

ESTIMATING THE SIZE OF THE GREATER SNOW GOOSE POPULATION

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Abstract: Accurate and precise estimation of the size of animal populations is critical to sound management and conservation. The size of the greater snow goose (*Chen caerulescens atlantica*) population has been monitored since 1965 by means of an aerial photographic survey conducted every spring in southern Quebec, Canada. As the population increased, the estimation of its size evolved from total counts of the birds on photographs (1965–1990) to sampling the photographed flocks (1991–2000). From 1998 to 2000, we implemented a protocol to estimate the proportion of flocks missed by the photographic survey. This was achieved using radiomarked geese that were tracked by independent observers during the aerial survey. The proportion of radiomarked geese detected during the survey was used to estimate the proportion of the population that was photographed. The estimated size of the photographed population was based on a combined stratified ratio estimator using partial counts and visual estimates of flocks in 3 size classes. The estimated size of the photographed population had a coefficient of variation (CV) of 2–6%. This precision was achieved by counting only 15% of the photographed geese on average, which was a large gain in logistical efficiency considering the size of the population. We found no evidence for overdispersion of the number of radiomarked birds ($n = 70$ in 1998, $n = 41$ in 2000) encountered in each flock. In 1999, technical problems with radiotransmitters prevented a reliable total population size estimate. In 1998 and 2000, we estimated that the photographic crew missed 11 and 29%, respectively, of the radiomarked geese present. The CV of the total population size estimates were 5.8% in 1998 and 11.1% in 2000. As the proportion of missed flocks increases, the number of radiomarked birds required to obtain a CV of 5% increases with a concomitant increase of cost. We highlight spatial and temporal changes in the spring distribution of greater snow geese staging in southern Quebec and suggest that adjustments of timing and coverage of the surveys will be required to maintain and improve the accuracy of the population size estimates at low cost.

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Estimating the size of animal populations is a prerequisite for effective conservation and management of both harvested and endangered species. The accuracy of population size estimates has always received considerable attention (Seber 1982, 1986). The difficulty of obtaining accurate estimates is especially evident for terrestrial mammals that are difficult to observe (Floyd et al. 1979, Crête et al. 1986, Karanth and Nichols 1998) and marine mammals that range over wide areas and spend most of their time underwater (Zeh 1999). However, even for large and conspicuous birds, visibility biases in ground or aerial counts may be an important source of inaccuracy in population size estimates (Caughley 1974, Heusmann 1990, Bromley et al. 1995).

Traditionally, population management of North American snow geese has been based on trends in numbers of geese detected from mid-winter surveys (Eggeman and Johnson 1989, Heusmann 1999). These surveys do not provide estimates of total numbers. The winter range is sampled by flying transects and using experienced observers to estimate visually the size of the flocks encountered. No attempt is made to adjust for visibility bias or to extrapolate to areas outside the transects. Researchers assume that an equal portion of the population is encountered each year, the visibility bias is constant each year, and the trends detected reflect those occurring in the overall population. Wintering snow geese range widely over large expanses of coastal marshes and agricultural fields (Hill and Frederick 1997), and midwinter surveys are unlikely to encounter the same proportion of the population each year. In the late 1960s, an aerial photographic survey was developed to monitor the greater snow goose population of the Atlantic Fly-

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way in southern Quebec (Heyland 1972, Gauvin and Reed 1987, Reed et al. 1998). Because the entire population occupied a restricted area along the St. Lawrence River in southern Quebec during the spring staging period, researchers assumed that all flocks were encountered during a survey flight. The white plumage of the geese facilitated detection of flocks and allowed the use of aerial photography to improve count accuracy.

From 1965 to 1990, all geese were counted on each photograph, yielding a complete census. With the increasing number of geese in the early 1990s, counting geese on all photographs became increasingly tedious and costly. In response to this problem, the survey procedure was changed in 1991 from counts of birds on all photographs to counting a sample of the photographed flocks. As goose numbers continued to increase throughout the 1990s, their range expanded into agricultural lands farther inland from the St. Lawrence River, and detecting all flocks in a single survey became difficult. In 1998–2000, we used radiomarked geese to estimate the proportion of flocks missed by the photographic survey.

Our objectives were to develop a statistical method to estimate the population size based on a sample of aerial photos. We then used a capture–recapture model with the radiomarked birds detected during the aerial survey to estimate the proportion of missed flocks. We also evaluated the number of radiomarked birds necessary to obtain a given precision on population size estimates. Finally, we determined the optimal timing of the surveys.

STUDY AREA

The spring photographic survey covers the entire area used by staging greater snow geese in southern Quebec, Canada. Until the mid-1980s, this area was limited to the upper and lower estuary of the St. Lawrence River (i.e., east of Quebec City). Thereafter, the area gradually expanded so that, in 2000, we extended the survey from Lake Champlain to Lake St. Pierre, then to Matane and Baie-Comeau along the St. Lawrence River, and finally to the Lake St. Jean region (Reed et al. 1998).

METHODS

Photographic Survey

We conducted aerial surveys using a high-winged, twin-engine aircraft (Islander™), which allowed coverage of the staging area in 1 or 2 days. Because of the short-term spatial stability of

flocks along the St. Lawrence River (Béchet et al. 2003), we assumed that conducting the survey over 2 days did not affect the overall estimate. We established standardized transects according to the known distribution of geese in southern Quebec (i.e., mostly along the shore of St. Lawrence River and main tributaries). Three observers, including the photographer, were on board the plane, and flight altitude varied between 600 and 900 m. The same photographer was involved with all the surveys conducted between 1991 and 2000. Flocks were identified visually and photographed using a hand-held, motor-driven, 35-mm reflex camera with a 70–210-mm zoom lens and 200 ISO color print film. A few small flocks could not be photographed because they were too far from the plane or in rapid movement; the photographer estimated visually the size of these flocks.

We conducted 3 surveys each spring during 1991–1995, and 2 each spring thereafter. Surveys were conducted when all geese had left the wintering grounds, as indicated by personnel of the most northern United States refuges used by greater snow geese (e.g., Forsythe National Wildlife Refuge, New Jersey, USA), and before the geese departed for the Arctic, which is highly synchronized and occurs between 15 and 25 May (Gauthier et al. 1988).

Radiotracking and Ground Visual Estimates

As part of a long-term study of the ecology of the greater snow goose, 310 adult females were captured and radiomarked on their breeding area at Bylot Island, Nunavut, Canada (73°00'N, 80°00'W), in August between 1996 and 1999 (Demers et al. 2003). The radio package weighed 59 g (i.e., about 2.5% of female mean body mass), had a life expectancy of ≥ 1 year, and had a signal that could be detected at least 5 km from the air.

From 1998 to 2000, ground radiotracking was done daily from the beginning of the staging period in southern Quebec (mid-Mar) to the departure of the last marked birds for the Arctic (late May). Our aim was to determine the number of radiomarked birds alive and with functioning radiotransmitters during each photographic survey. We assumed that the number of radiomarked geese detected both before and after a given survey was equal to the number of radiomarked birds (M) present in the population during the survey. Six crews covered the entire staging area of southern Quebec using vehicle-mounted directional antennas. To check for birds that might have escaped detection after the

survey because of departure for the breeding grounds, we also conducted radiotracking on the breeding grounds in June (Reed et al. 2003). Each time that a radiotransmitter was detected, we scored the signal quality as good, average, or poor based on regularity and strength relative to the distance to the bird.

In 1998, 1999, and 2000, 2 additional observers recorded the presence of radiomarked geese in flocks photographed during the survey. Two omni-directional antennas were mounted on the airplane (McAuley et al. 1993). Each observer scanned half of the radio frequencies (approx 40 each) at 3-sec intervals. When a radio signal was detected, we assigned the signal to the flock being photographed by the survey crew. Most of the time (80%), we could reliably assign a radiomarked goose to a flock because the airplane circled the flocks to improve quality of the photographs. Occasionally, we could not determine from which of 2 or more nearby flocks a signal was coming. In these cases, radiomarked geese were assigned to a group representing a combination of the flocks in question. Only the photographic crew located flocks, whereas the radiotracking crew operated independently and checked flocks for the presence of radiomarked geese. Flocks that were detected only by the radiotracking crew were not used in the analyses. Similarly, on the rare occasion that a radio signal was heard but no flocks seen, we considered these radiomarked birds as missed. We did not use radiotelemetry to locate goose flocks.

We performed ground visual estimates of number of geese daily at dawn in the larger roosting sites and once every 2 or 3 days in the smaller sites. We summed estimates across sites to obtain an index of the seasonal variation in the total number of geese present in southern Quebec. The mean of 2 estimates was used for sites with irregular coverage. We compared our index of population variation to the seasonal variations in the number of radiomarked geese present in the survey area based on our first and last detections of radiomarked geese in the season.

Estimation of the Size of the Photographed Population

We reconstituted flocks that were covered by >1 photograph by overlapping the photos. Starting in 1991, each photographed flock was assigned to a size class or stratum (small, $S \leq 2,000$ geese; medium, $2,000 < M \leq 5,000$; and large, $L > 5,000$) based on visual estimates of 10×15 -cm prints.

Sampling was conducted in 2 stages. We initially selected a random sample of flocks within each size stratum. These flocks were the primary sampling units, and we sampled about 25, 50, and 80% of the flocks in stratum S , M , and L , respectively. These sampling rates were based on an optimal allocation in which the sampling rates increase with flock size. Occasionally, we encountered flocks that were much larger than most, and we considered these flocks as an extra stratum. We overlaid a square grid on each sampled flock, and we counted geese using a systematic sample of squares. We counted geese in one-ninth of the S and M strata and one-fourth of the L and extra strata. Sampling rates at both stages were aimed at providing a CV of 5% on the estimated number of geese photographed. We counted individual geese on the photograph using a 10X binocular microscope and an automatic counting device (a pen attached to a digital tally).

We estimated the total number of geese in the photographed flocks (Y_p) with a combined stratified ratio estimator (S rmdal et al. 1992). The ratio of the counts to visual estimates was estimated globally for all sampled flocks and was then multiplied by the total number of geese estimated visually. If

N_h is the total number of flocks photographed in strata h ,

n_h is the number of flocks sampled for count in strata h ,

x_{hi} is the visual estimate of flock i in strata h , $i = 1, \dots, N_h$,

M_{hi} is the number of squares covering flock i in strata h , $i = 1, \dots, n_h$,

m_{hi} is the number of squares counted for flock i in strata h , $i = 1, \dots, n_h$, and

y_{hij} is the number of geese counted in square j for flock i in strata h , $i = 1, \dots, n_h$, $j = 1, \dots, m_{hi}$,

then the size of the photographed population is estimated by

$$\hat{Y}_p = X \frac{\sum_h N_h \hat{y}_h}{\sum_h N_h \bar{x}_h} = X \hat{R}, \tag{1}$$

where $X = \sum_h \sum_{i=1}^{N_h} x_{hi}$ is the total visual estimate,

$\sum_h N_h \hat{y}_h$ is the estimated number of geese based on partial counting of the sampled flocks, and

$\sum_h N_h \bar{x}_h$ is the estimated number of geese based on visual estimates of the sampled flocks with

$$\hat{y}_h = \frac{1}{n_h} \sum_{i=1}^{n_h} \frac{M_{hi}}{m_{hi}} \sum_{j=1}^{m_{hi}} y_{hij} \quad \text{and} \quad \bar{x}_h = \frac{1}{n_h} \sum_{i=1}^{n_h} x_{hi}.$$

The variance of \hat{Y}_p is estimated by

$$v(\hat{Y}_p) = \left[\frac{X}{\sum_h N_h \bar{x}_h} \right]^2 \left[\sum_h \frac{N_h(N_h - n_h)}{n_h} \sum_{i=1}^{n_h} \frac{(\hat{d}_{hi} - \bar{d}_h)^2}{n_h - 1} + \sum_h \frac{N_h}{n_h} \sum_{i=1}^{n_h} \hat{V}_{hi} \right], \quad (2)$$

where $\hat{d}_{hi} = \hat{y}_{hi} - \hat{R}x_{hi}$, $\bar{d}_h = \frac{1}{n_h} \sum_{i=1}^{n_h} \hat{d}_{hi}$ and

$$\hat{V}_{hi} = \frac{M_{hi}(M_{hi} - m_{hi})}{m_{hi}} \sum_{j=1}^{m_{hi}} \frac{(y_{hij} - \bar{y}_{hi})^2}{m_{hi} - 1} \text{ with } \bar{y}_{hi} = \frac{1}{m_{hi}} \sum_{j=1}^{m_{hi}} y_{hij}.$$

The stratified ratio was appropriate because the size distribution of flocks was not uniform with few large flocks and because visual estimates highly correlated with counts were easy to obtain (Särndal et al. 1992). Under the hypothesis that the relation between counts and visual estimates is a straight line through the origin and that the variance of the counts around this line is proportional to visual estimates, the ratio estimator is the best linear unbiased estimator (Cochran 1977). The combined estimate was preferred because the number of flocks sampled for counting was relatively small in some strata and because the ratio showed little variation relative to flock size. Counts of sampled flocks plotted against visual estimates supported the latter assumption, and Wald tests seemed to indicate that the ratio varied little, if any, among strata. Flocks that were only visually estimated by the photographer during the aerial survey were added to the total estimate.

Estimation of Total Population Size

We estimated the size of the total population (Y_t) as

$$\hat{Y}_t = \frac{1}{\hat{p}} \hat{Y}_p,$$

where \hat{Y}_p was the size of the photographed population and \hat{p} was the proportion of geese present in the survey area that was visually detected and photographed during the survey. We estimated \hat{p} using radiomarked geese (Rivest et al. 1998). We made 5 assumptions: (1) The population was closed to additions (immigration) or deletions (emigration or death) during a given survey. (2) All geese present in the survey area were equally likely to be detected. (3) Radiotransmitters were

not lost during the survey and were not overlooked by the radiotracking crew when present in a flock detected by the photographic crew. (4) No exchange of individuals among flocks occurred during the survey. (5) Radiomarked geese were independently distributed across the population.

Assumption (1) likely was met because of the short time needed for a survey and the relative short-term stability of flocks in southern Quebec (Béchet et al. 2003). We considered in our analyses only radiomarked geese detected in flocks that were visually detected and photographed so that assumption (2) was upheld. We considered only radiomarked geese with a good signal in the estimation of \hat{p} , and those geese considered to be present during the survey had to be detected at least once afterward; therefore, assumption (3) likely was met. Distinct flocks could eventually amalgamate when disturbed by the plane, but we then considered them as a new flock. We believe that geese likely were not photographed twice, so assumption (4) also was likely met. Assumption (5) could be violated if radiomarked geese were not homogeneously distributed across the population. If assumption (5) is true, the number of radiomarked geese encountered in each flock should approximate a Poisson distribution (Rivest et al. 1998). The method outlined by Dean and Lawless (1989) and Dean (1992) provides a score test for the overdispersion assumption (Appendix A).

The proportion of geese encountered during the survey relative to the total number of geese in the population has a binomial distribution $B(Y, p)$ and can be estimated from radiomarked birds. If M is the total number of radiomarked geese present during the survey and m is the number of radiomarked geese in flocks visually detected and photographed during the survey, then we can estimate \hat{p} by $\hat{p} = \frac{m}{M}$ with the expectation $E(\hat{p}) = p$ and the variance $V(\hat{p}) = \frac{p(1-p)}{M}$.

We estimated the variance of the population size estimates based on the univariate delta method (Bishop et al. 1975) as

$$V(\hat{Y}_t) = \frac{V(\hat{Y}_p)}{\hat{p}^2} + \frac{1-\hat{p}}{M\hat{p}^3} (Y_p^2 + V(\hat{Y}_p)). \quad (3)$$

We estimated the number of radiomarked geese required to achieve various levels of precision based on the CV. The CV of the estimator of the

Table 1. Estimates ($\hat{Y}_p \pm 95\% \text{ CI}$) of the size of the photographed population (photo), number of geese visually estimated (visual; not photographed), and precision (CV) of the annual photographic surveys of the greater snow goose population in southern Quebec, Canada, spring 1991–2000. The number of geese not photographed is not included in the photographic estimate.

Year	25 Apr–1 May			2 May–9 May			11 May–18 May		
	Photo	Visual	CV (%)	Photo	Visual	CV (%)	Photo	Visual	CV (%)
1991	259,900 ± 32,600	12,090	6.4	342,100 ± 30,800 ^a	10,487	4.6	287,500 ± 27,000	11,910	4.8
1992	417,600 ± 49,100	16,235	6.0	428,400 ± 38,600	5,615	4.6	436,100 ± 39,300 ^a	11,980	4.6
1993	349,200 ± 30,800	7,570	4.5	417,400 ± 42,500	165	5.1	496,000 ± 40,800 ^a	2,365	4.2
1994	403,900 ± 49,900	1,748	6.3	418,100 ± 35,200	1,916	4.3	587,900 ± 51,900 ^a	3,450	4.5
1995	501,300 ± 60,900	3,210	6.2	563,900 ± 47,500	4,039	4.3	611,800 ± 49,200 ^a	4,820	4.0
1996				579,700 ± 48,900	5,443	4.3	664,500 ± 66,400 ^a	4,586	5.0
1997				586,800 ± 55,200	8,902	4.8	657,500 ± 54,800 ^a	6,745	4.2
1998				694,200 ± 34,400	1,379	2.5	739,300 ± 58,500 ^a	1,930	4.0
1999				796,700 ± 63,400 ^a	6,704	4.0	754,600 ± 67,700	6,811	4.5
2000				571,700 ± 55,700 ^a	5,566	4.9	502,200 ± 50,700	7,643	5.1

^a Highest annual estimates.

size of the population \hat{Y} is estimated by $\beta = \frac{\sqrt{v(\hat{Y})}}{\hat{Y}}$, where $v(\hat{Y})$ is the estimator of $V(\hat{Y})$. Hence, having a CV of $\beta_{\hat{p}}$ for \hat{Y}_p , we want to achieve a CV of β_t ($\beta_t > \beta_p$) on \hat{Y}_t . Therefore,

$$v(\hat{Y}_p) = (\beta_p \hat{Y}_p)^2, \tag{4}$$

and similarly, $v(\hat{Y}_t) = \left(\frac{\beta_t \hat{Y}_t}{\hat{p}} \right)^2$. (5)

Using Equation (3), we estimated the total number of radiomarked geese required to obtain the desired precision by:

$$\hat{M} = \frac{\left[\frac{1 - \hat{p}}{\hat{p}^3} (\hat{Y}_p^2 + v(\hat{Y}_p)) \right]}{\left[v(\hat{Y}_t) - \frac{v(\hat{Y}_p)}{\hat{p}^2} \right]}. \tag{6}$$

Rearranging with Equations (4) and (5), Equation (6) becomes

$$\hat{M} = \frac{(1 - \hat{p}) (1 + \beta_p^2)}{\hat{p} (\beta_t^2 - \beta_p^2)}.$$

Hence, the number of radiomarked geese required to achieve a given precision on the estimation of the size of the total population depends on the proportion of geese detected during the survey and on the precision of the photographic estimate. We applied calculations to the size of the photographed population, omitting flocks with no photographs that could be added to afterward. We performed all calcula-

tions using application POPCREST (Population Combined Ratio Estimator), which we developed in SAS language (SAS Institute 1999). The program is available from the authors as supplementary information.

RESULTS

Estimation of the Size of the Photographed Population (1991–2000)

The CV of the estimated size of the photographed population averaged 4.7% (range = 2.5–6.4%; Table 1). In 1991, 1999, and 2000, the early May survey yielded the highest population size estimate, whereas the mid-May survey was highest in the 7 other years. Because the late April surveys always gave the lowest values, these surveys were abandoned in 1996. We obtained estimates from the photographic surveys after counting only 15% of the geese for an average of 47 ± 3 hr of work per survey. In 1990, the aerial survey took 6.5 hr of flight and 52 hr to enumerate all the geese; whereas in 2000, the survey took 9.2 hr and >81 hr would have been required to count all the geese (i.e., twice the time actually used), which confirms the logistical efficiency of the sampling method. The visual estimates of the number of birds that were not photographed averaged 6,132 (CV = 66%) per survey and were <4 % of the photographic estimates.

Estimation of Total Population Size (1998–2000)

The number of radiomarked geese present in southern Quebec generally decreased from the early May to the mid-May survey (Table 2). Because this decrease presumably reflected, in part, the early departure of some birds for the Arctic, we

Table 2. Number of radiomarked geese present (M) in the survey area, number detected (m), and proportion detected (%) during annual photographic surveys in southern Quebec, Canada, 1998–2000.

Year	Survey date	M	m	Detected (%)
1998	Early May	70	53	75.7
	Mid-May ^a	70	62	88.6
1999	Early May	31	21	67.7
	Mid-May	19	9	47.4
2000	Early May ^a	41	29	70.7
	Mid-May	20	20	100.0

^a Surveys used to correct the photographic population estimate.

planned to use the survey when the highest number of radiomarked birds was present on the staging grounds. In 1998, this number was the same in both surveys, but a higher proportion of flocks were missed during the first survey (24%) than during the second survey (11%; Table 2). In this case, we used the second survey to estimate population size to increase precision of the estimate. In 1999, 32 and 53% of the radiomarked birds

were missed during the first and second surveys, respectively, and in 2000, 29% were missed during the first survey and none during the second. However, the number of radiomarked geese present had decreased by $\geq 40\%$ between the first and second surveys in both years. We therefore used the first estimate in these 2 years. Estimating total population size in 1999 yielded a large estimate with large CV (1,176,100; CV = 13%). Because of technical problems with the radiotransmitter antenna and the small number of radiotransmitters with a good signal, we suspect that not all radiomarked birds were detected. We thus chose to discard the total population size estimate for 1999.

On some occasions (9 in 1998, 13 in 2000), radiomarked geese could not be assigned to a flock because of high goose concentrations. We estimated an overall flock size as the sum of the visual estimates of each flock. The mean number of radiomarked geese per flock was 0.68 (CV = 28%, $n = 91$) in 1998 and 0.19 (CV = 16%, $n = 151$) in 2000. We found no evidence for overdispersion of the radiomarked birds among flock sizes (1998: $z = 1.52$, $P > 0.05$; 2000: $z = 0.44$, $P > 0.3$).

The total population size estimate was 834,700 (CV = 5.9%) in 1998 and 808,300 (CV = 11.2%) in 2000. The number of geese that were counted but not photographed (1,930 in 1998, 5,566 in 2000; Table 1) can be added to these estimates. The number of radiomarked geese required to provide a CV of 5% would have been 127 in 1998 and 3,098 in 2000. A CV of 7% in 2000 still would have required 121 radiomarked birds. The number of radiomarked geese required to obtain an acceptable level of precision on the population size estimate rapidly declined with an increase in both the proportion of radiotransmitters detected and the level of precision of the photographic estimate (Fig. 1).

Ground Visual Estimates and Migration Chronology

During 1997–2000, we obtained the maximum number of geese estimated during the ground surveys about 20 April (Fig. 2). After that date, we observed a fragmentation of the flocks and dispersion toward small satellite roosting sites, which made exhaustive coverage more difficult. The maximum number of geese that we estimated on the ground was 650,000 in 1998 and 790,000 in 2000, which represented 78 and 98% of the population size estimates, respectively. During our study, both aerial surveys were carried out at least 10 days after the peak estimate (Fig. 2).

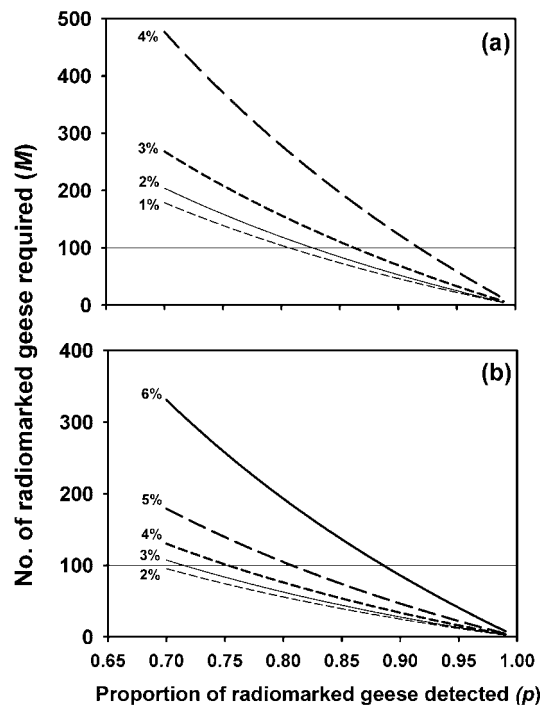


Fig. 1. Number of radiomarked geese (M) required to obtain a coefficient of variation of 5% (a) and 7% (b) on the total population size estimate in relation to the proportion of radiomarked geese detected (p) during annual surveys in southern Quebec, Canada. Each line corresponds to the coefficient of variation (% in bold) obtained on the size of the photographed population. For a given M (e.g., 100), drawing a horizontal line allows prediction of the precision required on the photographic estimate to obtain a given coefficient of variation on the total population size estimate for various p .

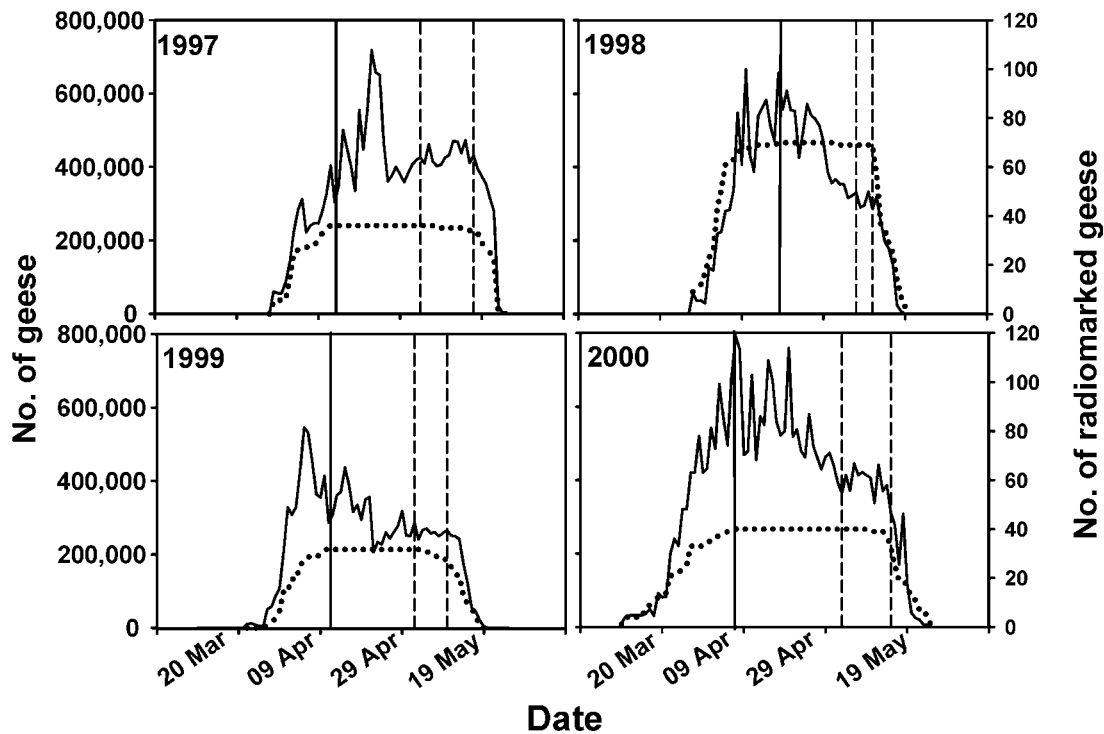


Fig. 2. Total ground counts of the greater snow goose population conducted daily at major roosting sites (plain line) and total number of radiomarked birds present (dotted line) in southern Quebec, Canada, 1997–2000. Solid vertical lines indicate the arrival date of the last radiomarked goose. Dashed vertical lines indicate the date of the 2 aerial photographic surveys each year.

Aerial surveys also were conducted at least 10 days after the arrival of the last radiomarked goose in Quebec (range = 7–19 Apr in 4 yr of radiotracking) and sometimes after the date when we started to lose signals of radiomarked geese (range = 22 Apr–10 May; Fig 2). These missing birds did not necessarily represent departure for the Arctic but may reflect dispersal of geese to small, less-accessible roosting sites outside our study area.

DISCUSSION

Photographic surveys provide more accurate estimates of the size of the snow goose population than visual aerial or ground surveys (Boyd 2000). The 2-stage, stratified sampling with a combined ratio estimator yielded a precise estimate of the photographed population at low cost. We did not estimate the accuracy of the visual estimates of small flocks made by the photographer. However, visual estimates of small flocks are less likely to be biased (Boyd 2000) and non-photographed flocks always represented <4% of the final estimate. We are confident that these visual estimates did not introduce significant biases in the final estimates of the total population.

A potential weakness of the photographic surveys was our assumption that all flocks were encountered during the survey. Our capture–recapture approach using radiomarked geese confirmed that some flocks were missed during the 1998–2000 surveys. Nonetheless, the relatively small proportion of flocks missed during the 1998 survey (approx 11%) suggests that the photographic estimate provided a reliable estimate of the population up to this date, especially in previous years when the population was smaller and less dispersed. The relatively large proportion of birds missed in 2000 (29%) may be a consequence of the spring hunt, a conservation measure introduced in 1999 that considerably altered the movements and distribution of geese in southern Quebec (B chet et al. 2003). Previous capture–recapture methods developed to estimate population size relied heavily on ground counts (Frederiksen et al. 2001) or on the number of birds checked for marks (Hestbeck and Malecki 1989, Routledge et al. 1999) to correct for such biases. Our methodology used a highly accurate tool (i.e., photographic counts) to estimate the total size of the surveyed population

with an associated variance. This estimate corresponds to the total number of geese checked for the presence of radiocollars during the survey.

Radiomarked individuals have been used to estimate population size with ratio estimators or capture–recapture models using natural marks, individually marked tags, or radiotransmitters (Crête et al. 1986, Bordage et al. 1998, Karanth and Nichols 1998). The use of radiotransmitters allowed us to check for the presence of a known number of radiomarked individuals present in the population, which is an advantage over methods in which this number has to be estimated from the resighting histories of marked individuals using a Jolly-Seber approach (Sheaffer and Jarvis 1995). Moreover, with radiotransmitters, we can reasonably assume that marks were not overlooked and that all radiomarked geese in photographed flocks were detected (i.e., capture probability = 1). This increased the precision of the population size estimate because the variance associated with a capture probability <1 will inflate the overall variance of the estimate.

None of the previously cited capture–recapture studies have checked for overdispersion of the marked individuals within the studied population when estimating population size. Yet, the assumption that marked individuals represent a random sample of the population is important to derive unbiased population size estimates. Frederiksen et al. (2001) mentioned that this was an important assumption in their analyses, but they did not validate it. We have presented a simple method to test this assumption.

The precision obtained with our radiotracking protocol in 1998 demonstrates the usefulness of our method. However, the lower precision in 2000—due to the high proportion of missed flocks and the unrealistic population size estimate in 1999—also highlight the limitations of our method. The method is inherently constrained by the total number of radiomarked individuals in the population, and this number was too small in 1999 given the low proportion of radiomarked geese detected. Having a large number of radiomarked geese in the population is expensive and also increases the time required to scan for all radiotransmitters. We consider that 50 frequencies represent a maximum per observer; otherwise, the chance of missing radio signals between successive scans would increase. Hence, individuals missed by a photographic survey can satisfactorily be taken into account by radiotracking only if the proportion of missed individuals is

not too high. A high proportion of missed geese requires such high numbers of radiomarked geese that additional radiotelemetry observers should be aboard the plane to check for all radiotransmitters accurately. The precision of the total population size estimate also depends on the precision of the photographic estimate. Therefore, a reduced precision due to an increased number of missed flocks can be partly offset by increasing precision of the photographic estimate, but this may be time consuming and hence costly. These considerations highlight the need to plan the spatial coverage of the photographic survey carefully to limit the number of missed individuals.

The staging area of the greater snow geese expanded into southwestern Quebec in the mid-1980s (Reed et al. 1998). As snowmelt occurs earlier in this region than in the traditional staging regions of the estuary, the geese now arrive earlier in Quebec (Reed et al. 1998). In our study, all radiomarked geese arrived in Quebec by 15 April, and the total number of geese estimated in the range regularly covered by the ground crews decreased after 20 April. This cannot be explained by the departure of geese for the Arctic, which normally does not occur until 15 May (Gauthier et al. 1988). Rather, it reflects the dispersal of flocks to small, scattered roosting sites. A further possible complication for timing of the survey arose in 1999 when the spring conservation hunt was implemented in Quebec but not in Ontario (Canadian Wildlife Service 2001). A number of greater snow geese may have remained in Ontario or Vermont in early May or may have returned there after experiencing the hunt (Béchet et al. 2003). Similar distribution changes have been recorded in other goose populations causing drops in counts conducted in traditional areas that did not reflect genuine trends for the whole population (Clausen et al. 1998, Ganter and Madsen 2001).

MANAGEMENT IMPLICATIONS

The recent shift in management priorities for several snow goose populations in eastern and central North America, from sustained harvest with an objective of population growth to one of population stabilization and reduction (Johnson 1997, Giroux et al. 1998), reinforces the need to estimate the size of these large populations accurately. This also applies to other increasing goose populations in Europe and North America (Madsen et al. 1999). In addition, accurate estimates of population size are important when population

goals are set on the basis of biological parameters (e.g., estimation of the carrying capacity of the habitat; see for instance Massé et al. 2001). The photographic sampling we described is 1 alternative to population size indices obtained by the traditional midwinter surveys conducted in North America (Heusmann 1999). We provided a framework that may help in designing similar surveys for other bird species. The combination of aerial photographic survey and radiotracking can be used to estimate the size of large populations of conspicuous and gregarious species. Our method also estimates the precision of the population size estimate. However, the capture, radiomarking, and ground radiotracking required involved substantial costs.

Optimal scheduling of the aerial survey to minimize the proportion of missed individuals is critical. In our case, we propose that the survey date should be a compromise between the chances of missing geese not yet arrived in Quebec and those that have already dispersed to satellite roosting sites or left the area to continue the migration. Hence, 2 surveys performed between 20 April and 10 May and covering the Ontario and Vermont borders should minimize the number of missed geese. Flying with 2–3 planes simultaneously (each covering a different portion of the range), around mid-day on sunny, warm days (when birds are grouped around roosting sites on the St. Lawrence River and other large bodies of water), also should improve the quality of the survey. Due to high cost, radiotracking could be performed once every 5 years to ensure the adequacy of the timing and spatial coverage of the photographic survey, to provide a total population size estimate, and to determine an associate precision on the estimate.

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LITERATURE CITED

- BÉCHET, A., J.-F. GIROUX, G. GAUTHIER, J. D. NICHOLS, AND J. E. HINES. 2003. Spring hunting changes the regional movements of migrating greater snow geese. *Journal of Applied Ecology* 40:553–564.
- BISHOP, Y. M. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. Discrete multivariate analysis. Massachusetts Institute of Technology, Boston, Massachusetts, USA.
- BORDAGE, D., N. PLANTE, A. BOURGET, AND S. PARADIS. 1998. Use of ratio estimators to estimate the size of common eider populations in winter. *Journal of Wildlife Management* 62:185–192.
- BOYD, W. S. 2000. Comparison of photo count versus visual estimates for determining the size of snow goose flocks. *Journal of Field Ornithology* 71:686–690.
- BROMLEY, R. G., D. C. HEARD, AND B. CROFT. 1995. Visibility bias in aerial survey relating to nest success of Arctic geese. *Journal of Wildlife Management* 59:364–371.
- CANADIAN WILDLIFE SERVICE. 2001. Migratory game bird hunting regulations in Canada. Canadian Wildlife Service Migratory Birds Regulatory Report 3.
- CAUGHLEY, G. 1974. Bias in aerial survey. *Journal of Wildlife Management* 38:921–933.
- CLAUSEN, P., J. MADSEN, S. M. PERCIVAL, D. O'CONNOR, AND G. Q. A. ANDERSON. 1998. Population development and changes in winter site use by the Svalbard light-bellied brent goose, *Branta bernicla hrota* 1980–1994. *Biological Conservation* 84:157–165.
- COCHRAN, W. G. 1977. Sampling techniques. Third edition. Wiley, New York, New York, USA.
- CRÉTE, M., L. P. RIVEST, H. JOLICOEUR, J. M. BRASSARD, AND F. MESSIER. 1986. Predicting and correcting helicopter counts of moose with observations made from fixed-wing aircraft in southern Quebec. *Journal of Applied Ecology* 23:751–761.
- DEAN, C. 1992. Testing for overdispersion in Poisson and binomial regression models. *Journal of the American Statistical Association* 87:451–457.
- , AND J. F. LAWLESS. 1989. Tests for detecting overdispersion in Poisson regression models. *Journal of the American Statistical Association* 84:467–742.
- DEMERS, F., J.-F. GIROUX, G. GAUTHIER, AND J. BÉTY. 2003. Effect of collar-attached transmitter on behaviour, pair bond, and breeding success of snow geese *Anser caerulescens atlanticus*. *Wildlife Biology* 9:161–170.
- EGGEMAN, D. R., AND F. A. JOHNSON. 1989. Variation in effort and methodology for the midwinter waterfowl inventory in the Atlantic Flyway. *Wildlife Society Bulletin* 17:227–233.
- FLOYD, T. J., L. D. MECH, AND M. E. NELSON. 1979. An improved method of censusing deer in deciduous–coniferous forests. *Journal of Wildlife Management* 43:258–261.

- FREDERIKSEN, N., A. D. FOX, J. MADSEN, AND K. COLHOUN. 2001. Estimating the total number of birds using a staging site. *Journal of Wildlife Management* 65:282–289.
- GANTER, B., AND J. MADSEN. 2001. An examination of methods to estimate population size in wintering geese. *Bird Study* 48:90–101.
- GAUTHIER, G., Y. BÉDARD, AND J. BÉDARD. 1988. Habitat use and activity budgets of greater snow geese in spring. *Journal of Wildlife Management* 52:191–201.
- GAUVIN, J., AND A. REED. 1987. A simulation model for the greater snow goose population. *Canadian Wildlife Service Occasional Paper* 64.
- GIROUX, J.-F., B. D. J. BATT, S. BRAULT, G. COSTANZO, B. FILION, G. GAUTHIER, D. LUSZCZ, AND A. REED. 1998. Conclusions and management recommendations. Pages 81–88 in B. D. J. Batt, editor. *The greater snow goose: report of the Arctic Goose Habitat Working Group*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA, and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- HESTBECK, J. B., AND R. A. MALECKI. 1989. Mark–resight estimate of Canada goose midwinter number. *Journal of Wildlife Management* 53:749–752.
- HEUSMANN, H. W. 1990. Evaluation of air/ground count comparisons for wintering American black ducks. *Wildlife Society Bulletin* 18:377–381.
- . 1999. Let's get rid of the midwinter waterfowl inventory in the Atlantic Flyway. *Wildlife Society Bulletin* 27:559–565.
- HEYLAND, J. D. 1972. Vertical aerial photography as an aid in wildlife population studies. *Proceedings of the Canadian Remote Sensing Symposium* 1:121–136.
- HILL, R. J., AND R. B. FREDERICK. 1997. Winter movements and habitat use by greater snow geese. *Journal of Wildlife Management* 61:1213–1221.
- JOHNSON, M. A. 1997. Management strategies to address the mid-continent lesser snow goose overpopulation problem. Pages 101–111 in B. D. J. Batt, editor. *Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA, and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- KARANTH, K. U., AND J. D. NICHOLS. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- MADSEN, J., G. CRACKNELL, AND A. D. FOX. 1999. Goose populations of the Western Palearctic. A review of status and distribution. *Wetland International Publications* 48. Wetland International, Wageningen, The Netherlands, and National Environmental Research Institute, Rønde, Denmark.
- MASSÉ, H., L. ROCHEFORT, AND G. GAUTHIER. 2001. Carrying capacity of wetland habitats used by breeding greater snow geese. *Journal of Wildlife Management* 65:271–281.
- MCAULEY, D. G., J. R. GOLDSBERRY, AND J. R. LONGCORE. 1993. Omnidirectional aircraft antennas for aerial telemetry. *Wildlife Society Bulletin* 21:487–491.
- REED, A., J.-F. GIROUX, AND G. GAUTHIER. 1998. Population size, productivity, harvest and distribution. Pages 5–31 in B. D. J. Batt, editor. *The greater snow goose: report of the Arctic Goose Habitat Working Group*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA, and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- REED, E. T., J. BÉTY, J. MAINGUY, G. GAUTHIER, AND J.-F. GIROUX. 2003. Molt migration in relation to breeding success in greater snow geese. *Arctic* 56:76–81.
- RIVEST, L. P., S. COUTURIER, AND H. CREPEAU. 1998. Statistical methods for estimating caribou abundance using postcalving aggregations detected by radio telemetry. *Biometrics* 54:865–876.
- ROUTLEDGE, R. D., G. E. J. SMITH, L. SUN, N. DAWE, E. NYGREN, AND J. S. SEDINGER. 1999. Estimating the size of a transient population. *Biometrics* 55:224–230.
- SÄRNDAL, C. E., B. SWENSSON, AND J. WRETMAN. 1992. *Model assisted survey sampling*. Springer-Verlag, New York, New York, USA.
- SAS INSTITUTE. 1999. *SAS/STAT user's guide*. SAS Institute, Cary, North Carolina, USA.
- SEBER, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Macmillan, New York, New York, USA.
- . 1986. A review of estimating animal abundance. *Biometrics* 42:267–292.
- SHEAFFER, S. E., AND R. L. JARVIS. 1995. Bias in Canada goose population size estimates from sighting data. *Journal of Wildlife Management* 59:464–473.
- ZEH, J. E. 1999. Correcting for missed observations in a shore-based count of whales. Pages 127–136 in G. W. Garner, S. C. Amstrup, L. L. Laake, B. F. J. Manly, L. L. McDonald, and D. G. Robertson, editors. *Proceedings of the symposium on marine mammal survey and assessment methods*, Seattle, Washington, USA.

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(Appendix on next page)

APPENDIX A

Overdispersion Test

If X_i is the number of radiomarked birds in the flock i , then X_i follows a Poisson distribution such as $X_i \sim P(N_i c)$, where N_i is the size of the flock and c is a normalizing constant (Rivest et al. 1998). If n is the number of photographed flocks, this constant can be estimated as:

$$\hat{c} = \frac{\sum_{i=1}^n X_i}{\sum_{i=1}^n N_i}$$

Therefore, we have

$$P(X_i = k) = \frac{(N_i c)^k e^{-N_i c}}{k!} = \frac{e^{k(\ln N_i + \ln c)} e^{-N_i c}}{k!}$$

$$\text{or } P(X_i = k) = \frac{e^{(a(\theta)k - g(\theta) + c(k))}}{k!}$$

with $a(\theta) = \theta = \ln(c)$, $g(\theta) = e^\theta$, and $c(k) = k \ln(N_i) - N_i$. Then

$$\hat{\theta} = \ln \left(\frac{\sum_{i=1}^n X_i}{\sum_{i=1}^n N_i} \right)$$

and $g(\theta) = e^\theta$ and $g'(\theta)$, $g^{(2)}(\theta)$, $g^{(3)}(\theta)$, and $g^{(4)}(\theta) = e^\theta$.

Hence, from Dean and Lawless (1989) and Dean

(1992), we have

$$Z_{obs} = \frac{\sum_{i=1}^n [(X_i - E(X_i))^2 - E(X_i)]}{\sum_{i=1}^n [E(X_i) + 2[E(X_i)]^2] - \frac{\left[\sum_{i=1}^n E(X_i) \right]^2}{\sum_{i=1}^n E(X_i)}}$$

so we obtain

$$Z_{obs} = \frac{\sum_{i=1}^n [(X_i - N_i \hat{c})^2 - N_i \hat{c}]}{\sum_{i=1}^n [N_i \hat{c} + 2[N_i \hat{c}]^2] - \frac{\left[\sum_{i=1}^n N_i \hat{c} \right]^2}{\sum_{i=1}^n N_i \hat{c}}}$$

and finally

$$Z_{obs} = \frac{\sum_{i=1}^n [(X_i - N_i \hat{c})^2 - N_i \hat{c}]}{\left[2 \sum_{i=1}^n [N_i \hat{c}]^2 \right]^{-1/2}}$$

The N_i were estimated as the product of the visual estimate of flock i by the combined stratified ratio estimated for the corresponding photographic survey. The null hypothesis H_0 that radiomarked birds are randomly distributed among flock size is rejected at the 0.05 level if $Z_{obs} > 1.645$ (1-tailed).