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Research Papers

Colony Dynamics and Persistence of Ivory Gull Breeding in Canada

Dynamique et pérennité de colonies de Mouette blanche au Canada

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ABSTRACT. Despite the importance of assessing the viability of small and endangered populations, often few demographic data are available. However, when counts are available from discrete sites, a colony- or site-based approach can be useful. We used recent counts of Ivory Gull, *Pagophila eburnea*, a rare species that breeds at remote sites in the high Arctic, to model colony dynamics and population persistence. Dramatic declines in numbers of pairs nesting in Canada led to the uplisting of this species to Endangered by the Committee on the Status of Endangered Wildlife in Canada in 2006. Colonies continued to decline from 2004 to 2006, with sites at the southern edge of the breeding range on Baffin Island almost completely extirpated; only one pair remained in 2005 and 2006. We used colony counts at 24 sites on southern Ellesmere Island and Devon Island from 2002 to 2006 to model extinction and colonization rates. Extinction rates were high at 0.735 ± 0.077 (mean ± SE) and increased for smaller colonies. Colonization rates were low at 0.189 ± 0.054 (mean ± SE), new colonies were small (mean: 7.7 pairs), and there was no evidence of local rescue effects from nearby colonies. Based on these rates, a population projection model was constructed using a starting population of 225 pairs at the 24 sites. The projected population reached an equilibrium of approximately 30 pairs in only 8 yr. The large and isolated colony on Seymour Island has declined at 2.7%/yr (95% confidence limits: –13.9, 8.5) since 1974, and had low but wide-ranging probabilities of going extinct within 20 yr. The suggestion that Ellesmere Island may be the only site where breeding Ivory Gull will persist in the future is supported by the recent discovery of new colonies there in 2006.

RÉSUMÉ. En dépit de l’importance d’évaluer la viabilité de petites populations en voie de disparition, il existe souvent peu de données démographiques. Toutefois, lorsqu’on dispose de dénombrements pour des sites isolés, une méthode d’analyse par colonie ou par site peut s’avérer utile. Nous avons utilisé des dénombrements récents de Mouettes blanches, *Pagophila eburnea*, une espèce rare qui se reproduit dans des sites reculés dans le Haut-Arctique, pour modéliser la dynamique des colonies et la pérennité des populations. Les déclins importants observés dans le nombre de couples nichant au Canada sont à l’origine de l’attribution nouvelle du statut « en voie de disparition » à l’espèce par le Comité sur la situation des espèces en péril au Canada en 2006. Le déclin des colonies s’est poursuivi de 2004 à 2006, les sites à la limite méridionale de l’aire de nidification sur l’île de Baffin étant pratiquement tous abandonnés : un seul couple était toujours présent en 2005 et 2006. Nous avons utilisé les dénombrements de 24 colonies dans le Sud de l’île d’Ellesmere et sur l’île Devon, de 2002 à 2006, pour modéliser les taux d’extinction et de colonisation. Les taux d’extinction étaient élevés (0,735 ± 0,077 [moyenne ± erreur-type]) et ont augmenté dans le cas des plus petites colonies. Les taux de colonisation étaient faibles (0,189 ± 0,054 [moyenne ± erreur-type]), les nouvelles colonies étaient petites (moyenne : 7,7 couples) et il ne semblait pas y avoir d’effets « de sauvetage » local par les colonies voisines. À partir de ces taux, un modèle de projection de population a été construit en utilisant une population de départ de 225 couples aux 24 sites. La population projetée a atteint un équilibre d’environ 30 couples en seulement huit ans. La grosse colonie isolée sur l’île Seymour a diminué à un rythme de 2,7 % par année (limites de confiance à 95 % : -13,9; 8,5) depuis 1974, et a une probabilité faible, mais très incertaine, de s’éteindre d’ici 20 ans. L’hypothèse selon laquelle l’île d’Ellesmere puisse être le seul site où des couples nicheurs de Mouette blanche vont subsister est appuyée par la découverte récente de nouvelles colonies à cet endroit en 2006.

Key Words: *colony dynamics; endangered species; Ivory Gull; Pagophila eburnea; population modeling*

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INTRODUCTION

For small and endangered populations, an assessment of their ability to persist can be an important tool to guide management and recovery efforts (Morris et al. 2002). Various forms of population viability analysis or population modeling are commonly used to assess the risk of local extinction and diagnose causes of population decline (Caswell 2001, Beissinger and McCullough 2002). A challenge for rare and endangered species is that detailed demographic data may not be available for any number of reasons such as logistics, expense, and the fact that disturbance involved with monitoring a species may impinge on its recovery (Morris and Doak 2002). Also, there remain concerns with the use of population persistence models, especially when data are sparse (Beissinger and Westphal 1998, Coulson et al. 2001).

In general, avian species are relatively easy to monitor and population modeling has been conducted using rich demographic data sets (Lande 1988, Wiese et al. 2004, Calvert et al. 2006, Koons et al. 2006). Esler (2000) showed that when birds exhibit spatial structure and site fidelity, important insights into avian population dynamics can be determined using a spatially explicit approach. Avian colony dynamics have been recently explored and have led to insights into where bird colonies are formed and how they persist in time and space (Erwin et al. 1998, Oro and Ruxton 2001, Barbraud et al. 2003, Chaulk et al. 2006). How local colony size and recent colony trends influence the ability of colonies to persist and the importance of rescue effects from nearby occupied colonies have all been considered (Barbraud et al. 2003, Martínez-Abraín et al. 2003, Chaulk et al. 2006). Although colony- or site-level analyses preclude detailed inferences about the demographic processes that are hampering the recovery of a population, they can provide more insight into the dynamics of a population than can analyses based simply on overall trends.

The Ivory Gull, *Pagophila eburnea,* is an Arctic species that breeds in the north Atlantic and Arctic oceans above the Arctic Circle and winters in the Atlantic and Pacific oceans near ice edges (Haney and MacDonald 1995). Breeding sites are generally discrete, either on nunataks (mountain peaks that project from glaciers), flat offshore islands, or windswept hills on gravel plateaus. In Canada, all breeding locations share the characteristics of isolation from mammalian predators and support only Ivory Gull, i.e., there are no mixed-species colonies (Haney and MacDonald 1995).

Recent aerial surveys in Canada have shown a 70–80% decline in Ivory Gull numbers from the 1980s to the early 2000s (Gilchrist and Mallory 2005), corroborating information received through local ecological knowledge (Mallory et al. 2003). These observations supported a recommended change in the status of the species from *special concern* to *endangered* in 2006 (Committee on the Status of Endangered Wildlife in Canada 2006). Given its remote breeding locations, detailed demographic data on the species are severely limited. For North America, a single estimate of adult survival based on recovery data was available spanning 28 yr (Stenhouse et al. 2004). Limited breeding success data were available for one site in the 1970s (MacDonald 1976, Haney and MacDonald 1995). There are no data on post-fledging and juvenile survival for this species. However, colony surveys have continued at most known sites from 2002 to 2006, providing an opportunity to examine the colony dynamics of this rare and declining species.

Our purpose was to evaluate the current colony site dynamics of Ivory Gull breeding in Canada. Specifically our objectives were: to provide updated information for 2004–2006 (earlier data are presented in Gilchrist and Mallory 2005) on the population status of Ivory Gull breeding in Canada; to assess colony extinction and colonization rates using data collected between 2002 and 2006; and to determine if extinction rates are related to colony size and whether rescue effects are possible. Finally, we evaluated whether these colonies can persist under the current conditions, including for the relatively large and isolated colony on Seymour Island using a separate and more traditional count-based assessment of the population trend and viability. Here, extinction rate is defined as the probability of an occupied site becoming unoccupied, and colonization rate is defined as the opposite. A number of mechanisms can lead to these transitions.

METHODS

Prior to 2001, 33 Ivory Gull colonies were known to exist in Arctic Canada (Thomas and MacDonald 1987, Haney and MacDonald 1995); these had been discovered over several years. Beginning in 2002, we conducted annual, comprehensive surveys of the known breeding range in Canada. The results for 2002 and 2003 were presented elsewhere (Gilchrist and Mallory 2005) and increased the number of known colonies to 49. From 2004 to 2006, we continued to focus our surveys on these sites and nearby habitats (Fig. 1).

Because of their remote locations, all surveys were conducted by helicopter between 0900 and 1700 EDT, and survey dates occurred between 29 June and 16 July each year, which fell during the incubation stage. The weather was sunny with little cloud on all flights. We surveyed mountain nunataks by flying 80–100 m from cliff faces at 40–60 km/h in a Bell 206 L4 helicopter. We flew from one nunatak to the next, assuming that no birds nested on the glacial ice between them. Gulls were easily spotted; at the approach of the helicopter, some gulls remained on their nests, white against the dark rock, whereas others flew away from the cliff and circled over the colony, bright against the blue sky. When birds were spotted, the helicopter slowed to a hover so that all three crew members could count the numbers of individual birds sitting on cliff ledges and flying.

In every region in which we conducted surveys, we flew over alternative areas of suitable habitat to determine if the Ivory Gull had moved to nest elsewhere. We examined more than 300 alternate cliffs or nunataks across years, in addition to the known or new colonies. This coverage represents a significant portion of the potential breeding range because cliff and nunatak colonies are restricted to select granulite-facies granitoids, which are limited to southeastern Ellesmere Island and Devon Island (Frisch 1984*a*,*b*,*c*). In 2003, helicopter surveys were supplemented by fixed-wing transect surveys on the Brodeur Peninsula of Baffin Island (Gilchrist and Mallory 2005). Information on unoccupied locations was required to determine whether any detected population changes at colonies were the result of colony redistribution or numerical declines in the number of nesting birds.

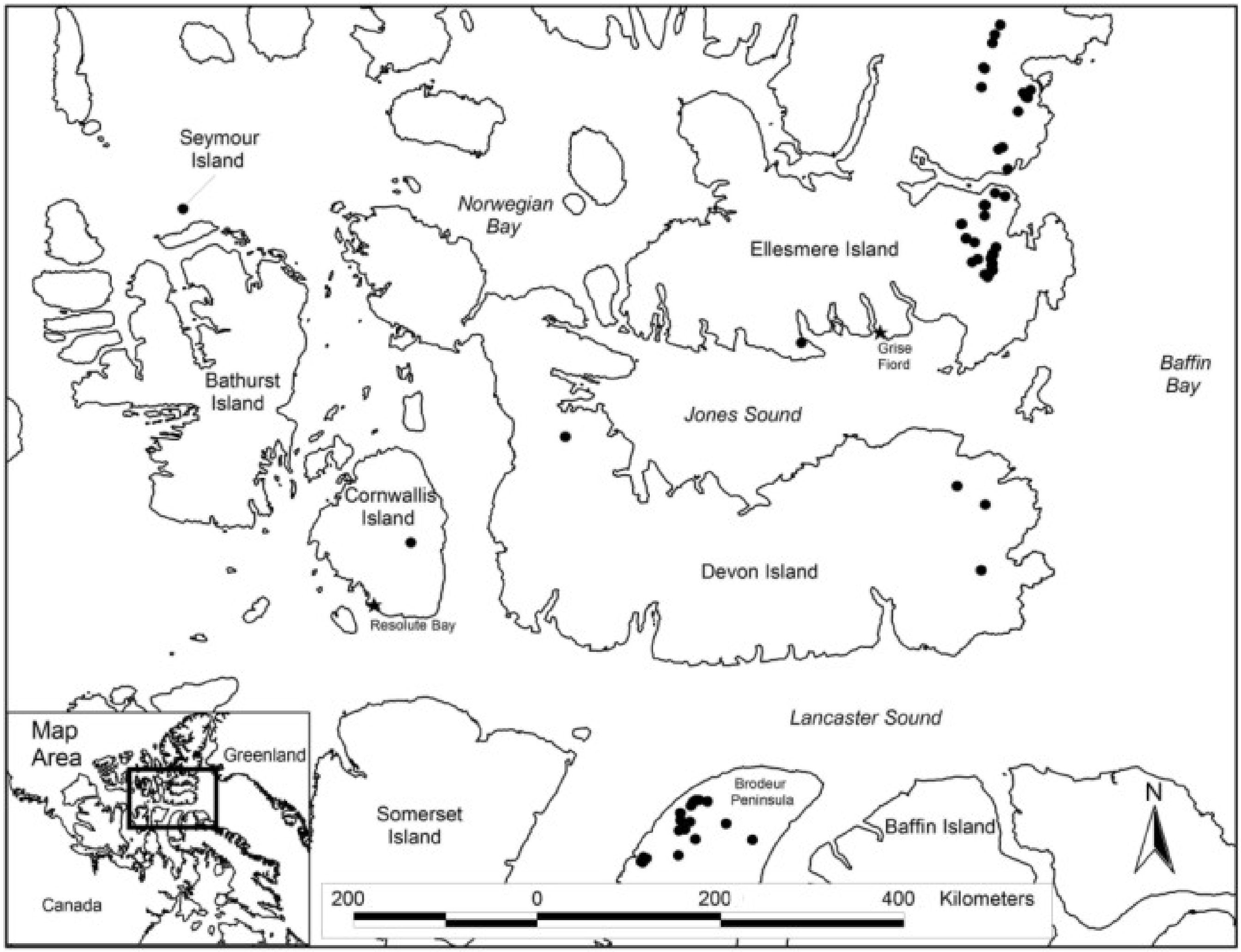
We confirmed breeding by the observation of fresh nesting material or eggs. Counts for each colony represented the total number of birds observed; we could not distinguish between active, failed, or nonbreeders. One member of a breeding pair is always present at the nest during the breeding cycle (Mallory et al. in press), so active colonies will always have at least one bird present. For the purposes of our study, we assumed that one bird represented a breeding pair because the other member of the pair is generally away collecting nest material or foraging during incubation and chick rearing (Mallory et al. in press). This approach will overestimate the number of breeding pairs if both members of the pair are at the nest during the survey. Ideally, repeated surveys are preferred to assess the detection rates of colonies (MacKenzie et al. 2002) and estimate the variability in the counts (Morris and Doak 2002). The latter is done to remove sampling and observer variation from the true process or temporal variation. However, a variety of constraints, including the remote location of the breeding areas, appropriate weather for conducting surveys, the expense of helicopter time, and a desire to minimize disturbance at the colonies, made repeated surveys unfeasible for this species.

Data analysis

Twenty-four colonies had at least one active breeding pair on Ellesmere Island and Devon Island from 2002 to 2006. Extinction and colonization rates were calculated based on these 24 colonies. To calculate these rates, the frequency of the event, i. e., extinction or colonization, was divided by the number of times the event could have occurred, with binomial error calculated in the standard manner. In this way, individual colonies could contribute more than one sample to the data set, and the rates have different sample sizes depending on the overall occupancy rate; i.e., if few colonies were occupied, few extinctions, but many colonizations, were possible. This approach is similar to that used by Barbraud et al. (2003) using the program MARK; however, we did not use MARK because we assumed that all colonies were detected.

To assess what factors were related to colonization or extinction rates, we used a generalized linear model approach with colony state (i.e., occupied or unoccupied) as a binomial response and colony site as a subject (Martínez-Abraín et al. 2003), using generalized estimating equations (GEE) available in PROC GENMOD in SAS version 9.1 (SAS Institute 2004). When a colony was occupied, the extinction probability in the subsequent year was modeled against the size of the colony (i.e., the number of birds counted at the site). For colonization rates, we examined whether colony isolation influenced the probability with which a colony was recolonized. This was indexed by the

Fig. 1. Locations (circles) of Ivory Gull colonies in Arctic Canada. Stars represent human settlements.



number of colonies sites within 10 km, which we considered a reasonable dispersal distance for Ivory Gull (Bateson and Plowright 1959); in addition, a radius of 10 km provided a good range in the number of neaby colonies, from zero to seven. Simple descriptive statistics and colony size frequencies were also calculated for the 20 sites on southern Ellesmere Island and Devon Island that were counted every year from 2002 to 2006.

Because only four sites on Baffin Island had breeding birds present from 2003 to 2006, and only one pair remained by 2005 and 2006, meaningful analyses of factors related to extinction and colonization rates were not possible. For the same reason, population models were not constructed for Baffin Island.

Population models

A colony-based model for southern Ellesmere Island and Devon Island was constructed using MATLAB software, using the values or functions presented in Table 1. Initial starting values for the population were taken from the first breeding census, usually 2002, because more birds were present at the beginning than at the end of the recent census period, which provided optimistic starting values for the population. The starting population comprised 225 pairs. The model projected each colony through repeated time steps and evaluated whether it went extinct or persisted if previously occupied or was colonized if previously unoccupied by comparing the value provided for colonization rates or calculated for extinction rates based on the current population size (Table 1) with a randomly drawn number from a uniform distribution. The resulting colony sizes for colonies that persisted or were newly colonized were chosen randomly. In the case of colonies that persisted, a normal random deviate was drawn, multiplied by 0.132 (the SE of the function) and added to 0.755; the resulting value was multiplied by the colony size in the previous year. For colonies that were newly colonized, a set of skew-normal random deviates were chosen to reflect the right skew observed in the real data. These random deviates were extracted from http://tango.stat.unipd.it/SN/index.html#se, based on work by Azzalini and Capitianio (1999). Any random values that resulted in colony sizes less than one were ignored. We assessed model sensitivity to determine the importance of the various parameters used in the model, i.e., extinction and colonization rates and sizes of new colonies and those that persisted. This was done by adding 10% to each starting value used in the model while holding all other values at their starting values and comparing the effect on the resulting output with the baseline output.

For Seymour Island, the largest and most persistent colony in Canada, a longer time series starting in 1974 was available. This colony was extant in all 11 surveys except 2002, so 10 counts were available for analysis. The count of zero in 2002 was not used because it merely represented that the population was not available to be counted in that year. Population growth rate and process variance was calculated following Morris and Doak (2002) for density-independent count-based data (based on Lande and Orzack 1988 and Dennis et al. 1991). Briefly, the mean (μ) and variance (σ^2) of the log population growth rates were calculated by regressing the log population growth rates between subsequent counts at i and $i + 1$ (i.e., $\log[N_{i+1}/N_i]$) divided by the square root of the interval between i and $i + 1$ (i.e., $\sqrt{[t_{t+i} - t_i]}$) against $\sqrt{(t_{t+i} - t_i)}$. The term $\sqrt{(t_{t+i} - t_i)}$ was required to address counts that were conducted > 1 yr apart, which was the case in this data set. More sophisticated methods to assess process variance were not possible because of the gaps in the time series (e.g., Staples et al. 2004). Regression diagnostics were examined for possible outliers and evidence of serial autocorrelation. Again, following Morris and Doak (2002), values of μ and σ^2 were used to calculate the cumulative distribution function of the probability of extinction or quasi-extinction. Confidence limits of the cumulative distribution function were based on 5000 bootstraps of randomly drawn values of μ and σ^2 based on their confidence limits. Given that Ivory Gull will nest solitarily, an extinction threshold of only one pair was considered, as well as a larger quasi-extinction threshold of 10 pairs. The median time to the extinction and quasi-extinction thresholds and the probability of reaching these thresholds after 20 yr were extracted from the cumulative distribution functions, along with their associated 95% confidence limits. In the case of the median times, the 95% confidence limits represent the earliest time when 0.5 (the median) was included in the 95% confidence limits of the cumulative distribution function.

RESULTS

Surveys: 2004–2006

By the end of the 2006 surveys, we knew of 65 Ivory Gull colony locations that had been occupied at least once since 1974, which were distributed as follows: Seymour Island, 1; Cornwallis Island, 1; Devon Island, 5; Brodeur Peninsula of Baffin Island, 17; Ellesmere Island, 41 (Fig. 1 and Table 2). Ivory Gull was not present at 26 of these locations (Devon Island, 2; Baffin Island, 13; Ellesmere Island, 11) during any of the recent surveys from 2002 to 2006 (Table 2), and we were unable to access one very remote colony on Ellesmere Island where 15 Ivory Gulls were spotted in 1977 (Thomas and MacDonald 1987).

We compared colony size for the 29 sites where gulls were counted at least once prior to 1991 and at least once during our surveys from 2002 to 2006. Using the maximum number of birds observed at each colony in each time period, colony sizes were significantly larger (68.3 ± 14.7 gulls, mean ± SE) prior to 1991 compared to during our surveys (8.5 ± 6.9 gulls; mean difference: 59.6 ± 11.6 gulls; 95% CL: 32.0, 87.2). At every one of these colonies, the highest number of birds ever observed occurred before 1991. The sum of the maximum colony sizes between 1974 and 1990 was 1981 gulls, whereas

Table 1. Parameters and their values or functions used to calculate their values used in the Ivory Gull colony persistence model for Ellesmere Island and Devon Island.

Parameter	Value or function
Number of colonies	24
Initial population size	225 pairs in 17 occupied colonies; 13 ± 31 pairs per occupied site (mean ± SD)
Probability of extinction	$p_{ext} = \frac{e^{-0.088N_t+2.100}}{1+e^{-0.088N_t+2.100}}$
Probability of colonization	0.189 ± 0.054 (mean ± SE)
Size of colonies that persist	$N_{t+1} = 0.755 \pm 0.132 N_t$
Size of colonies that are newly colonized	7.7 ± 12.3 (mean ± SD; drawn from a skewed distribution)

these same colonies and nearby sites supported a maximum of 558 gulls during our surveys, representing a possible 72% decline in gulls from earlier counts.

In 2004, we found a new colony in east-central Ellesmere Island that supported 92 to 131 gulls in each of three years. In 2006, we found seven new colonies located several kilometres west of this site. Collectively, this cluster of eight colonies accounted for 697 Ivory Gull individuals in 2006, or 83% of the 842 birds that we observed that year, which was the maximum count in any recent year from 2002 to 2006. Given that we had only 1 yr of counts for these colonies, we did not include these colonies in our model for Ellesmere Island. Of these eight colonies, four had *Xanthoria* lichen and graminoids growing on the cliff below the gulls, which is a characteristic of established colonies (Gilchrist and Mallory 2005), indicating that these colonies had gone undetected in earlier surveys (Thomas and MacDonald 1987). The other four colonies appeared to be relatively new.

Colony dynamics

At colonies that were surveyed each year from 2002 to 2006, Ivory Gull nesting on southern Ellesmere Island and Devon Island showed aggregated distributions, as indicated by high coefficients of dispersion (CD: variance to mean ratio) in colony size (Fig. 2). Although the time series is short, it also appeared that the birds became more aggregated over time, as indicated by higher CDs and lower numbers of sites occupied.

For the sites that had one breeding pair from 2003 to 2006 on Baffin Island, there were five opportunities for colonies to go extinct, and in four cases they did (0.80 ± 0.20, mean ± SE). Colonizations were possible in seven instances and occurred twice (0.29 ± 0.18). In both cases, only one pair occupied a previously unoccupied site.

For southern Ellesmere Island and Devon Island colonies, colony extinction was possible in 34 cases and occurred in 25 cases (0.735 ± 0.077, mean ± SE). Colonization events were rarer, with 10 (0.189 ± 0.054, mean ± SE) actual colonizations out of 53 possible colonizations. As expected, the probability of extinction decreased with increasing colony size

Table 2. Ivory Gull colony locations, counts in 2004–2006, and maximum recorded colony sizes from surveys or literature.

Island	Latitude	Longitude	Birds counted at the colony			Maximum size
			2004	2005	2006	
Ellesmere	76.38	84.97	0	0	0	287
Ellesmere	76.71	80.13	0	0	0	70
Ellesmere	76.80	80.26	0	0	0	90
Ellesmere	77.18	79.59	0	2	0	4
Ellesmere	76.86	79.75	0	0	0	20
Ellesmere	76.83	79.85	0	0	0	19
Ellesmere	76.82	79.84	0	0	0	20
Ellesmere	76.80	79.92	0	0	0	28
Ellesmere	76.76	79.92	0	0	0	28
Ellesmere	76.73	79.90	0	0	0	2
Ellesmere	76.71	80.00	0	0	0	2
Ellesmere	76.69	80.06	0	1	0	11
Ellesmere	76.79	80.42	0	0	0	70
Ellesmere	77.44	79.35	0	0	0	
Ellesmere	77.45	79.23	0	0	0	125
Ellesmere	77.32	79.17	0	0	0	
Ellesmere	77.72	78.35	0	0	0	
Ellesmere	77.73	78.37	2	0	0	2
Ellesmere	77.76	78.45	0	0	0	
Ellesmere	77.75	78.32	0	0	0	
Ellesmere	77.77	78.23	50	23	0	50
Ellesmere	77.72	78.35	2	0	0	2
Ellesmere	77.73	78.38	42	1	0	42
Ellesmere	77.12	79.89	0	0	0	1
Ellesmere	77.06	79.94	0	0	0	2

(con'd)

Ellesmere	77.12	79.91			0	1
Ellesmere	77.12	79.93	0		0	
Ellesmere	77.17	79.33	0	0	0	50
Ellesmere	76.94	80.51		0	0	
Ellesmere	76.94	80.52	0	0	0	60
Ellesmere	77.02	80.59	0	0	0	1
Ellesmere	77.02	80.57	0	0	0	24
Ellesmere	79.97	76.92				15
Ellesmere	78.18	78.83	131	92	100	131
Ellesmere	77.65	78.67			25	25
Ellesmere	76.91	80.29			2	2
Ellesmere	78.13	79.02			150	150
Ellesmere	78.08	79.12			20	20
Ellesmere	77.82	79.60			150	150
Ellesmere	77.93	79.44			200	200
Ellesmere	77.94	79.47			50	50
Devon	75.47	81.37	0	0	0	25
Devon	75.34	80.74	0	2	1	30
Devon	74.95	81.00	0			30
Devon	75.80	90.82		3	0	3
Devon	74.77	80.70				6
Seymour	76.80	101.27	120	110	143	351
Cornwallis	75.08	94.25		7	0	7
Baffin	73.66	87.48	0	0	0	75
Baffin	73.66	87.55	0	0	0	175
Baffin	73.62	87.66	0	0	0	6
Baffin	73.64	87.61	0	0		37
Baffin	73.58	87.87	0	0	0	45
Baffin	73.48	87.77	0	0	0	13
Baffin	73.47	87.90	0	0	0	84

(con'd)

Baffin	73.31	88.63	0	0	0	130
Baffin	73.30	88.57	0	0	0	45
Baffin	73.27	88.65	0	0	0	25
Baffin	73.53	87.67	0	0		18
Baffin	73.53	87.87	0	0	0	30
Baffin	73.51	86.91	0	0	0	35
Baffin	73.65	87.30	1	0	0	20
Baffin	73.32	87.91	54	0	1	55
Baffin	73.42	86.35	0	0	0	26
Baffin	73.42	87.55	0	0	0	7

Note: For cases for which the maximum size is absent, the colonies are known from the literature, but original counts were not available and no gulls were observed in 2002–2006.

(β = –0.088, 95% CL: –0.145, –0.031, n = 34; Fig. 3). There was no detectable relationship between the probability of colonization and the number of colony sites within 10 km (β = 0.019, 95% CL: –0.278, 0.316, n = 53).

For colonies that persisted, previous colony size was regressed on current colony size using a model with no intercept; the slope of this relationship was 0.755 ± 0.132 (mean ± SE; n = 9). Thus, on average, colonies were approximately three-quarters of the size that they were in the previous year. For colonies that were newly established, we calculated a mean size of 7.7 ± 12.3 gulls (mean ± SD; median: 3.5, range: 1–42), and there was a large right skew in the distribution.

Model projections

Given the analysis of extinction and colonization rates, we used a function that depended on colony size to model colony extinction rates while colonization rates were held constant across all colonies. We provide an example of 10 randomly chosen runs along with the average trajectory of 5000 runs (Fig. 4). At first, the population declines steeply, reaching an equilibrium of about 30 pairs after 8 yr. Individual runs showed the same general pattern, with higher fluctuations once the equilibrium was reached after 8 yr. This equilibrium value is likely artificial because colonization rates would be expected to decline as the overall population size decreases, unless all colonizations were coming from outside the area, and the population eventually becomes extinct.

The model was relatively insensitive to increases of 10% in the input values. Increasing the colonization rate and size of newly formed colonies and decreasing the extinction rate resulted in minor changes; the time to reach the equilibrium was delayed by 1 yr (i.e., 9 yr) and the equilibrium number of birds was somewhat larger, i.e., by 32–34 pairs. The model was most sensitive to increases in the size of colonies that persisted; the equilibrium value remained the same, but the decline in total population size was slowed, reaching the equilibrium in 13 yr.

Seymour Island

From 1974 to 2006, μ (or logλ) was estimated at –0.0271 with 95% confidence limits that bound 0 (–0.1389, 0.0847). The process variance, σ^2, was

Fig. 2. Colony size distributions and descriptive statistics for Ivory Gull nesting on Devon Island and southern Ellesmere Island in 2002–2006. Only colonies that were counted every year were included (n = 20). CD is the coefficient of dispersion (variance to mean ratio).

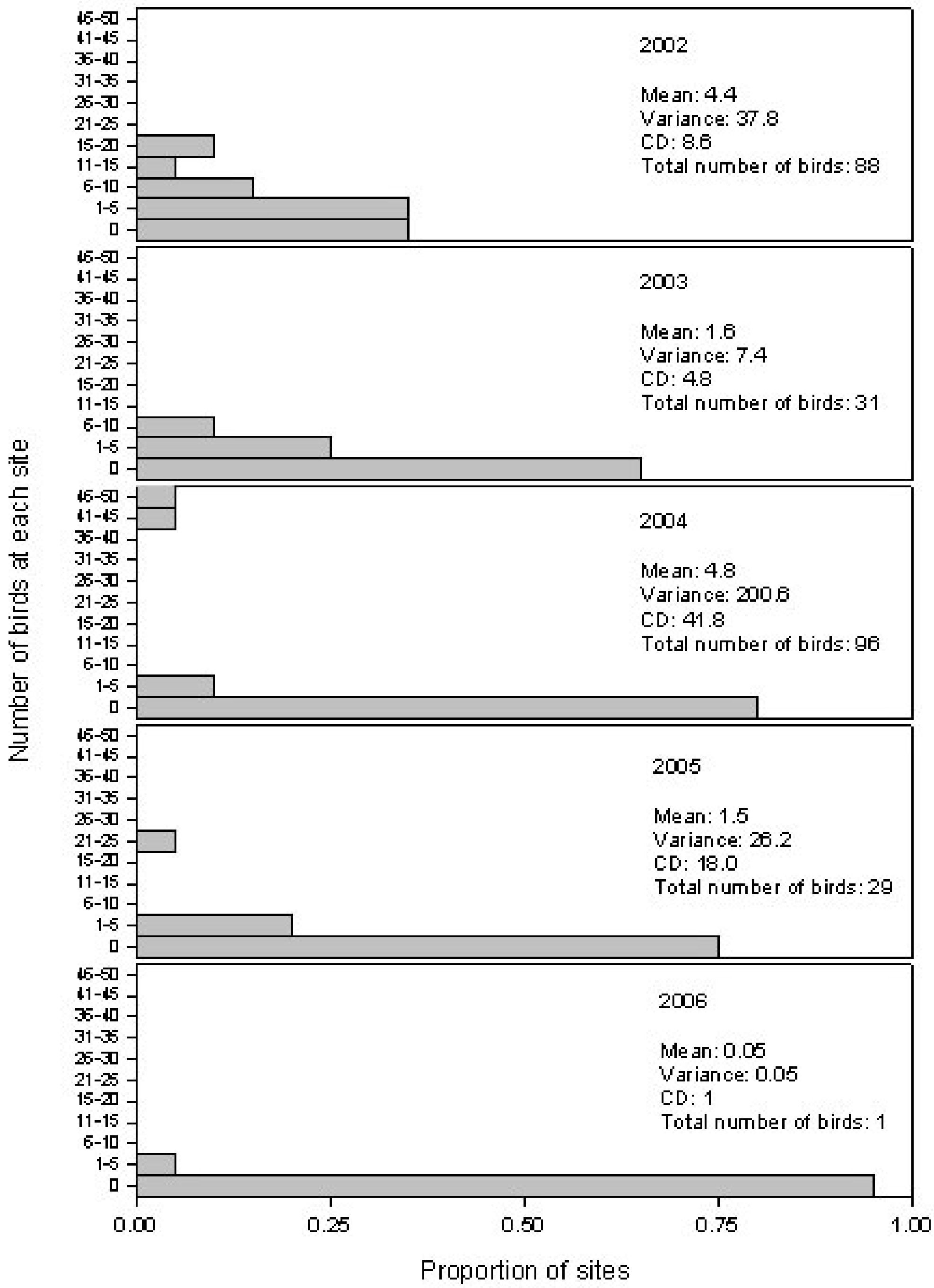
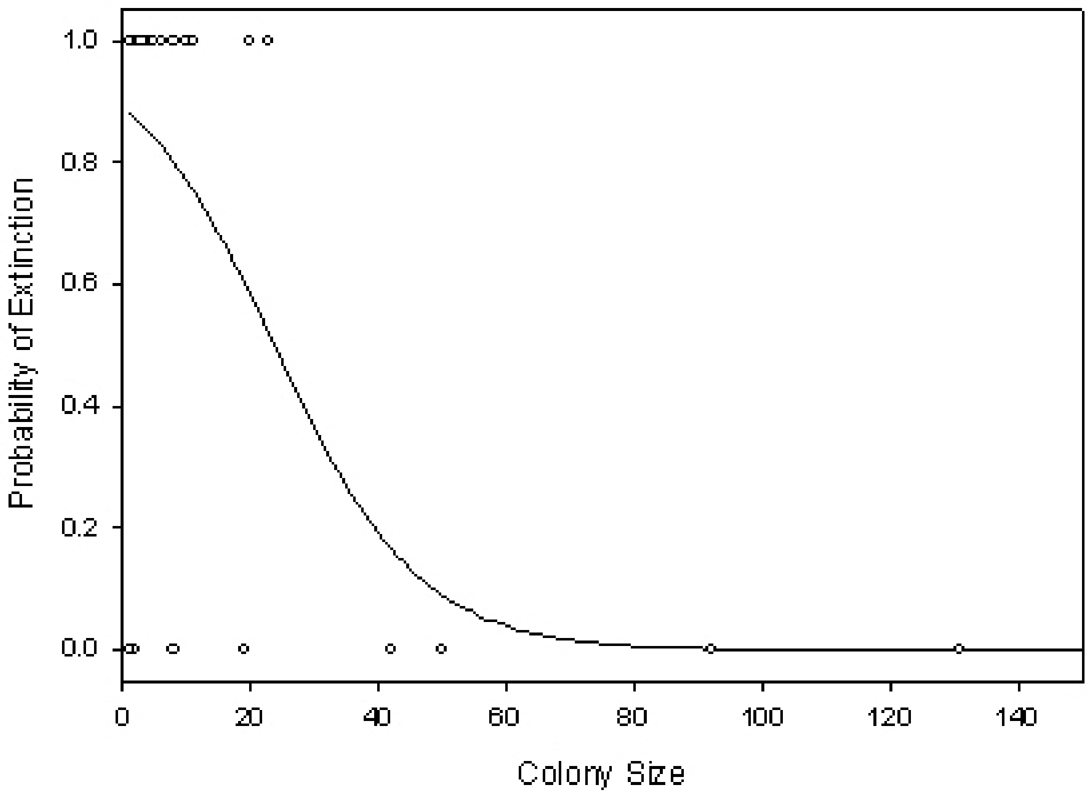


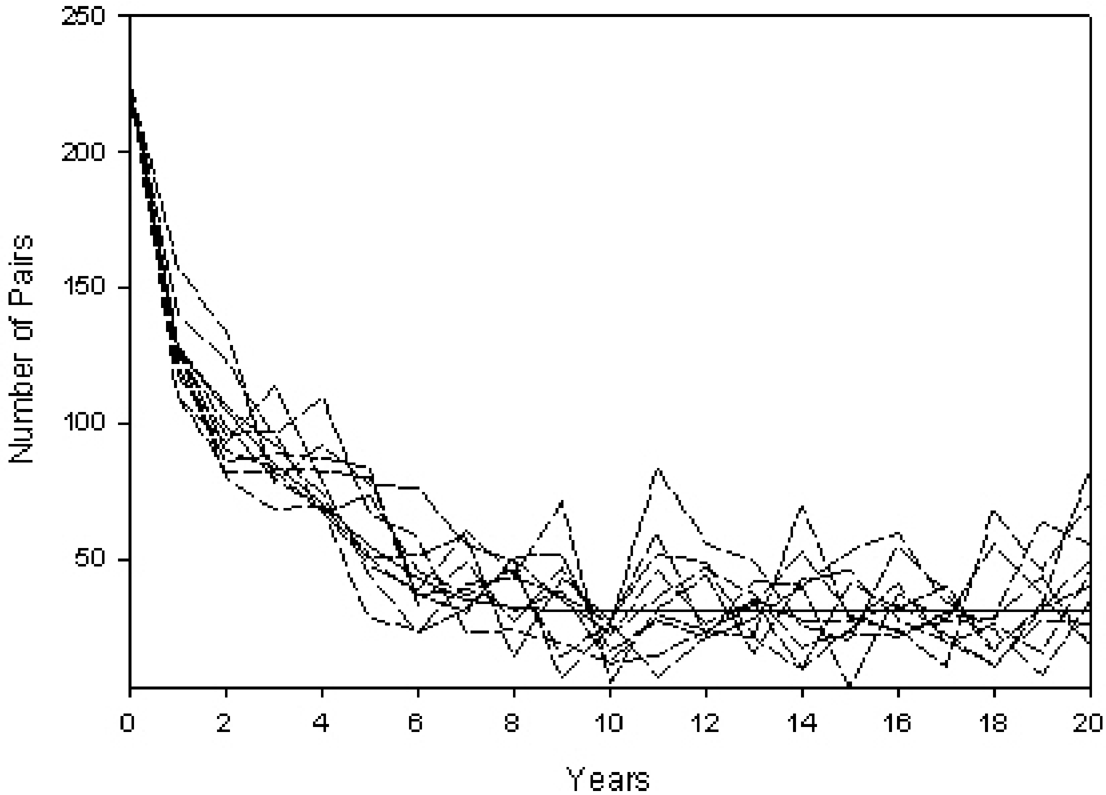
Fig. 3. Sizes and extinction rates of Ivory Gull colonies on Ellesmere Island and Devon Island in 2002–2006. Circles represent actual observations; the curve is a fitted binomial regression.



0.0752, with 95% confidence limits that did not bound 0 (0.0329, 0.3115). Regression diagnostics indicated that the long spans without data did not overly influence the results; rather, the large increase in gulls from 1983 to 1984 (225 to 351 gulls) and the large decline from 2003 to 2004 (200 to 120 gulls; Fig. 5) had the largest influences, indicated by studentized residuals > 2. There was little indication of first-order autocorrelation in the time series (r = –0.102). However, because of the gaps in the time series between 1977 and 1983 and between 1984 and 2003 and the limited data series, the interpretation of autocorrelation coefficients is difficult.

Based on these values of μ and σ^2 and their confidence limits, the median time to extinction (one pair) for Seymour Island is 145 yr (95% CL: 31, ∞; there was no time at which the population had a 50% chance of extinction at its lower 95% confidence limit), and the median time to a quasi-extinction threshold of 10 pairs is 66 yr (95% CL: 15, ∞). By 20 yr, the population had a probability of 0.0003 of reaching only one pair and a probability of 0.0728 of reaching 10 pairs, although there were extremely wide confidence limits on these estimates (0.0000, 0.2472 for a threshold of one pair; 0.0000, 0.6460 for 10 pairs).

Fig. 4. Simulation results for the overall population size of 24 Ivory Gull colonies on Ellesmere Island and Devon Island. Dashed lines indicate 10 individual runs of the model; the solid line is the mean of 5000 runs.

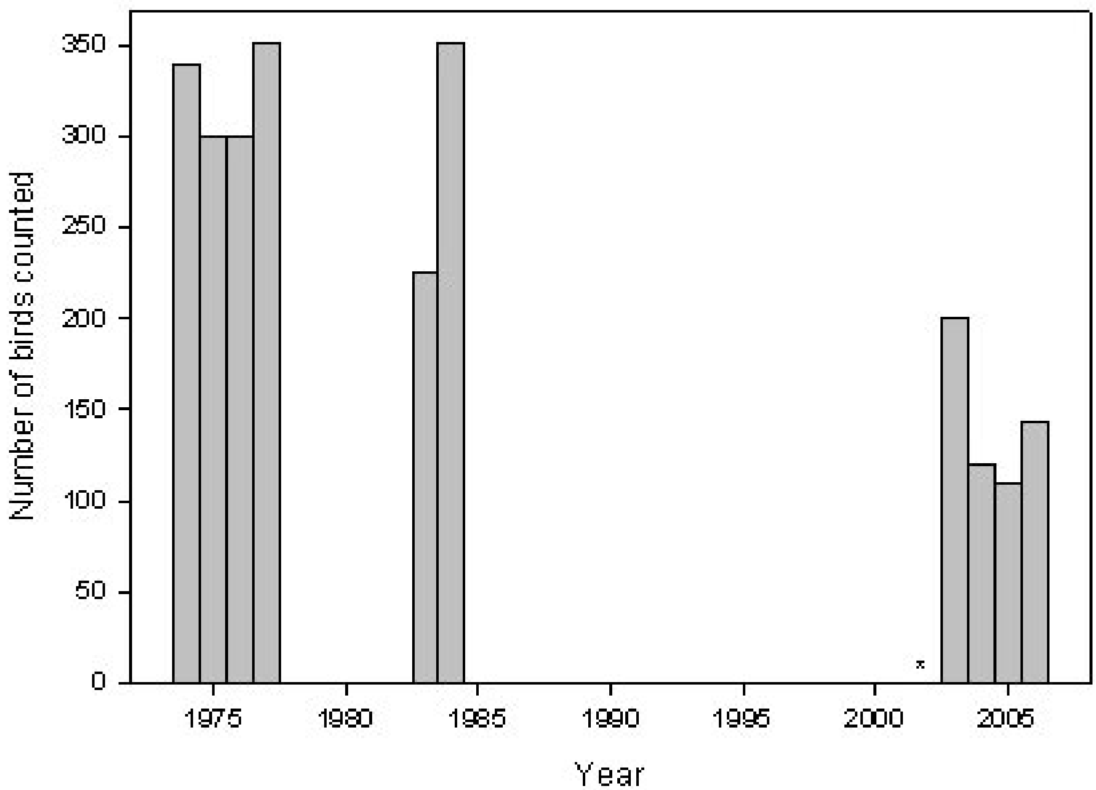


DISCUSSION

In the early 20th century, Ivory Gull colonies on the Brodeur Peninsula were so large that Inuit mistook them at a distance for snow (Bray 1943, Mallory *unpubl. data*). During research in the 1970s, Seymour Island supported > 200 Ivory Gull nests in three of five years (S. D. MacDonald *unpubl. data*). This situation has changed. The numbers of Ivory Gull occupying Canadian colonies have declined by more than 70% since the 1970s, a pattern that is consistent in all breeding regions and across five years of comprehensive surveys. The colony survey results corroborate information from Inuit residents of the Arctic (Mallory et al. 2003), residents of Newfoundland and Labrador (Ryan et al. 2006), and surveys at sea (Chardine et al. 2004). Although a long-term pattern of decline was evident, certain colonies were occupied by varying numbers of gulls in successive years. A colony-based analysis proved a useful tool with which to examine the dynamics of Ivory Gull breeding populations in Canada and showed that colony extinction rates were high and increased at lower colony sizes, whereas colonization rates were very low and did not appear to be influenced by the number of nearby colonies.

Several assumptions are required when using site occupancy and colony count data to determine trends over time. In the case of site occupancy, our methods assume that occupied sites are always

Fig. 5. Number of Ivory Gull individuals counted on Seymour Island between 1974 and 2006. The asterisk indicates that the colony was not occupied in 2002 and thus could not be counted.



identified; otherwise, the calculated colonization rate will be biased low. Similarly, with count data, all individuals in the population may not be counted. Apparent trends in numbers of birds may simply reflect a declining ability of observers to detect birds that are present or a change in the attendance patterns of bird at the colony, e.g., in recent years the second pair member was more likely to be absent from the colony or fewer failed or nonbreeding birds were present at the colony. Although such biases are likely present in the data, they are probably not large, as Ivory Gull individuals are counted relatively easily because of their conspicuous plumage and behaviour in the relatively barren habitat in which they breed (Gilchrist and Mallory 2005). The assumption that environmental conditions will not change over the time period of the projection is likely not to hold, but without a longer time series available, it is difficult to predict how conditions might change and how Ivory Gull might respond to these conditions. Density-dependent effects are likely to be important if the population continues to decline and will likely accelerate any declines through the Allee effect (e.g., Gilchrist 1999).

The model was not overly sensitive to the values of the colonization and extinction rates, likely because these two rates were so different. In models in which these rates are similar, changes in the values have greater effects on the model results. The size of colonies that persisted was the most sensitive parameter and delayed the population decline more than similar changes in other parameters. Given that the size of colonies that persisted was estimated based on only nine colonies, this is likely the largest source of uncertainty in the model projections.

A relationship between colony size and extinction or abandonment probability has been observed in other avian studies and is not unexpected (Barbraud et al. 2003, Chaulk et al. 2006). For very small colony sizes, demographic stochasticity and individual deaths of birds may lead to extinction. Further, small colonies may not be as attractive to recruiting or breeding birds, so birds settle in larger colonies (i.e., conspecific attraction; Stamps 1988). Although data were available for only 5 yr, the apparent clumping of the remaining birds breeding on southern Ellesmere Island and Devon Island, especially from 2002 to 2004, suggests that birds settle in fewer but larger colonies as the population declines. Levels of natal and breeding site fidelity are not known in this species, but in the related Black-legged Kittiwake, *Rissa tridactyla*, natal dispersal is not uncommon at local scales (e.g., tens of kilometres; Coulson and Nève de Mévergnies 1992), recruiting birds are attracted to more successful colonies, and established breeders will leave unsuccessful sites (Danchin et al. 1998).

No relationship was found between colonization rate and a measure of colony isolation (i.e., the number of colonies within 10 km). There are a number of possible reasons for this lack of relationship, including a limited sample size and/or an insufficient time series to detect a relationship. However, the estimate was close to zero and the confidence limits were wide, so there was no indication of even a weak relationship. The most obvious biological reason for the lack of a relationship is that the dispersal of breeding Ivory Gull is not limited to small distances such as 10 km. This suggests that pockets of colonies do not appear to act as units with movements of birds among them; isolated breeding sites were just as likely to be used as aggregated sites. Therefore, at the scale used in our analysis, there was no evidence of rescue effects from nearby colonies (i.e., the immigration of individuals from nearby colonies; Brown and Kodric-Brown 1977). Rescue effects in this species, if they are possible, may occur at larger spatial scales, e.g., from birds breeding further north on Ellesmere Island, western Greenland, or possibly Seymour Island.

The projections of colony dynamics based on the data collected from 2002 to 2006 show that if current conditions do not change, the population of Ivory Gull nesting on southern Ellesmere Island and Devon Island will persist only at low numbers, and this will happen relatively soon, within 10 years. An important component of the model is the colonization rate, which was found to be quite low compared to the extinction rate. If extant colonies were missed, especially at previously unoccupied sites, then the colonization rate calculated would be biased low. However, given the extensive survey coverage of potential sites on southern Ellesmere Island and Devon Island (Gilchrist and Mallory 2005), we do not think that the colonization rate is severely underestimated. Because of the variety of uncertainties inherent in any population viability analysis, the calculated time to extinction or to a quasi-extinction threshold should not be considered absolute (Beissinger and Westphal 1998). The important point is that unless conditions change, in the near future there may not be a viable breeding population of Ivory Gull on southern Ellesmere Island and Devon Island, as is already apparently the case for the breeding population on the Brodeur Peninsula of Baffin Island.

The large colony on Seymour Island also declined slowly from 1974 to 2006 at 2.7%/yr. The estimated median time to extinction was relatively long, at 145 yr, as was the estimated time to the quasi-extinction threshold of 10 pairs, at 66 yr. Thus, unlike Devon Island and southern Ellesmere Island, there is probably sufficient time for management activities to be introduced and implemented before the population breeding on Seymour Island is perilously small. Alternatively, given the large uncertainty in the estimates of time to extinction, continued monitoring at Seymour Island may be all that is warranted in the short term to determine if the population is truly in long-term decline.

The suggestion that Ellesmere Island will be the last region to support breeding Ivory Gull is supported by the recent discovery of colonies there in 2006. These sites were not detected in previous surveys; therefore, it is not known whether some of these colonies have always been occupied or whether they constitute birds that have moved north from southern Ellesmere Island and Devon Island. If these sites have always been occupied, as suggested by the vegetation present for four of the colonies, then it simply means that the Canadian breeding population has been consistently underestimated, e.g., by up to 700 pairs in 2006. If this represents the movement of birds from southern breeding areas, it means that the apparent declines have been overestimated. However, the range contraction from southern and western breeding areas is still cause for concern because previously occupied and presumably suitable habitat is no longer being used.

A particular advantage of colony-based dynamics study is that it deals with the issue of nonbreeding and colony movement, at least within the study area, better than detailed projections based on vital rates calculated from a single study site. Extinction rates are effectively the product of nonbreeding rates and colony abandonment via dispersal, death, or both, whereas colonization rates result from the return of birds to previously abandoned colonies and new colony establishment via immigration, recruitment, or both. In studies at single sites, both nonbreeding and colony movement can lead to survival rates that are underestimated (Pradel et al. 1997) and thus population growth rates that are underestimated. Multisite studies, including assessments of movement or telemetry studies, avoid this problem, but can be expensive, time consuming, and not always practical for rare species. Specific to Ivory Gull, all of the nunatak sites are essentially inaccessible, making Seymour Island the only appropriate study site for detailed work in Canada.

CONCLUSION

Overall, the models show that the Ivory Gull population breeding in Canada is at risk of local extirpation across much of its breeding range if current conditions continue. Southern areas such as the Brodeur Peninsula may already be extirpated. This continues an apparent pattern reported by Haney and MacDonald (1995), with the loss of Ivory Gull colonies previously extant in the western and northwestern Canadian Arctic archipelago. Clearly, diagnosing the cause of these declines is a priority. Human harvest (Stenhouse et al. 2004) and trace metal contamination (Braune et al. 2006) show promise as possible and avoidable causes of population decline. However, the shooting of Ivory Gull is no longer considered a major source of mortality in Canada or Greenland (it is unknown if they are shot in eastern Russia), and the reduction of trace metal contamination in the Arctic will be a long process requiring international collaboration. Several types of environmental change could be involved in the apparent declines (Gilchrist and Mallory 2005), but once again, little can be done in the short term to ameliorate climate conditions in the Arctic. Assessments of population trends and avian health from other parts of the Ivory Gull's circumpolar range would help to ascertain whether the declines in Canada are a regional issue or whether the entire global Ivory Gull population is under stress and declining.

Efforts should be made to protect existing colonies because they may provide the final refuges for this species in Canada, as well as a source of potential emigrants to colonize abandoned sites. Ivory Gull, like terns, will change breeding sites (but the distances moved tend to be limited; Bateson and Plowright 1959, Volkov and de Korte 1996), so the species appears to have the potential to colonize new sites when population numbers are sufficient. Recent genetic analyses indicate that there is little genetic structure among breeding populations of Ivory Gull in Canada, Greenland, and Norway (Royston 2007), again suggesting that dispersal and colonization is a normal part of the life history of this species. Estimates of natal and dispersal rates would be valuable for future population modelling and could lead to a better understanding of the overall risks to the Canadian population, although these estimates may have to come from other regions where larger and accessible colonies are located. It is also not known whether breeding and recruiting birds will move from flat island breeding or natal sites to cliff nesting habitat and vice versa; if they do not, there will less opportunity for population rescue. In spite of the slow decline in the last 30 yr observed on Seymour Island, which is the largest colony in Canada, projections suggest that there is sufficient time to intervene at this colony if useful and practical management actions to boost the population growth rates can be implemented. Further monitoring at this site is clearly warranted to determine if this population is truly in long-term decline.

Responses to this article can be read online at:
http://www.ace-eco.org/vol2/iss2/art8/responses/

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