 3. Observations of avian predators following bears foraging in a nesting lesser snow goose *Anser caerulescens caerulescens* colony. (A–C) A female polar bear *Ursus maritimus* and cub cause a female snow goose to abandon her nest. Following predation of the nest, four common ravens *Corvus corax* inspect the nest. (D–F) A lone grizzly bear *Ursus arctos* approaches and consumes a snow goose nest and is closely followed by at least three common ravens.



Table 4. Candidate logistic regression models for exploring factors impacting avian predator presence in a snow goose colony during events, with corresponding model rank, log likelihoods, AICc,  $\Delta$ AICc and Akaike weights.

Model	Model rank	Log likelihood	AICc	$\Delta$ AICc	Akaike weight
Day	1	-16.915	38.19	0	0.54
Day + Wind	2	-16.71	40.17	1.98	0.20
Day + Camera	3	-16.745	40.24	2.05	0.19
Day + Wind + Camera	4	-16.6	42.61	4.42	0.06
Intercept only	5	-24.45	51.02	12.83	0
Wind	6	-23.45	51.26	13.07	0
Camera	7	-24.35	53.06	14.87	0

nest attendance due to presence of bears, which may be due to high daily nest attendance evolved by snow geese to defend against avian predators.

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 (Harvey 1971, Inglis 1977, Prop et al. 1985). Larger raptors in these regions such as bald or golden eagles *Aquila chrysaetos* may occasionally kill females on nests (Cooke et al. 1995), but most avian predators require the absence of attendant parents to take eggs (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 (Harvey et al. 1968, Götmark and Åhlund 1984, Bêty and Gauthier 2001). Associations between bears and avian predators were clear in our study, and we found anecdotal evidence of avian predators acting more as scavengers rather than kleptoparasites, 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, but these lack detailed descriptions of methods for evaluating any such associations or causes of nest failures (Barry 1967, Rode et al. 2015). Gaston and Elliott (2013) report a combination of apparent kleptoparasitism by glaucous gulls *Larus hyperboreus* taking advantage of unattended thick-billed murre *Uria lomvia* nests made available by foraging polar bears, but also scavenging on unconsumed adults and chicks killed by polar bears. The complete consumption of eggs by bears without any spillage of egg contents (yolk, albumen, partially developed embryos) is unlikely, which could provide a supplementary food source for opportunistic scavenger species in Arctic environments. Any leftover contents could provide potentially low-cost, high-reward energetic resource for scavengers, especially if this resource is compounded across hundreds or thousands of snow goose nests in the region.

The behaviours exhibited by avian predators in association with foraging bears 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 mobbing of avian predators (Gilchrist and Gaston 1997). However, the inability to physically defend against bears may be a causal factor in the '...mass panic of adult murre [in response to polar

bears]' described by Gaston and Elliott (2013): p. 47, which creates foraging opportunities for kleptoparasitic gulls in the absence of protective parents. 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 vicinity of a disturbance source. Bêty and Gauthier (2001) hypothesized that investigator disturbance in a greater snow goose colony had a larger 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, we predict that bird colonies with higher nest densities may be more vulnerable to nest loss by avian predators during bear foraging.

For snow goose colonies along western Hudson Bay, the general lack of scavenging and kleptoparasite events resulting from avian predators on bear days in our study was likely mitigated due to high nest attendance by geese on these days. We originally hypothesized that geese would leave their nest in response to bear presence in their colony, but we did not observe this phenomenon while controlling for effects of DOI and camera placement type. 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 et al. 2000, Kovařík and Pavel 2011), which may be a more relevant strategy in predator-prey relationships where prey species are unable to physically defend against larger predators (Montgomerie and 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 a conspicuous attendant female (Samelius and Alisauskas 2001). It would seem that 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 (i.e. parent geese). Conversely, many Arctic shorebird species will leave their nest and perform distraction displays to lure predators away (Smith et al. 2012, Humphreys and Ruxton 2020) and shorebirds have evolved camouflaged eggs which reduces nest discovery in the absence of attendant parents (Skrade and Dinsmore 2013). However, snow geese with conspicuously white eggs must account for other predators with varying foraging patterns when leaving their nest, and this strategy would put nests at greater risk to associated avian predators with an aerial vantage point who can quickly cue in on unguarded nests (Opermanis 2004). Therefore, we suggest that our finding of geese maintaining their high nest attendance in the presence of bears is the result of evolved behaviours to reduce predation by associated avian predators in the area. This suggestion may seem to contradict previous work that show geese leave their nest far in advance of large mammal predators (Abraham et al. 1977, Cooke et al. 1995, Wiebe et al. 2009), however we emphasize here that we examined changes in daily nest attendance rates



in non-target individuals rather than proximate responses of individuals targeted by bears.

We observed variation in behavioural responses by individual geese, which may be due to differences in age classes of geese in our sample (although we were unable to measure this). Younger, less experienced females are less attentive to their nests, and may more readily leave their nests due to perceived predation risks (Cooke et al. 1981, 1995), possibly in favour of future breeding opportunities (Curio 1983, Montgomerie and 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, Jagielski et al. 2021a). However, the younger, less attentive female geese may be disproportionately at risk to any secondary predators associated with foraging bears due to increased time spent off nest. This difference in nest attentiveness among age classes 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 (Rockwell et al. 1993, Cooke et al. 1995). In this case, the nests that would have been most susceptible to avian predation in our study (through decreased nest attentiveness) may have already been removed from the population sample before observations began. Nest failure of younger geese early in the season 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 beneficial in understanding the relationship between individual age, nest attendance and bear presence.

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## Author contributions

**Andrew F. Barnas:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Brian J. Darby:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Software (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **David T. Iles:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Methodology (equal); Software (equal); Writing – original draft (equal); Writing – review and editing (equal). **David N. Koons:** Data curation (equal); Funding acquisition (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Robert F. Rockwell:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Christina A. D. Semeniuk:** Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Susan N. Ellis-Felege:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.vdncjxwxs>> (Barnas et al. 2021).

## Supporting information

The supporting information associated with this article is available from the online version.

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