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EFFECTS OF NEST VISITS ON PREDATOR ACTIVITY AND PREDATION RATE IN A GREATER SNOW GOOSE COLONY

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Abstract.—We assessed the effect of nest visits by researchers on the activity of nest predators and predation rate of eggs in a High Arctic Greater Snow Goose (*Chen caerulescens atlantica*) colony. The study was conducted in years of moderate (1996) and low (1997) overall nest predation rate. We first compared activity rate (number of presences per h) and behavior of nest predators in the colony with and without investigator disturbance. In one year out of two, activity rate and time spent in the colony were higher during nest visits than under undisturbed conditions for Glaucous Gulls (*Larus hyperboreus*) and Parasitic Jaegers (*Stercorarius parasiticus*). Moreover, presence of investigators significantly increased (4.8 times) the probability of nest attack by predators in one year. Nevertheless, the immediate revisit technique showed that the percentage of goose eggs robbed by predators in monitored nests was low (<0.7%) during a nest visit. In addition, we found no significant difference in mean clutch size at the end of incubation or nesting success between nests that were visited repeatedly (8 visits) and those less disturbed (<3 visits). Although some predators can be attracted by and take advantage of the presence of investigators, our results indicate that nesting parameters estimated for this snow goose colony are not biased by nest visits. However, the effect of investigator disturbance could be more important in other arctic nesting bird species that are unable to successfully defend their nest against predators or when predation pressure is very high.

EFECTOS DE VISITAS A LOS NIDOS SOBRE LA ACTIVIDAD DE DEPREDADORES Y TASAS DE DEPREDACIÓN EN UNA COLONIA DE *CHEN CAERULESCENS ATLANTICA*

Sinopsis.—Investigamos el efecto de las visitas de investigadores a los nidos en la actividad de depredación y de tasas de depredación de huevos en una colonia de *Chen caerulescens atlantica* en el ártico alto. El estudio se condujo en años de tasa de depredación total moderada (1996) y baja (1997). Al principio comparamos la tasa de actividad (número de presencias por hora) y conducta de los depredadores en la colonia con y sin disturbios de investigadores. En uno de dos años, la tasa de actividad y el tiempo en la colonia fueron mayores durante las visitas a los nidos que en colonias sin disturbios de *Larus hyperboreus* y de *Stercorarius parasiticus*. Más aún, la presencia de investigadores aumentó significativamente (4.8 veces) la probabilidad de ataques a nidos por depredadores en un año. Sin embargo, la técnica de revisitar inmediatamente mostró que el porcentaje de huevos de *Chen caerulescens atlantica* robados por depredadores en nidos bajo monitoreo, fue menor (<0.7%) durante una vista al nido. Asimismo, no hallamos diferencias significativas en el promedio del tamaño de la camada al final de la incubación o en el éxito en anidar entre nidos que fueron visitados repetidamente (8 visitas) y los que fueron menos molestados (<3 visitas). Aunque algunos depredadores pueden atraerse por la presencia de investigaciones y pueden tomar ventaja de eso, nuestros resultados indican que los parámetros de anidaje que se estimaron para la colonia de *Chen caerulescens atlantica* no fueron viciados por visitas a los nidos. Sin embargo, el efecto de disturbios por investigadores podrían ser más importantes en otras especies de aves árticas que no son capaces de defender exitosamente sus nidos ante depredadores o cuando la presión de depredación es muy alta.

Disturbance by researchers can potentially bias measures of nesting parameters in birds. For instance, repeated visits to nests may increase nest abandonment or predation rates (Livezey 1980; Westmoreland and Best

1985). Although the "biological uncertainty principle" recognizes the possibility that observers may inadvertently influence nesting success, it is almost impossible to determine failure rates of nests without visiting them (Lenington 1979). In a review of the effect of nest visits on breeding birds, Götmark (1992) concluded that researchers seeking unbiased estimates of nesting parameters should evaluate their own impact. Nevertheless, there are still few studies that use adequate methods to determine the effect of nest visits (Maye-Gross et al. 1997). In addition, many questions about the proximate mechanisms affecting nesting failure remain unanswered, particularly the impact of human activity on the behavior of nest predators (Strang 1980; Götmark et al. 1990; Götmark 1992; Mayer-Gross et al. 1997).

Many factors, including tolerance of the study species to disturbance, degree of disturbance, community of predators, and habitat structure, can influence the impact of nest visits (Major 1990; Götmark 1992; Hannon et al. 1993; Armstrong 1996; Olson and Rohwer 1998). The effect of the activity of researchers can also vary annually in relation to changes in biotic or abiotic factors (Ellison and Cleary 1978; White and Thurow 1985; Rodway et al. 1996; Ortega et al. 1997). Finally, species nesting in open habitats can be especially susceptible to disturbance by investigators because avian predators can more easily detect exposed eggs or people searching for nests (Götmark and Åhlund 1984).

We assessed the effect of nest visits by researchers on the activity of predators and predation rate in a High Arctic Greater Snow Goose (*Chen caerulescens atlantica*) colony. First, we compared the activity rate and behavior of predators in the presence and absence of investigators in the colony. Second, we tested for potential loss of eggs as a result of displacement of territorial goose pairs during visits using the immediate revisit technique. Third, we evaluated the impact of nest visits on partial clutch predation by comparing mean clutch size of control nests (undisturbed) with that of nests visited several times. Finally, we compared nesting success of highly and lightly disturbed nests.

STUDY AREA AND METHODS

We conducted the study in 1996 and 1997 at the migratory bird sanctuary of Bylot Island (72°53′N, 78°55′W), Nunavut Territory, Canada. We made observations and monitored nests in a large but patchy goose colony (typically >4000 nests) located around a narrow valley (ca. 0.5 km wide) surrounded by low hills with gentle slopes and extensive upland habitat. The nesting habitat had a low and sparse plant cover dominated by arctic willow (*Salix arctica*), bell-heather (*Cassiope tetragona*), and various graminoids (see Lepage et al. 1996 and Tremblay et al. 1997 for details of the areas).

The Greater Snow Goose is a ground-nesting precocial species. It is single-brooded and does not renest after loss of a clutch (Lepage et al. 2000). Nest initiation is typically very synchronized, and about 90% of the nests are initiated within eight d (Lepage et al. 1996). Duration of incubation period is approximately 24 d (Poussart et al. 2000). Nest desertion is rare (estimated at <2%; Tremblay et al. 1997), and predation is the main cause of nest failure for geese on Bylot Island (Lepage et al. 1996; Bêty et al., in press). Goose nest predators are, in decreasing order of importance, arctic foxes (*Alopex lagopus*), Parasitic Jaegers (*Stercorarius parasiticus*), Glaucous Gulls (*Larus hyperboreus*), and Common Ravens (*Corvus corax*) (Bêty et al. 2001).

General field methods.—Goose nests were found by systematic searches during the laying or early incubation period and marked with orange wooden sticks at a distance of 10 m from the nest. Eggs were individually marked with waterproof black ink. Nests were located with a Global Positioning System receiver (GARMIN GPS-75; ±25 m). Local nest density was defined for each goose nest as the total number of nests found at any time within a 1-ha circle centered on the focal nest (minimum nest density according to this method was thus 1 nest ha^{-1}; Lepage et al. 1996). This provided an index of spatial and temporal variations in nest aggregation and genuine nest density. Nest visits were conducted by two or three people walking close together (generally <30 m between each person) and eggs were covered with nest material at each visit. Typically, a researcher stayed a few minutes (<5 min) at a nest to collect data (count, mark, or weigh eggs or young). When a fox approached to 100 m of researchers during nest visits, they left the disturbed area until the fox moved far away (>1 km).

Response of predators.—In 1996 and 1997, we compared the activity rate (number of presences per h) and behavior of predators in the goose colony during nest visits by investigators (treatment) and when investigators were absent (undisturbed conditions: control). All observations were conducted at one experimental plot (ca. 50 ha) where conditions (habitat and nest dispersion) were typical of those encountered in the overall goose colony. Each year, four observation sessions of 240 min were conducted without investigator presence in the goose colony (1996: 24, 30 June, 4 and 6 July; 1997: 24, 28 June, 3 and 5 July) and were used as control. A total of five sessions were done during nest visits by investigators, i.e., the treatment (three sessions in 1996: 25, 26 June and 9 July; two sessions in 1997: 21 June and 6 July). Duration of observations for the treatment ranged from 90 to 180 min per session and was a function of the time that investigators were in the colony. Overall, 16 h of observations were conducted under undisturbed conditions in each year, and 6.25 and 5 h during nest visitations in 1996 and 1997, respectively. All sessions occurred during the incubation period between 0700 and 1100 because normal nest visits occurred between 0700 and 1800 and were concentrated in the morning.

Observations were conducted from a blind located at the highest elevation point in one corner of the experimental plot. Observations generally started 10 min after entering the blind because predators were unaffected by our presence as soon as we disappeared inside the blind. We recorded the number of predators staying within the plot for at least

1 min (including predators flying over the experimental plot). The 1-min criterion was used to eliminate the few observations of avian predators that were traveling at high speed across the plot and clearly not foraging. We noted the time spent in the plot (±1 min). The behavior of predators was classified as ''attack'' (predator attempting to rob one or more goose nests during its presence) or ''passage'' (presence without nest attack). Although predators were not marked, individuals that were seen moving out and then back inside the plot were counted only once. No predators were breeding on the plot. We used binoculars to detect and identify predators and a spotting scope to determine the outcome of their attacks. Nest attacks were considered successful if at least one egg was preyed upon.

Immediate revisit technique.—Goose nests used for the immediate revisit experiments (Sedinger 1990) will be referred to as the highly disturbed nests. All nests used in this experiment were located at >1 km from the 50 ha experimental plot used to study predator activity (see above). Following an initial visit to all nests, investigators moved far enough (>300 m) to allow nesting pairs to return to their territories. When virtually all pairs had returned (≤ 30 min after the end of the initial visit), nests were immediately revisited. The number of eggs depredated between the two visits was recorded. In 1996 and 1997, we did immediate revisits three times during the incubation period (early, mid and late incubation stages). The behavior of geese in response to researchers visiting nests was recorded at nests randomly selected among the highly disturbed group (1997 only). We recorded the distance of the observer from the nest when the female flushed (estimated to nearest 5 m) and the presence or absence of nest material over the eggs when researchers arrived at the nest. Covered nests were defined as nests with $>75\%$ of the clutch covered by nest material.

Disturbance and partial clutch predation.—In 1997, to evaluate the effect of nest visits on partial clutch predation, we compared mean clutch size of highly disturbed versus undisturbed nests. All undisturbed nests were located at >150 m from any disturbed area (150 m is the maximum distance at which females flushed when approached during incubation; see results). Highly disturbed nests were those monitored for the immediate revisit experiment and were visited a total of eight times, once at the end of laying and seven times during the incubation period (including three revisits). Undisturbed nests were visited only once at the end of the incubation to sample clutch size, and no nest markers were used. We compared the date at which incubation started (incubation date) for a random sample of undisturbed and disturbed nests. Incubation date was determined using a linear relationship between an egg density index [mass/(length $\times$ breadth)^2] and stage of incubation (Lepage et al. 1996; Gauthier, unpubl. data). In Greater Snow Geese, there is a steep seasonal decline in clutch size (-0.20 egg d^{-1}; Lepage et al. 2000). Because median incubation date did not differ either between undisturbed and highly disturbed nests $\bar{x} = 14.5$ June, range 10–20, $n = 19$ and $\bar{x} = 14$ June, range 10–21, $n = 38$, respectively; $Z = -0.33$, $P = 0.74$ Wilcoxon's rank sum test, we assumed that these two groups had the same initial mean clutch sizes.

Disturbance and total nest failure.—To evaluate the effect of nest visits on total nest failure, we compared nesting success of lightly and highly disturbed nests in 1997. Lightly disturbed nests were visited only once or twice during incubation. Highly disturbed nests were those used for the immediate revisit experiment and were visited seven times during incubation (see above). All nests were found during the laying or early incubation period and were visited during the hatching period to determine their fate. A nest was considered successful if at least one egg hatched. For nests found after the laying period, laying date (start of egg laying) was determined by estimating incubation stage (see above) or by backdating from hatching date (Lepage et al. 1999). Total clutch size was defined as the total number of eggs marked in a nest. Nests completely depredated during egg laying were excluded from analysis of clutch size.

Data analysis.—Generalized Linear Models (procedure GENMOD of SAS Institute Inc. 1996) were used to examine the response of predators to investigator presence in the colony. Poisson regressions were used to model the activity rate of predators. Poisson regressions are well suited for counts where the variance increases with the mean, as was the case here (Agresti 1996). The loglinear model used was

$$\log(\mu) = \log(\mathrm{dr}) + \beta_0 + \beta_1(\mathrm{Year}) + \beta_2(\mathrm{Treatment}) + \beta_3(\mathrm{Year}\cdot\mathrm{Treatment})$$

where μ is the expected number of predators observed, dr is the duration of observation (min), and β_i are the regression coefficients. The model included the variables Year (1996 = 1, 1997 = 0), Treatment (nest visit = 1, control = 0) and the interaction term. The deviance was used to evaluate model fit (Agresti 1996). Overdispersion (defined as greater variability than predicted by the random component of the model) is common in the modeling of Poisson counts (Agresti 1996). If data were overdispersed (deviance/df >2), we used an overdispersion parameter to adjust standard errors and likelihood ratio statistics (DSCALE option of the GENMOD procedure). Standard errors of parameter estimates are inflated in models using an overdispersion parameter (SAS Institute Inc. 1993), which increases risks of type II error. In these cases, we also analyzed each year separately and suppressed the overdispersion parameter if the data fitted the model well (deviance/df <2). Likelihood ratios were used to test the significance of a variable in the model with other variables already included. If the interaction term was not significant, it was deleted from the model. Exponentiating the slope (β) associated with the treatment variable gave the ratio of predator activity rate observed in the treatment relative to control (a ratio of 1 means no effect of treatment; Agresti 1996). The 95% confidence intervals for parameters were based on the profile likelihood function (LRCI option of the GENMOD procedure).

The length of time predators stayed in the plot was compared using Wilcoxon's rank sum tests (Siegle and Castellan 1988). In this analysis, we pooled data for all sessions of observation for control and treatment to increase sample size.

We used logistic regression (LOGISTIC procedure, SAS Institute Inc. 1996) to evaluate the impact of investigator presence in the colony on the probability of nest attack by a predator (attack = 1, passage = 0). This model incorporated the variables Year (1996 = 1, 1997 = 0), Treatment (nest visit = 1, control = 0) and the interaction term. If the interaction term was not significant, it was deleted from the model. Because the total number of attacks was low (zero cell count: Hosmer and Lemeshow 1989), we pooled data for all predator species and sessions of observation for control and treatment. Exponentiating the slope (β) associated with the treatment gave the ratio of the treatment effect relative to control (a ratio >1 means that probability of nest attack by predators is higher for treatment relative to control). The RISKLIMITS option of the LOGISTIC procedure was used to obtain the 95% Wald confidence intervals for these ratios.

Laying dates were compared using Wilcoxon's rank sum tests. We compared mean nest density and mean clutch size using t-tests. When variances were heteroscedastic, an approximate t-test based on unequal variances was used to test for differences in group means. Logistic regression was also used to evaluate the effect of repeated nest visits on nesting success (success = 1, failure = 0). This model incorporated the variables Type (highly disturbed nests = 1, lightly disturbed nests = 0), Density (nest density calculated for each goose nest) and the interaction term. Because we showed in an earlier analysis that the fate of a goose nest is independent of the fate of its nearest neighbors (Bêty et al. 2001), we considered each goose nest as an independent observation in all analyses. Statistical tests were two-tailed and significance levels were set at 0.05. Values provided are mean ± SE unless stated otherwise.

RESULTS

Percentage of successful nests in the monitored colony was near average in 1996 (61%) and high in 1997 (86%; 1994 to 1999, mean ± SD = 60 ± 24%; range, 22 to 86%; Bêty et al. 2001). Goose nest density was higher in 1997 than in 1996, with 5.7 ± 0.2 and 4.2 ± 0.2 nests ha^{-1}, respectively ($t = 5.59$, df = 539, $P < 0.0001$; 1994 to 1999, mean ± SD = 5.5 ± 1.1; range, 4.1 to 6.7; Bêty et al. 2001).

Response of predators.—The impact of investigator presence on the activity rate of avian predators was variable across predator species and years (Fig. 1, Table 1). In 1997, the activity estimate for Glaucous Gulls was 11.9 times (95% CI = 5.5 to 29.7) higher during nest visits than under undisturbed conditions. However, activity of gulls was not affected by nest visits in 1996 (ratio = 0.7, 95% CI = 0.3 to 1.6). In contrast, we detected a slight increase in Parasitic Jaeger activity rate during nest visits only in 1996 (ratio = 2.6, 95% CI = 1.18 to 5.57). No significant effect of investigator presence on the activity of ravens was detected. In 1997, gulls and jaegers spent more time in the plot during nest visits than under undisturbed conditions (gulls, 3.7 ± 0.7 min [n = 26] vs 1.1 ± 0.2 min [n = 7], $Z = 2.77$, $P = 0.006$; jaegers, 2.3 ± 0.9 min [n = 3] vs 1.2 ± 0.1 [n = 18], $Z = 1.96$, $P = 0.05$, respectively, for disturbed and undisturbed conditions). The time spent in the plot was not significantly affected by investigator disturbance for ravens in 1997 and all avian predator species in 1996 (all $P > 0.10$). The total number of arctic foxes observed on the experimental plot was too low ($n = 12$) to allow statistical analysis.

About 10% of predator observations in the colony resulted in attacks on goose nests (Table 2). The impact of nest visits on the behavior of predators was different in 1996 and 1997 (as shown by the significant interaction term, Table 3). In 1997, the probability that a predator attacked a nest was 4.8 times (95% CI = 1.4 to 17.0) higher during nest visits than during undisturbed conditions. In contrast, the probability of attack tended to be lower during nest visits in 1996 but the difference was not significant (ratio = 0.4, 95% CI = 0.1 to 1.6). Nevertheless, the total number of successful attacks was low in both years. In 1996, only two out of four nest attacks observed during nest visits were successful compared to five out of 17 under undisturbed conditions. Comparable figures in 1997 were three successes out of 11 nest attacks during nest visits and zero out of five under undisturbed conditions.

Immediate Revisit Technique.—Female geese flushed from their nest when an investigator approached (flushing distance, 75 ± 5 m; range, 15-150 m; $n = 32$). When disturbed, some females covered their nest with material before leaving (32%, 41% and 47% of the females during the early [n = 95], mid [n = 95] and late [n = 94] incubation periods, respectively). Typically, males and females stayed within 150 m when an investigator was around their nest and they came back near their nest (<10 m) less than 10 min after the investigator's departure. Virtually all nesting pairs were at their nest, or close to it, after 30 min. In both 1996 and 1997, nest predation was rare during nest visits by investigators. Predation events that occurred during a nest visit were always partial clutch losses of 1 egg/nest. Percentage of eggs lost during nest visits ranged from 0.0 to 0.7% and did not vary within incubation stage or between years (Table 4).

Disturbance and partial clutch predation.—Average clutch size of highly disturbed nests declined slightly during the incubation period (early incubation, 3.9 eggs ± 0.1; end of incubation, 3.8 eggs ± 0.1; paired t-test, $t = 2.5$, $P = 0.01$, $n = 94$). Nest density did not differ between undisturbed (5.7 ± 0.4 nests ha^{-1}, $n = 63$) and highly disturbed nests (4.9 ± 0.2, $n = 94$) at the end of incubation ($t = 1.54$, df = 100.4, $P = 0.13$). Despite repeated nest visits, we did not detect a difference in average clutch size recorded at the end of the incubation period between undisturbed (3.8 eggs ± 0.1, $n = 63$) and highly disturbed nests ($t = 0.04$, df = 155, $P = 0.97$; difference between means, 0.006; 95% CI = −0.345 to 0.357). We considered a difference in clutch size of 0.38 egg (10%) as a

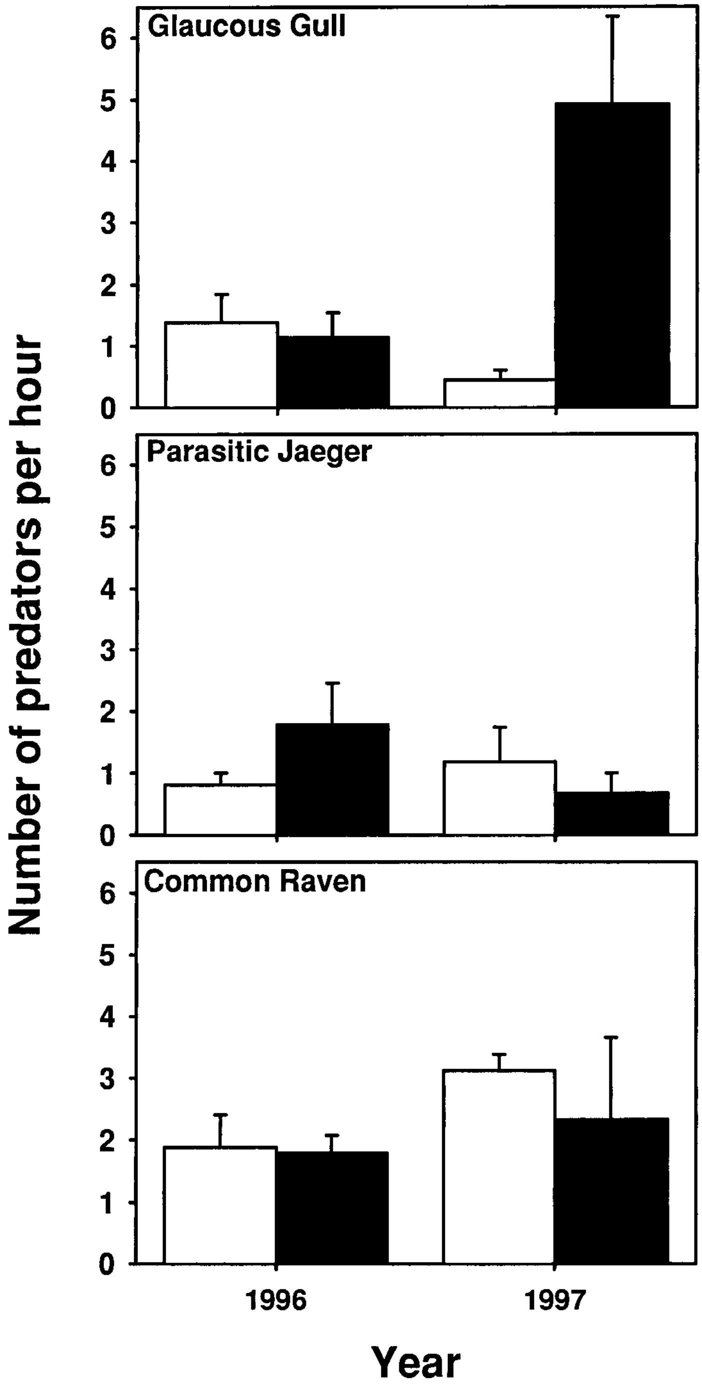
Glaucous Gull
Parasitic Jaeger
Common Raven
0
1
2
3
4
5
6
Number of predators per hour
1996
1997
Year

TABLE 1. Regression models[a] estimating the impact of nest visits (treatment) on the activity rate of avian predators observed in a Greater Snow Goose colony during the incubation period, Bylot Island, Nunavut Territory, 1996–1997.

Predator species	Year	Variables	df	β	SE	χ^2	P
Glaucous Gull	1996–97	Intercept	1	−4.92	0.38		
		Year	1	1.15	0.43	0.75	0.385
		Treatment	1	2.48	0.43	10.12	0.002
		Year * Treatment	1	−2.84	0.63	25.28	<0.001
Common Raven	1996–97	Intercept	1	2.98	0.14		
		Year	1	−0.46	0.20	5.42	0.020
		Treatment	1	−0.09	0.23	0.16	0.685
		Year * Treatment	1	0.21	0.46	0.20	0.653
Parasitic Jaeger	1996	Intercept	1	4.30	0.28		
		Treatment	1	0.94	0.40	5.54	0.02
	1997	Intercept	1	−3.92	0.44		
		Treatment	1	−0.68	1.20	0.38	0.54

[a] Models assume that predator number follows a Poisson distribution. The fit of the full model was satisfactory for the gull and raven data (deviance = 15.4 and 12.5, respectively, df = 9). A correction for overdispersion was used for the Parasitic Jaeger data in 1997 (deviance = 15.0, df = 4) but not in 1996 (deviance = 5.2, df = 5).

minimum for a biologically significant effect in our system (see Steidl et al. 1997). This value is lower than the inter-annual variations observed in clutch size (1994 to 1999, mean ± SD = 3.8 ± 0.4 eggs; range, 3.1 to 4.2 eggs; Bêty et al. 2001). Because the 95% confidence interval of the observed difference between means excludes this value, we therefore consider the null hypothesis of no biologically significant effect of nest visits on partial nest predation to be true.

Disturbance and total nest failure.—At the beginning of incubation, mean nest density was slightly higher in lightly disturbed nests (5.7 ± 0.2 nests ha^{-1}, $n = 291$) than in highly disturbed nests (5.0 ± 0.2, $n = 98$; $t = 2.33$, df = 225.6, $P = 0.02$). Median laying date was similar between the two groups (10 June, range 8–13, $n = 291$, for lightly disturbed and 11 June, range 7–19, $n = 39$, for highly disturbed; $Z = 1.10$, $P = 0.27$). Mean initial clutch size was slightly higher for lightly disturbed nests (4.2 ± 0.1, $n = 258$) than for highly disturbed nests (4.0 ± 0.1, $n = 95$; $t = 1.96$, df = 351, $P = 0.05$). Nesting success was not related to nest density ($\chi^2 = 0.16$, df = 1, $P = 0.69$) and did not differ between highly (87.8%, $n = 98$) and lightly disturbed nests (85.6%, $n = 285$; $\chi^2 = 0.46$, df = 1, $P = 0.50$; interaction term, $P = 0.88$, was dropped from the model). If

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FIGURE 1. Activity rate of avian predators (mean ± SE number of predators observed per hour) at a Greater Snow Goose colony during nest visits by investigators (treatment: *black bars*) and in absence of investigator disturbance (control: *white bars*) during the incubation period, Bylot Island, Nunavut Territory, 1996–1997 (control, $n = 4$ in both years; treatment, $n = 3$ in 1996 and $n = 2$ in 1997.

TABLE 2. Behavior of nest predators at a Greater Snow Goose colony during nest visits by investigators, (treatment) and in the absence of investigator disturbance (control), Bylot Island, Nunavut Territory, 1996–1997.

	1996		1997	
Behavior	Control	Treatment	Control	Treatment
Attack[a]	14 (14%)	3 (7%)	4 (4%)	8 (17%)
Passage[b]	83 (86%)	41 (93%)	92 (96%)	38 (83%)
Total	97	44	96	46

[a] Predator attempting to rob ≥1 goose nest during its presence in the colony.

[b] Presence of a predator in the colony without a nest attack.

we again consider a difference of 10% as a minimum for a biologically significant effect, then the 95% confidence interval of the observed difference between nesting success in highly disturbed and lightly disturbed areas (2.2%, 95% CI = −5.5 to 9.9%) excludes this value. This threshold of 10% is much lower than the inter-annual variations observed in snow goose nesting success (see above). We therefore consider the null hypothesis of no biologically significant effect of repeated nest visits on nesting success to be true.

DISCUSSION

We found that presence of researchers in a Greater Snow Goose colony affected the activity of nest predators (Glaucous Gulls and, to a lesser extent, Parasitic Jaegers), but these effects were variable among years. Moreover, investigator presence increased probability of nest attack by predators in only one year out of two. Few papers have reported data on the behavior of nest predators in response to visits by researchers (Götmark 1992; Mayer-Gross et al. 1997). Previous studies also suggested that jaegers and gulls could be attracted to disturbed areas in open habitats and sometimes take eggs in unattended nests of other waterfowl species (Strang 1980; Götmark and Åhlund 1984). Unlike Götmark and Åhlund (1984), we did not find evidence that corvids were repelled by human presence at our study site.

Despite the effect of human presence in the colony on the behavior of predators, our observations showed that nest visits had little effect on

TABLE 3. Logistic model estimating the impact of nest visits (treatment) on the probability of nest attacks by predators in a Greater Snow Goose colony during the incubation period, Bylot Island, Nunavut Territory, 1996–1997.

Variables	df	β	SE	χ^2	*P*
Intercept	1	−3.14	0.51	37.69	<0.001
Year	1	1.36	0.59	5.34	0.02
Treatment	1	1.58	0.64	6.04	0.01
Year * Treatment	1	−2.41	0.92	6.82	0.009

TABLE 4. Number of eggs lost during visits to Greater Snow Geese nests. Numbers were estimated by the immediate revisit technique conducted during early, mid, and late incubation stages, Bylot Island, Nunavut Territory, 1996–1997.

Incubation stage	Year	n[a]	No. of eggs Before	After	Lost
Early	1996	88	301	300	1
	1997	95	374	374	0
Mid	1996	85	285	283	2
	1997	95	368	367	1
Late	1996	82	275	275	0
	1997	94	360	359	1

[a] n = number of nests.

Greater Snow Goose nest predation. First, few successful nest attacks by predators were observed during nest visits. Second, the percentage of eggs depredated during nest visits was extremely low (<0.7%) in both years of the study. Third, mean clutch size at the end of incubation did not differ between highly disturbed and undisturbed nests. Finally, repeated nest visits did not reduce nesting success. Therefore, even if predators can sometimes rob a few eggs during nest visits, the overall impact on nesting parameters seems to be low. However, because we lack spatial replications of our experiments and we conducted our study in years of moderate to low nest predation rate, we must be careful with generalization to other areas and years.

Under undisturbed conditions, Greater Snow Goose breeding pairs are highly attentive to their nests (Reed et al. 1995), and females cover their eggs with nest material before departing for a recess. They can successfully defend their clutch against foxes and avian predators when they are at their nest or close to it (<10 m; Bêty et al. 2001). However, when researchers visit nests, nesting pairs vacate their territory and leave their clutch without protection. Consequently, human presence in the colony creates a temporary disturbed area with many exposed nests. Avian nest predators, because of their high mobility, can rapidly find this potential source of food in open habitats. As the number of unattended nests located in the disturbed area mainly depends on local nest density and nest aggregation, human presence can create more opportunities for predators at high nest density. Because goose nest density was higher in 1997, this might explain why activity of avian nest predators was more influenced by investigator disturbance in that year than in 1996.

Overall abundance of predators and availability of alternative prey might also have an effect on the response of predators to disturbance created by investigators. The activity rate of gulls and jaegers observed in the goose colony under undisturbed conditions (control) was very similar in 1996 and 1997 (Figure 1), a pattern that was confirmed by additional observations conducted over the whole 24-h period (J. Bêty and G. Gauthier, unpubl. data). This suggests that changes in predator abundance did not contribute to between-year variation in the response of avian predators to human disturbance. In the arctic tundra, the abundance of lemmings, the primary prey of many predator species, follows fairly regular cycles of three to five years (Krebs 1964; Sittler 1995). These fluctuations can affect the predation pressure on nesting birds, and predation intensity is generally higher when lemmings are scarce (Martin and Baird 1988; Underhill et al. 1993; Bêty et al., in press). At our study site, lemming abundance reached a peak in 1996 but declined considerably in 1997 (2.34 versus 0.91 lemmings 100 trap-nights^{-1}; Bêty et al. 2001). Therefore, differences in response of predators to investigator disturbance in the colony might also be explained by variation in the availability of alternative prey for nest predators. However, despite the large difference in lemming abundance, egg loss during nest visits was low in both years of the study.

Many researchers have pointed out that mammals like foxes may discover nests by following human tracks in the vegetation or human scent (Götmark 1992). However, there is little evidence that researcher disturbance increases mammalian predation rates (Götmark 1992; Skagen et al. 1999; Lloyd et al. 2000). We believe that human trails or scent did not increase the predation rate by foxes at our study colony for several reasons. First, we frequently walked criss-crossing paths inside and outside the colony (up to 3 km from any goose nest) to accomplish activities other than nest visits. Under such circumstances, it could be unprofitable for scent predators to follow human trails, as suggested by Hannon et al. (1993). Second, predators must associate human tracks or scent with food (Götmark 1992). Even if foxes could find a nest by following human scent, the probability of robbing eggs remains low if parents are at the nest, which reduces the likelihood that foxes could associate human scent with food. However, if arctic foxes are already present in the colony during nest visits, they can rapidly take advantage of the displacement of territorial pairs to rob eggs, as some foxes were not afraid by investigators (J. Bêty, pers. obs.). Thus, the temporary interruption of nest visiting that we made when a fox was close to investigators (<100 m) most likely reduced the impact of disturbance on nest predation.

Conclusions.—Our observations confirm that nest predators can be attracted by and take advantage of investigator presence in a goose colony. Nevertheless, our results show that few eggs were robbed during nest visits at our study site in years with moderate to low nest predation. Several factors could contribute to this low impact. First, parents came back close to their nest rapidly after visits. Second, they can successfully protect their nest against predators. Third, precautions were taken during nest visits to reduce opportunities for predators. In our annual nest monitoring program, goose nests are generally found during the laying period, visited once during incubation, and revisited during hatching to determine their fate (Lepage et al. 2000). Our results suggest that activities of researchers do not bias nesting parameters obtained in this way. However, the effect of investigator disturbance could be more important in other arctic nesting bird species that are less tenacious to their nest, unable to successfully defend their nest against predators, or that rely more on cryptic nests for defense against predators.

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LITERATURE CITED

Agresti, A. 1996. An introduction to categorical data analysis. Wiley, New York.

Armstrong, T. 1996. Effects of research activities on nest predation in arctic-nesting geese. J. Wildl. Manage. 60:265–269.

Bêty, J., G. Gauthier, J.-F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos. 93:388–400.

Ellison, L. N., and L. Cleary. 1978. Effects of human disturbance on breeding of Double-crested Cormorants. Auk 95:510–517.

Götmark, F. 1992. The effects of investigator disturbance on nesting birds. Curr. Ornithol. 9:63–104.

———, and M. C̊hlund. 1984. Do field observers attract nest predators and influence nesting success of common eiders? J. Wildl. Manage. 48:381–387.

———, R. Neergaard, and M. C̊hlund. 1990. Predation of artificial and real Arctic Loon nests in Sweden. J. Wildl. Manage. 54:429–432.

Hannon, S. J., K. Martin, L. Thomas, and J. Schieck. 1993. Investigator disturbance and clutch predation in Willow Ptarmigan: methods for evaluating impact. J. Field Ornithol. 64:575–586.

Hosmer, W. H., Jr., and S. Lemeshow. 1989. Applied logistic regression. Wiley, New York.

Krebs, C. D. 1964. Lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. Arctic Inst. North Am. Tech. Pap. 15:1–104.

Lenington, S. 1979. Predators and blackbirds: the ''uncertainty principle'' in field biology. Auk 96:190–192.

Lepage, D., A. Desrochers, and G. Gauthier. 1999. Seasonal decline of growth and fledging success in snow geese *Anser caerulescens:* an effect of date or parental quality? J. Avian Biol. 30:72–78.

———, G. Gauthier, and S. Menu. 2000. Reproductive consequence of egg-laying decisions in snow geese. J. Anim. Ecol. 69:414–427.

———, ———, and A. Reed. 1996. Breeding-site infidelity in Greater Snow Geese: a consequence of constraints on laying date? Can. J. Zool. 74:1866–1875.

Livezey, B. C. 1980. Effects of selected observer-related factors on fates of duck nests. Wildl. Soc. Bull. 8:123–128.

Lloyd, P., R. M. Little, and T. M. Crowe. 2000. Investigator effects on the nesting success of arid-zone birds. J. Field Ornithol. 71:227–235.

Major, R. E. 1990. The effect of human observers on the intensity of nest predation. Ibis 132:608–612.

Martin, A. P., and D. Baird. 1988. Lemming cycles—which Palearctic migrants are affected? Bird Study 35:143–145.

MAYER-GROSS, H., H. Q. P. CRICK, AND J. J. D. GREENWOOD. 1997. The effect of observers visiting the nests of passerines: an experimental study. Bird Study 44:53–65.

OLSON, R., AND F. C. ROHWER. 1998. Effects of human disturbance on success of artificial duck nests. J. Wildl. Manage. 62:1142–1146.

ORTEGA, C. P., J. C. ORTEGA, C. A. RAPP, S. VORISEK, S. A. BACKENSTO, AND D. W. PALMER. 1997. Effect of research activity on the success of American Robin nests. J. Wildl. Manage. 61:948–952.

POUSSART, C., J. LAROCHELLE, AND G. GAUTHIER. 2000. The thermal regime of eggs during laying and incubation in Greater Snow Geese. Condor 102:292–300.

REED, A., J. R. HUGHES, AND G. GAUTHIER. 1995. Incubation behavior and body mass of female Greater Snow Geese. Condor 97:993–1001.

RODWAY, M. S., W. A. MONTEVECCHI, AND J. W. CHARDINE. 1996. Effect of investigator disturbance on breeding success of Atlantic Puffins. Biol. Conserv. 76:311–319.

SAS INSTITUTE. 1993. Technical report P-243 SAS/STAT software: the GENMOD procedure. Release 6.09. SAS Institute, Inc., Cary, North Carolina.

———. 1996. SAS/STAT user's guide. Release 6.12. SAS Institute, Inc., Cary, North Carolina.

SEDINGER, J. S. 1990. Effects of visiting Black Brant nests on egg and nest survival. J. Wildl. Manage. 54:437–443.

SIEGLE, S., AND N. J. CASTELLAN, JR. 1988. Non-parametric statistics for the behavioral sciences. Second ed., McGraw-Hill, New York.

SITTLER, B. 1995. Response of stoats (*Mustela ermina*) to fluctuating lemming (*Dicrostonyx groendlendicus*) populations in North East Greenland: preliminary results from long-term study. Ann. Zool. Fennici 32:79–92.

SKAGEN, S. K., T. R. STANLEY, AND M. B. DILLON. 1999. Do mammalian nest predators follow human scent trails in the shortgrass prairie? Wilson Bull. 111:415–420.

STEIDL, R. J., J. P. HAYES, AND E. SCHAUBER. 1997. Statistical power analysis in wildlife research. J. Wildl. Manage. 61:270–279.

STRANG, C. A. 1980. Abundance of avian predators near people searching for waterfowl nests. J. Wildl. Manage. 44:220–222.

TREMBLAY, J.-P., G. GAUTHIER, D. LEPAGE, AND A. DESROCHERS. 1997. Factors affecting nesting success in Greater Snow Geese: effects of habitats and association with Snowy Owls. Wilson Bull. 109:449–461.

UNDERHILL, L. G., R. P. PRYS-JONES, E. E. SYROECHKOVSKI, N. M. GROEN, V. KARPOV, H. G. LAPPO, VAN M. W. ROOMEN, A. RYBKIN, H. SCHEKKERMAN, H. SPIEKMAN, AND R. W. SUMMERS. 1993. Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. Ibis 135:277–292.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102:774–780.

WHITE, C. M., AND T. L. THUROW. 1985. Reproduction of Ferruginous Hawks exposed to controlled disturbance. Condor 87:14–22.

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