Condor, 81:232–235

DEMOGRAPHIC PARAMETERS OF A NESTING COLONY OF SNOW GEESE

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Mark and recapture data can be used to estimate some of the demographic parameters of a natural population (e.g., Jackson 1939, Leslie and Chitty 1951, Orians 1958, Imber and Williams 1968). Several analytical techniques are available (Seber 1973); the method presented independently by Jolly (1965) and Seber (1965) is particularly suited for open populations (i.e., populations in which the number of individuals may change during the course of the study due to emigration, mortality and recruitment). We present the results of a Jolly-Seber analysis of data collected at a nesting colony of Snow Geese (*Anser caerulescens caerulescens*). We estimate survival, emigration and population size, and use the survival estimates to calculate potential natural longevity.

METHODS

The Snow Goose colony at La Pérouse Bay (58°24′N, 94°24′W), Manitoba, has been studied since 1969. Each year during the flightless molt period, occurring in late July and early August, entire flocks of geese were captured (for technique, see Cooke and Sulzbach 1978) in separate banding drives in different parts of the colony. Each bird was marked with a Canadian Wildlife Service aluminum leg band, and its sex and age class (i.e., gosling or adult) were recorded. Capture-recapture data from 1969–1974 for both color phases (blue and white) were used in our analyses. Data for the two color phases were combined because samples of blue morphs were small; a previous examination found no consistent differences in mortality of the two (Sulzbach 1975).

The rationale of a Jolly-Seber analysis has been presented elsewhere (Seber 1973) but will be briefly reviewed here. Assuming random sampling, the proportion of marked birds in a captured sample at time t_i is the same as that in the population from which the sample was drawn. That is:

$$m_i/n_i = M_i/N_i \qquad (i = 2, 3, \ldots, L - 1), \qquad (1)$$

where m_i is the number of marked birds recaptured at t_i, n_i is the total (marked + unmarked) number of birds captured at t_i, M_i is the number of marked birds in the colony at t_i, N_i is the total (marked + unmarked) number of birds in the colony at t_i, and L is the number of sampling periods. It follows that $m_1 = M_1 = 0$; as we will show, M_L cannot be estimated. Upon rearranging (1) one obtains:

$$N_i = (M_i n_i)/m_i \qquad (i = 2, 3, \ldots, L - 1). \qquad (2)$$

Since m_i and n_i are known quantities, one can estimate the population size at t_i if one can estimate the number of marked birds at t_i (i.e., M_i). Immediately after time t_i there are two types of marked birds in the colony, those released after the ith sample (n_i) and those previously marked birds which were not recaptured at t_i (i.e., $M_i - m_i$). If the subsequent return rate of marked birds is the same regardless of whether or not they were caught at t_i, then the proportion of marked birds caught after t_i will be the same for both groups. Hence, if r_i is the number of birds captured and released at t_i (this includes both recaptured birds and birds banded for the first time at t_i) which are subsequently recaptured in later years, and z_i is the number of birds marked in years prior to t_i that were not recaptured at t_i but were recaptured in years subsequent to t_i, and all birds captured at t_i are released, then

$$r_i/n_i = z_i/(M_i - m_i) \qquad (i = 2, 3, \ldots, \mathrm{L} - 1), (3)$$

and

$$\hat{M}_i = [(z_i n_i)/r_i] + m_i \qquad (i = 2, 3, \ldots, \mathrm{L} - 1). \quad (4)$$

One can see that $z_1 = z_L = r_L = 0$. It follows from (2) and (4) that

$$\hat{N}_i = [(z_i n_i^2)/(r_i m_i)] + n_i \qquad (i = 2, 3, \ldots, \mathrm{L} - 1). (5)$$

$\hat{M}_i$ and $\hat{N}_i$ are estimates of the number of marked birds and of the total population size at t_i. $\hat{M}_i$ can also be used to estimate the rate of return of birds to the colony. If the return rate to the colony (incorporating both mortality and emigration) is the same for all birds, the ratio of marked birds at t_{i+1} to the number present immediately after sampling at t_i estimates the proportion of birds returning to the colony. That is:

$$\hat{S}_i = \hat{M}_{i+1}/[(\hat{M}_i - m_i) + n_i] (i = 2, 3, \ldots, \mathrm{L} - 2), \quad (6)$$

where $\hat{S}_i$ estimates the probability of a bird alive at t_i surviving and returning to the colony at t_{i+1}.

Estimates of the variances of population size and return rate are given by Seber (1973). The formulas are asymptotic and valid for large expectations of n_i, m_i, r_i, and z_i.

RESULTS

We banded 15,492 geese during the five-year period. Table 1 includes the numbers of each age class banded each year and the numbers of recaptures. The 1,457 recaptures involved 1,292 different birds (i.e., some individuals were caught more than once.

The Jolly-Seber method assumes that: (1) all individuals in a population have equal probabilities of being captured; (2) marked birds have equal probabilities of returning to the area sampled; (3) every animal captured has the same probability of being returned to the population; (4) marks are not lost during the course of the study; (5) sampling time is negligible (Seber 1973). An analysis of our data indicated that the first assumption may not be satisfied because we found that the probability of capture increased for the first few years of life of female birds (Sulzbach and Cooke 1978). The second assumption did not appear to hold for males banded as goslings, whose subsequent recaptures were rare (Sulzbach and Cooke 1978). Thus, we have limited our analysis to birds captured as adults. An examination of the data on captures of marked birds visually identified at the nest indicated our total yearly catches to be random samples of the nesting adults (Sulzbach 1975). We found, however, that mate captures were highly interrelated events (Sulzbach and Cooke 1978). Consequently, male and female data were analyzed separately. Recent findings indicate the existence of two distinct brood-rearing areas during the period of banding (unpubl. data), with little movement of individuals between these areas from year to year. Capture locations in the past were chosen without benefit of this knowledge, and our choices might have artificially altered the probability of subsequent recapture. This would affect the estimates of population size and return rate, but probably to only a minor extent.

The third assumption is satisfied, as virtually all adult birds captured were returned to the population, and the fourth assumption is also met. We applied plastic leg bands in addition to the aluminum leg bands; no birds were recaptured with plastic bands but not aluminum bands. Hickey (1952) found aluminum band loss to be low for at least five years for all species he examined, including waterfowl. Thus it is unlikely that bands were lost during the period of this study. The fifth assumption is true since the capture and banding of a flock takes only one day.

An indirect method of assessing the applicability of the underlying model was presented by Leslie et al. (1953). One can compare the increase in the marked population at some time t_i due to the release of newly marked individuals, with an estimate of this increase obtained from an analysis of the marked population of animals captured at least twice. Seber (1973:225) gave formulas for calculating the estimated number of newly released individuals ($\hat{V}_i$) and its variance. Table 2 includes the estimated and actual numbers of newly released individuals for this study. While agreement between the figures is not spectacular, it is as good as that of other studies where the technique of analysis has been accepted as valid (Leslie et al. 1953, Seber 1973:227). With only one exception, the actual values are within one standard deviation of the estimated values. In this paper we report only those parameters for which the variance could be estimated.

TABLE 1. Number of birds banded and recaptured at La Pérouse Bay from 1969 to 1974.

Year	Number banded		Number recaptured
	Adults	Goslings	
1969	71	580	—
1970	1,041	2,768	41
1971	561	863	107
1972	1,128	2,483	361
1973	1,071	2,680	467
1974	692	1,554	481
Total	4,564	10,928	1,457

Estimates of adult return rates are shown in Table 3. Values ranged from 0.71 to 0.85 for females and 0.53 to 0.71 for males. In all three years females returned at a higher rate than males. Cooke et al. (1975) predicted that male return rates in any year for the La Pérouse Bay colony should be approximately equal to the square of the female rate for that year. This is due to the high rate at which males whose mates die emigrate to larger colonies. This prediction was supported in all three years (Table 3). Differences between male rates and the square of female rates were not significant. The rates of female return probably reflect adult survival, while those of male return reflect survival coupled with an emigration rate equal to the adult mortality rate.

Estimates of the number of adult birds in the colony are shown in Table 4. The 7,347 for the number of males in 1970 is very unreliable because of the small number of recaptures up to that time. Estimates based on the combined data of both sexes agree well with the sum of the separate estimates for males and females. The known interdependence of mate captures (Sulzbach and Cooke 1978) did not greatly affect the esti-

TABLE 2. Actual (V_i) and estimated ($\hat{V}_i$) numbers (with SD) of newly marked individuals released at banding.

		Year		
		1971	1972	1973
Males	V_i	288	633	617
	$\hat{V}_i$	490 ± 123	636 ± 160	546 ± 138
Females	V_i	285	550	584
	$\hat{V}_i$	293 ± 259	395 ± 173	640 ± 120

TABLE 3. Estimates of return rate (with SD) for adult birds based on the Jolly-Seber method. The rate for males is expected to approximate the square of the female rate because of emigration by a large percentage of males who lose their mates.

	1970–1971	1971–1972	1972–1973
Male return rate	0.68 ± 0.08	0.71 ± 0.09	0.53 ± 0.07
Female return rate	0.85 ± 0.07	0.84 ± 0.08	0.71 ± 0.08
Square of female return rate	0.73	0.72	0.50

mates of population size. Apparently, the captures of marked and unmarked birds are essentially equiprobable events.

The Jolly-Sever estimates indicate that the colony consisted of roughly 6,000 to 7,000 birds during the period of 1970–1973. Visual estimates made during the nesting period are lower in every year (Table 4). This is especially true for 1971, a year when weather conditions during the nesting period were poor, resulting in a low number of successful nesters. A likely explanation for the discrepancy between the figures is that the Jolly-Seber estimates pertain to the population of potentially nesting birds, but the fraction of this number that successfully nests varies annually as a result of climatic fluctuations. Our banding samples appear to be drawn primarily from those birds that nest successfully (Sulzbach 1975). However, as indicated in the equations, if the proportion of marked birds among the nesting adults is the same as the proportion among all adult birds in the colony, the Jolly-Seber estimates will pertain to the entire population of adults and not just to the fraction that nests successfully.

DISCUSSION

The adult survival estimates range from 0.71 to 0.85 and agree with those reported previously in Cooke and Sulzbach (1978), which were based on visual identifications of adult birds at the nest. Cooch (1958) estimated a 0.7 survival rate of adult Snow Geese. Rienecker (1965), using band recoveries from white-phase individuals captured on California wintering areas, estimated the combined adult and yearling survival to be 0.75 per year. Adult mortality probably varies from year to year owing to many factors, including weather, hunting pressure, and food availability on wintering areas. But on the average, the yearly survival rate of adult Snow Geese is near 0.75.

Longevity in the wild is difficult to measure directly, but can be estimated from survival values. Assuming mortality to be constant annually and approximately uniform within any year, the expectation of further life for adult birds (i.e., for this study, birds two years old) can be calculated as

$$e = (2 - D)/D, \qquad (7)$$

where D is the annual mortality rate (Botkin and Miller 1974). Assuming D to equal 0.25, e is 3.5 years. Potential natural longevity can be calculated as

$$A = \ln P/\ln (1 - D), \qquad (8)$$

where A is the number of years survived, P the probability of survival to age A, and D the annual mortality rate (Botkin and Miller 1974). The value of A obtained depends on P. We have arbitrarily set P equal to 0.01 since a value this low will insure that only a small fraction of the population will consist of birds older than A. Again assuming D equals 0.25, the potential natural longevity of adult birds is 16 years. We do not have data allowing us to assess the accuracy of this figure, but we have captured one foreign-banded adult that was at least 13 years old.

Mortality of immature birds is difficult to estimate since it requires a method of analysis incorporating both time- and age-dependence of mortality rates. Band recover-

TABLE 4. Estimates of size of the adult segment of population at La Pérouse Bay based on Jolly-Seber method. Those for total population size are based on combined data for males and females. Visual estimates of number of nesting birds were made during nesting season.

	1970	1971	1972	1973
Males	7,347 ± 7,903	3,407 ± 665	3,044 ± 410	3,413 ± 518
Females	2,631 ± 963	3,295 ± 485	2,769 ± 265	3,446 ± 406
Males + females	9,978	6,702	5,813	6,859
Total	6,606 ± 2,359	6,801 ± 805	5,918 ± 469	6,919 ± 646
Visual estimates	5,000	3,200	5,600	6,000

ies indicate that mortality of immature birds from hunting is 1.86 times as high as that of adults (Sulzbach 1975). If hunting is the major cause of adult and juvenile mortality, this would indicate a juvenile survival rate of 0.46–0.72 for the La Pérouse Bay colony. Rienecker (1965) estimated survival of immature birds to be approximately 0.46 for white-phased individuals. Cooch (1958) estimated immature survival to be 0.5. Our lower estimates agree well with these other studies, while the higher values probably reflect the weakness of assuming that hunting is the single major cause of immature mortality.

Our estimates of population size indicate that the La Pérouse Bay colony contained 3,000–3,500 pairs of adult birds during 1970–1973. We were unable to reliably estimate numbers of prebreeding geese because of sampling difficulties (Sulzbach and Cooke 1978). The discrepancy between visual estimates of numbers of breeding pairs and estimates of numbers of adult birds based on recapture data caution against relying solely on one or the other in attempts to understand the dynamics of the colony. Environmental fluctuations can affect the colony's size through changes in the fraction of the population that successfully nests. Reliance on recapture estimates alone would fail to detect these changes and could lead to overestimates of productivity. Reliance on visual estimates alone could lead to an underestimation of the adult population and, consequently, the long term productivity of the colony.

ACKNOWLEDGMENTS

This research has been supported by the Canadian Wildlife Service, National Research Council of Canada, Wildlife Management Institute, and Manitoba Department of Mines, Energy and Resource Management. Field work was carried out at the Queen's University Tundra Biology Station.

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