

ESTIMATES OF MOVEMENT AND SITE FIDELITY USING MARK-RESIGHT DATA OF WINTERING CANADA GEESE¹

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Abstract. Population ecologists have devoted disproportionate attention to the estimation and study of birth and death rates and far less effort to rates of movement. Movement and fidelity to wintering areas have important ecological and evolutionary implications for avian populations. Previous inferences about movement among and fidelity to wintering areas have been restricted by limitations of data and methodology. We use multiple observation data from a large-scale capture-resighting study of Canada Geese in the Atlantic flyway to estimate probabilities of returning to previous wintering locations and moving to new locations. Mark-resight data from 28 849 Canada Geese (*Branta canadensis*) banded with individually coded neck bands in the mid-Atlantic (New York, Pennsylvania, New Jersey), Chesapeake (Delaware, Maryland, Virginia), and Carolinas (North and South Carolina) were used to estimate movement and site fidelity. Two three-sample mark-resight models were developed and programmed using SURVIV to estimate the probability of moving among or remaining within these three wintering regions. The model (MV2) that incorporated “tradition” or memory of previous wintering regions fit the data better than the model (MV1) that assumes that a first-order Markov chain described movement among regions. Considerable levels of movement occurred among regions of the Atlantic flyway. The annual probability of remaining in the same region for two successive winters, used as a measure of site fidelity, was 0.710 ± 0.016 (estimated mean \pm SE [SE]), 0.889 ± 0.006 , and 0.562 ± 0.025 , for the mid-Atlantic, Chesapeake, and Carolinas, respectively. The estimated probability of moving to the Chesapeake from the mid-Atlantic or from the Carolinas was $3\times$ and $25\times$ as high, respectively, as the probability of moving in the opposite directions. Changes in estimated probabilities of moving between years corresponded to changes in winter harshness. In warm years, geese moved north and in cold years, they moved south. Geese had a high probability of moving to and remaining in the Chesapeake. Annual changes in the movement probabilities did not correspond to annual changes in the United States Fish and Wildlife Service midwinter survey. Considerable numbers of geese from the Carolinas appeared to be wintering in more northerly locations (“short-stopped”) in subsequent winters.

Key words: *Branta canadensis*; Canada Goose; mark-resight data; movement rates; neck bands; site fidelity; winter distribution.

INTRODUCTION

All changes in population size result from changes in birth, death, immigration, and/or emigration. Population ecologists have devoted disproportionate attention to the estimation and study of birth and death rates and far less effort to rates of movement. The inability to account for observed population changes solely in terms of birth and death rates has led to an increased awareness of the potential importance of movement to population dynamics (e.g., Krebs et al. 1973, Lidicker 1975, Hestbeck 1982, 1986, 1988, Connor et al. 1983, Pienkowski and Evans 1985).

Movement and fidelity to wintering areas have im-

portant ecological and evolutionary implications for avian populations. Possible survival and future reproductive “benefits” of returning to the same wintering area include familiarity with the distribution of food resources, roost sites, cover, and predators (Raveling 1969, Spaans 1977, Nichols et al. 1983). However, if the relative suitability of different wintering sites with respect to factors affecting fitness varies from year to year, and if this variation can be perceived by birds, then opportunistic selection of the “most suitable” wintering grounds could occur each year (Nichols et al. 1983).

Previous inferences about movement among and fidelity to wintering areas have been restricted by limitations of data and methodology. Annual variation in bird counts on wintering areas and in winter band re-

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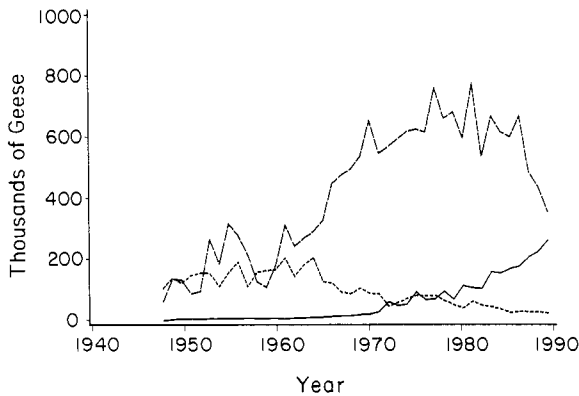


FIG. 1. Number of Canada Geese $\hat{N}_{i,j}$, wintering in the mid-Atlantic (—), Chesapeake (---), and Carolina (-----) regions of the Atlantic flyway from 1948 to 1989.

covery distribution patterns has provided evidence of variation in wintering ground location (Pulliam and Parker 1979, Nichols et al. 1983, Terrill and Ohmart 1984, Diefenbach et al. 1988a, b). Recapture or resighting of marked individuals in the same wintering area in different years has provided evidence of fidelity (Koerner et al. 1974, Raveling 1979). Such methods sometimes permit tests for differences in fidelity among groups (Diefenbach et al. 1988a, b), but they do not permit estimation of the proportion of birds alive in a particular winter that return to the same wintering area used the previous year.

During the last three decades, dramatic changes in the number of Canada Geese wintering in different regions have occurred for the Atlantic population (Fig. 1), as well as other North American populations (e.g., Mississippi Valley population [Reeves et al. 1968, Rusch et al. 1985], Eastern Prairie population [Vaught and Kirsch 1966, Humburg et al. 1985], Hi-Line population [Szymczak 1975], and Rocky Mountain population [Krohn and Bizeau 1988]). It is generally believed that Canada Geese have a strong propensity to use the same geographical locations for migration and wintering grounds year after year (Raveling 1969, 1970, 1979, Bellrose 1980). Yet, as new habitat has become available in more northern states, Canada Geese appear to have abandoned wintering locations in the southern states (Reeves et al. 1968).

In the Atlantic flyway during the 1960s, the number of geese wintering in the Chesapeake (Delaware, Maryland, Virginia) increased, while the number wintering in the Carolinas (North and South Carolina) decreased. In recent years, numbers of geese have subsequently decreased in the Chesapeake and increased in the mid-Atlantic (New York, Pennsylvania, New Jersey). These changes may have resulted from lower survival for geese migrating to more southerly locations, from geese moving into newly created habitat in the north (short-stopped), or from changes in both movement and survival (Cridler 1967, Hankla and Rudolph 1967, Addy

and Heyland 1968, Crissey 1968). In the Atlantic flyway, Trost et al. (1986) found that survival differences between Maryland and North Carolina were consistent with the direction of change in relative numbers during the 1960s, but that the difference was not large enough to account for the observed change in relative number between these two states. Hestbeck and Malecki (1989) also found that regional survival differences in the Atlantic flyway have contributed to changes in relative numbers occurring in the 1980s. The role of movement in causing these changes is unknown and remains to be explored.

In this paper, we use multiple observation data from a large-scale capture-resighting study of Canada Geese in the Atlantic flyway to estimate probabilities of returning to previous wintering locations and moving to new locations. We first develop two different models to test the hypothesis that wintering ground selection is described by a first-order Markov chain (i.e., that wintering ground location in year i depends only on wintering location in year $i - 1$), vs. the alternative that wintering ground selection involves a second-order stochastic process (i.e., that location in year i depends on wintering location in years $i - 1$ and $i - 2$). We then use estimates under the appropriate model to evaluate current ideas about fidelity of Canada Geese to particular wintering grounds, the directionality of shifts in wintering grounds (e.g., short-stopping), and possible influences of weather on shifts in wintering ground location. Finally, we combine these estimates with United States Fish and Wildlife Service midwinter survey estimates of goose numbers to evaluate the role of movement in recent changes in relative numbers of geese in regions of the Atlantic flyway.

METHODS

Field methods and data sources

Information about numbers of geese was obtained from the United States Fish and Wildlife Service midwinter survey. Since the total midwinter estimate of geese changed annually, the estimated percentage of geese present within each region was used for comparisons. The percentage was estimated by summing the midwinter counts for each state within a region, dividing the regional totals by the midwinter total for all three regions, and multiplying by 100.

Information on climate was obtained from monthly summaries of "Climatological Data" (NOAA). Recordings for the mid-Atlantic came from airport stations in Rochester, New York, Erie, Pennsylvania, and Atlantic City, New Jersey. Recordings for the Chesapeake and Carolinas came from airport stations in Salisbury, Maryland and New Bern, North Carolina, respectively. Individuals from the mid-Atlantic population (Bellrose 1980) start migrating from northern Quebec in September and arrive at their southern terminus from November to January (Bellrose 1980).

The number of days with a minimum temperature recording $\leq 0^\circ\text{C}$ during November, December, and January was used as a measure of winter severity to illustrate the effect of weather on the regional movement of geese. Lincoln (1935) found that movement of the 2°C isotherm appeared to govern the speed at which Canada Geese migrate north. The measure of winter severity for the mid-Atlantic was the mean of recordings for the three stations. A temperature gradient was estimated by subtracting the total number of days $\leq 0^\circ$ for the Carolinas from the total for the mid-Atlantic.

Project personnel banded 28 849 adult and subadult Canada Geese with uniquely coded yellow neck bands during the fall and winter of 1983–1984, 1984–1985, and 1985–1986 in the mid-Atlantic, Chesapeake, and Carolinas. Observers travelled specific routes within the eight states and recorded 101 732 resightings. Each state was surveyed every 1–3 wk from October to April, 1983 through 1988. Because we were concerned with only the migrant population, observations were also made during summer 1987 to detect resident geese. All marked individuals found within the wintering states during summer were classified as residents and were removed from the analyses.

The sampling period used to estimate movement rates was defined as 4 January to 15 February. This period excludes the fall migration and corresponds to the time when most geese are at their southern terminus. The hunting season for Canada Geese generally began in early to mid-October and ended in mid- to late January. The hunting season was closed in South Carolina from the fall of 1985 to present. The effect of harvest on movement appears to be strongest during the early stages of the hunting season (J. B. Hestbeck, *personal observation*).

The analysis was applied to three independent, regional cohorts of geese for each year (1984–1986) where $n_{i,j}$ represented the number of geese banded or observed during the sampling period of year i in region j . Observations of these geese during the subsequent two sampling periods provide the observation histories used for estimation. We denote the three regions as A for the mid-Atlantic, B for the Chesapeake, and C for the Carolinas. We also use 0 to denote the event that an individual was not observed during a given sample period. Let XYZ denote a particular observation history where $X = A, B,$ or C depending upon the region of initial observation, $Y = 0, A, B,$ or C depending on whether and where the goose was observed, and $Z = 0, A, B,$ or $C,$ also depending on whether and where the goose was observed. For example, history $A0B$ denotes a goose captured or observed in region A during year i , not seen during year $i + 1$, and observed in region B during year $i + 2$. The raw data for each analysis included the number of geese in each of three regional cohorts and the number of geese associated with each possible capture history. If a goose was ob-

served in > 1 region during a particular sampling period, the observation was randomly assigned to one region. This occurred for only 1% of the individuals included in the analysis.

Mark-resight models

We developed two three-sample mark-resight models to estimate movement probabilities. One model, MV1, appears to be equivalent to that of Arnason (1972, 1973) and is parameterized with transition and sighting probabilities defined as:

- $\phi_{i,j,k}$ = probability that a bird alive and present in region j during year i survives and is present in region k during year $i + 1$,
 $P_{i,j}$ = probability that a bird present in region j during year i is observed during that period.

Sighting probabilities, $P_{i,j}$, are similar to the capture probabilities of the standard Jolly-Seber model (Jolly 1965, Seber 1965) and differ only in that they are defined for region j . Transition probabilities, $\phi_{i,j,k}$, are similar to Jolly-Seber survival probabilities but differ in specifying the location of the goose at the beginning (region j) and ending (region k) of the transition period (i to $i + 1$). Movement in MV1 is described by a first-order Markov chain, i.e., movement between two consecutive sampling periods depends only on location of a bird in the prior sampling period. For example, the $\phi_{i+1,j,k}$ (transition probabilities) depend only on the location (j) of the goose during $i + 1$.

The assumptions required by model MV1 are similar to those required by the standard Jolly-Seber model (Seber 1982, Pollock et al. 1990): (1) time- and region-specific sighting and transition probabilities are the same for all marked birds found in a particular region and in a particular sampling period, (2) birds behave independently with respect to sighting probability, survival, and movement, (3) marked birds do not lose their marks, (4) all samples are instantaneous, and (5) losses to the population through emigration are permanent. These assumptions are testable, to some degree, with model goodness-of-fit statistics.

The effect of violation of the assumptions has not been examined for model MV1; however, because the sighting and transition probabilities of model MV1 are similar to the capture and survival probabilities of the standard Jolly-Seber model, respectively, an idea of possible biases due to violation of the assumptions of MV1 can be obtained by examining the effects of violation of the assumptions of the Jolly-Seber model.

Carothers (1979) found that biases in the estimation of survival rates (hence transition rates) due to heterogeneity in probability of capture among individuals were negligible even when the test of equal catchability revealed significant variation in capture probabilities.

For the second assumption, birds behave independently with respect to sighting probability, survival,

and movement. This assumption will be violated for geese because geese are not independent entities (Sulzbach and Cooke 1978). Although this will not bias any estimators, the true sampling variances are larger than those computed from the statistical models for the data (Pollock and Raveling 1982).

The third assumption is that marked birds do not lose their marks. If geese lose their neck bands, estimates of survival will be negatively biased. However, when the transition probabilities are decomposed into survival and movement components, as noted below, the bias due to tag loss will be associated with the survival and not the movement component.

The assumption that sampling is instantaneous can never be strictly met. Because all mortality for the Jolly-Seber model and all movement and mortality for model MV1 should occur between samples, estimation of survival or transition probabilities is sensitive to the length of the sampling and intersampling periods. To guarantee this, the length of the sampling period should be small compared to the length of time between sampling, and sampling should not occur during periods of high mortality, such as the opening of hunting seasons, or high movement, such as times of migration. As noted earlier, sampling for this experiment occurred 3 mo after the opening of the hunting season in the northern states and during the time when geese are more sedentary and at their southernmost terminus.

The assumption regarding nonpermanent emigration can be important for a study of survival and movement. For studies on a flyway level, nonpermanent emigration will be very small because almost all regions are sampled. However, for smaller scale projects, nonpermanent emigration can be a greater problem. The best way to restrict this problem is to conduct the estimation during a period of time when migration or smaller scale movement will be small.

In addition to model MV1, we developed a more general model, MV2, which incorporated "tradition" or memory of previous wintering regions into a probabilistic model. In this model, movement was described by a second-order stochastic process such that the transition probabilities, $\phi_{i-1,j,k}$, depend on the location not only at $i + 1$ but also the location during the previous year at i . Specifically, we allow the transition probability from location j at $i + 1$ to location k at $i + 2$ to differ for geese that were located in region k at time i ($\phi'_{i-1,j,k}$) vs. geese that were not located at k during time i ($\phi^*_{i-1,j,k}$).

The assumptions for model MV2 are similar to those for model MV1 except that the first assumption is modified to allow that all marked birds with the $\phi'_{i-1,j,k}$ or $\phi^*_{i-1,j,k}$ transition probabilities have the same probability of moving from region j to k given that the bird was either inside or outside of region k at time i and was in region j at time $i + 1$.

The likelihood functions for models MV1 and MV2 can be written as the product of the three multinomial

distributions corresponding to birds initially released from each region at time i . The likelihood function is conditioned on the numbers of released birds, $n_{i,j}$. Each cell of the multinomial corresponds to a particular observation history. The probability associated with each cell is modeled using the transition and sighting probability parameters of the respective model, MV1 or MV2. A listing of the 48 possible capture histories with their associated probabilities under each model is available from the authors. The observed numbers of birds exhibiting each observation history are then used in conjunction with program SURVIV (White 1983) to obtain maximum likelihood estimates under each model. We made no attempt to derive closed-form estimators, but note that Arnason (1973) derived moment estimators for MV1. We tested fit of our models (and hence model assumptions) using the goodness-of-fit test of SURVIV and tested the more biologically interesting hypothesis of an influence of memory and tradition, using a likelihood ratio test between models MV1 and MV2.

We were primarily interested in movement probabilities, but the transition probabilities we estimated actually represent products of movement and survival probabilities. We can write the transition probabilities as:

$$\phi_{i,j,k} = S_{i,j} \psi_{i,j,k}, \quad (1)$$

where $S_{i,j}$ represents the probability that a goose alive during time i in region j survives (does not die or permanently emigrate) until time $i + 1$, and $\psi_{i,j,k}$ denotes the probability that a goose in region j during time i moves to region k at time $i + 1$, given that the goose survives from i to $i + 1$.

Because $\sum_{k=1}^3 \psi_{i,j,k} = 1$, we can write an identity for $\psi_{i,j,k}$ as:

$$\psi_{i,j,k} = \frac{S_{i,j} \phi_{i,j,k}}{S_{i,j} \left(\sum_{k=1}^3 \psi_{i,j,k} \right)}. \quad (2)$$

An estimator for $\psi_{i,j,k}$ can be obtained using Eqs. 1 and 2 as:

$$\hat{\psi}_{i,j,k} = \frac{\hat{\phi}_{i,j,k}}{\sum_{k=1}^3 \hat{\phi}_{i,j,k}}. \quad (3)$$

Because the $\phi_{i,j,k}$ must be estimated, we used the modified estimator and associated variance presented in Appendix A to estimate $\hat{\psi}_{i,j,k}$ instead of the method implied in Eq. 3. We used Z statistics to compare estimates of $\hat{\psi}_{i,j,k}$ among years and regions (Brownie et al. 1985:180–182).

Population projections

To project the relative, regional abundance of geese that would be expected to result solely from the esti-

mated movement probabilities, we viewed regional movement as a first-order Markov chain and used the average estimated annual movement probabilities, $\hat{\psi}_{j,k}$, to construct a matrix of probabilities of moving among the three regions, T' (e.g., see Quirin 1978):

$$T' = \begin{bmatrix} \hat{\psi}_{A,A} & \hat{\psi}_{A,B} & \hat{\psi}_{A,C} \\ \hat{\psi}_{B,A} & \hat{\psi}_{B,B} & \hat{\psi}_{B,C} \\ \hat{\psi}_{C,A} & \hat{\psi}_{C,B} & \hat{\psi}_{C,C} \end{bmatrix}$$

Assuming the $\hat{\psi}_{j,k}$ are constant through time, we can compute an equilibrium distribution of movement probabilities by taking T' to the n th power until it converges to an equilibrium matrix W . Each row of W is equivalent and corresponds to the equilibrium probability distribution of being located in the three regions (e.g., Quirin 1978).

The transient effects of movement on population size of each region were examined by comparing estimated immigration, $\hat{I}_{i,j}$, and emigration, $\hat{E}_{i,j}$, for year i and region j . Immigration and emigration were estimated using the estimated movement probabilities, $\hat{\psi}_{i,j,k}$, survival rates, $\hat{S}_{i,j}$, for year i and region j from Hestbeck and Malecki (1989), and population number, $\hat{N}_{i,j}$, for year i and region j from the United States Fish and Wildlife Service midwinter survey. For example, immigration and emigration for the mid-Atlantic region for year i were estimated as:

$$\hat{I}_{i,A} = \hat{N}_{i,B}\hat{\psi}_{i,B,A}\hat{S}_{i,B} + \hat{N}_{i,C}\hat{\psi}_{i,C,A}\hat{S}_{i,C}$$

$$\hat{E}_{i,A} = \hat{N}_{i,A}\hat{S}_{i,A}(\hat{\psi}_{i,A,B} + \hat{\psi}_{i,A,C})$$

Variances were estimated as (Goodman 1960):

$$\widehat{\text{Var}}[\hat{I}_{i,A}] = \hat{N}_{i,B}^2(\hat{S}_{i,B}^2\widehat{\text{Var}}[\hat{\psi}_{i,B,A}] + \hat{\psi}_{i,B,A}^2\widehat{\text{Var}}[\hat{S}_{i,B}] - \widehat{\text{Var}}[\hat{\psi}_{i,B,A}]\widehat{\text{Var}}[\hat{S}_{i,B}]) + \hat{N}_{i,C}^2(\hat{S}_{i,C}^2\widehat{\text{Var}}[\hat{\psi}_{i,C,A}] + \hat{\psi}_{i,C,A}^2\widehat{\text{Var}}[\hat{S}_{i,C}] - \widehat{\text{Var}}[\hat{\psi}_{i,C,A}]\widehat{\text{Var}}[\hat{S}_{i,C}])$$

$$\widehat{\text{Var}}[\hat{E}_{i,A}] = \hat{N}_{i,A}^2(\hat{S}_{i,A}^2\widehat{\text{Var}}[\hat{\psi}_{i,A,B}] + \hat{\psi}_{i,A,B}^2\widehat{\text{Var}}[\hat{S}_{i,A}] - \widehat{\text{Var}}[\hat{\psi}_{i,A,B}]\widehat{\text{Var}}[\hat{S}_{i,A}]) + \hat{N}_{i,A}^2(\hat{S}_{i,A}^2\widehat{\text{Var}}[\hat{\psi}_{i,A,C}] + \hat{\psi}_{i,A,C}^2\widehat{\text{Var}}[\hat{S}_{i,A}] - \widehat{\text{Var}}[\hat{\psi}_{i,A,C}]\widehat{\text{Var}}[\hat{S}_{i,A}])$$

Because variances for the $\hat{N}_{i,j}$ are not known or estimated, variances for $\hat{I}_{i,j}$ and $\hat{E}_{i,j}$ are underestimated. Net movement, $\hat{M}_{i,j}$, for region j and year i was estimated as $\hat{M}_{i,j} = \hat{I}_{i,j} - \hat{E}_{i,j}$. The variance of $\hat{M}_{i,j}$ was estimated as $\widehat{\text{Var}}[\hat{M}_{i,j}] = \widehat{\text{Var}}[\hat{I}_{i,j}] + \widehat{\text{Var}}[\hat{E}_{i,j}]$.

RESULTS

Midwinter survey

The distribution of geese within the Atlantic flyway has greatly changed from 1948 to the present. During

the period of this study (1983–1988), the relative abundance of geese wintering in the mid-Atlantic has increased while decreasing in the Chesapeake. From 1984 to 1988, the midwinter percentages have gone from 19 to 32% in the mid-Atlantic, 77 to 65% in the Chesapeake, and 4 to 3% in the Carolinas. Of particular interest, from 1984 to 1986 the midwinter percentages were approximately constant for the three regions. Then between 1986 and 1987, the midwinter percentage increased from 20 to 29% for the mid-Atlantic, dropped from 77 to 68% in the Chesapeake, and remained at 3% in the Carolinas.

Climate data

Our data for winter harshness varied over time (Table 1). The number of days with a minimum temperature $\leq 0^\circ$ during November, December, and January ranged from 58 to 67 d for the mid-Atlantic, 48 to 57 d for the Chesapeake, and 26 to 36 d for the Carolinas, and the temperature gradient ranged from 22 to 41. The winter of 1985–1986 was warmest in the mid-Atlantic (58 d) and coldest in the Carolinas (36 d), and the gradient was 22. The winter of 1986–1987 was coldest in the mid-Atlantic (67 d) and warmest in the Carolinas (26 d), and the gradient was 41 d.

Mark-resight models

Goodness-of-fit tests for MV1 indicated rejection of this model ($P < .001$) for data from each year. Examination of the observed and expected numbers of geese for each observation history and the corresponding contribution to the total χ^2 statistic showed that only a few specific histories were responsible for the lack of fit. The number of geese making a particular transition from $i + 1$ to $i + 2$ was larger than expected when the locations at times i and $i + 2$ were the same, and smaller than expected when the locations were different.

Model MV2 fit the data from the 1984 ($\chi^2_{15} = 21.3$, $P = .13$) and 1985 ($\chi^2_{15} = 19.7$, $P = .19$) cohorts adequately, but did not fit the 1986 cohort data ($\chi^2_{15} = 41.0$, $P < .001$). However, 47% of the total χ^2 value for the 1986 cohort was contributed by a single cell. When this cell was omitted, the model fit the data adequately ($\chi^2_{14} = 21.6$, $P = .09$). Under MV2, comparison of estimated average annual transition products ($\phi^*_{i+1,j,k}P_{i-2,k}$ vs. $\phi'_{i-1,j,k}P_{i+2,k}$) demonstrated that geese located in region k at time i had consistently higher probabilities of being found in region k at time $i + 2$ than geese that were not located in region k at time i (Table 2). Comparison of MV2 and MV1 using a likelihood ratio test also provided strong evidence of the need to incorporate memory and tradition into the model (1984, $\chi^2_9 = 31.6$, $P < .001$; 1985, $\chi^2_9 = 95.1$, $P < .001$; 1986, $\chi^2_9 = 90.9$, $P < .001$). These results indicated that the assumption that a first-order Markov chain described movement was not appropriate.

Estimated annual sighting and transition probabili-

TABLE 1. Climatic data for the mid-Atlantic, Chesapeake, and Carolinas for winters 1983–1984 through 1986–1987.

Region	Number of days min. temp. $\leq 0^{\circ}\text{C}$				Temp. grad.* (d)
	Novem-ber	Decem-ber	Janu-ary	Total	
1983–1984					
Mid-Atlantic	11	23	29	63	30
Chesapeake	4	19	28	51	
Carolinas	2	12	19	33	
1984–1985					
Mid-Atlantic	15	18	30	63	33
Chesapeake	16	13	28	57	
Carolinas	8	4	18	30	
1985–1986					
Mid-Atlantic	6	25	27	58	22
Chesapeake	2	23	25	50	
Carolinas	0	16	20	36	
1986–1987					
Mid-Atlantic	15	23	29	67	41
Chesapeake	8	18	22	48	
Carolinas	1	11	14	26	

* Temperature gradient is computed as the difference in total number of days $\leq 0^{\circ}\text{C}$ between mid-Atlantic and Carolina regions.

ties varied among years and regions (Table 3). Annual sighting probabilities were 0.605 ± 0.024 ($\bar{X} \pm \text{SE}$), 0.433 ± 0.013 , and 0.542 ± 0.036 , for the mid-Atlantic, Chesapeake, and Carolinas, respectively. The estimated probabilities of moving also varied among years and regions (Table 4). Geese had a higher probability of moving north during the winter of 1985–1986 than during 1984–1985. The probability increased for geese moving from the Chesapeake to the mid-Atlantic ($Z = 2.89$, $P = .002$) and from the Carolinas to the Chesapeake ($Z = 1.66$, $P = .048$). During the winter of 1986–1987, geese had a higher probability of moving south when compared to the previous winter. The probability increased for geese moving from the mid-Atlantic to the Chesapeake ($Z = 1.96$, $P = .025$) and from the Chesapeake to the Carolinas ($Z = 3.53$, $P < .001$). The probability decreased for geese moving from the Chesapeake to the mid-Atlantic ($Z = 3.07$, $P = .001$) and for geese moving from the Carolinas to the Chesapeake ($Z = 4.52$, $P < .001$). Also during the 1986–1987 winter, the probability of remaining in the Carolinas dramatically increased from 0.464 in 1985–1986 to 0.717 ($Z = 4.77$, $P < .001$).

The mean annual probabilities of geese moving into the Chesapeake from the mid-Atlantic or from the Carolinas were three times (0.096 to 0.287) and 25 times (0.015 to 0.371) as high, respectively, as those of moving in the opposite directions. In regard to short-stopping geese from the Carolinas, the mean probability of moving into the Carolinas from the mid-Atlantic or Chesapeake was smaller than the probability of moving from the Carolinas to the mid-Atlantic ($Z = 6.37$, $P < .001$) or Chesapeake ($Z = 14.8$, $P < .001$).

The probability of remaining in the same region for two successive years (a measure of site fidelity) was 0.710 ± 0.016 ($\bar{X} \pm \text{SE}$), 0.889 ± 0.007 , and 0.562 ± 0.025 , for the mid-Atlantic, Chesapeake, and Carolinas, respectively. The average probability of remaining in the Chesapeake was higher than that of remaining in the mid-Atlantic ($Z = 10.3$, $P < .001$), and the probability of remaining in the mid-Atlantic was higher than that of remaining in the Carolinas ($Z = 4.99$, $P < .001$).

Population projections

The transition matrix of mean estimated movement probabilities, $\hat{\psi}_{j,k}$, yielded an equilibrium relative abundance of 0.247, 0.727, and 0.027 for the mid-Atlantic, Chesapeake, and Carolinas, respectively. These projected proportions of Atlantic flyway geese in each of the three regions resulted from the repeated application of the average annual movement probabilities from Table 4 and are very similar to independent estimates of relative abundance based on the mid-winter survey.

No consistent patterns were found in the annual estimates of the number of geese moving among regions (Table 5). In the Carolinas, net losses of geese occurred during 1984–1985 and 1985–1986, but a net gain occurred for 1986–1987. Changes in the annual estimates of the number of geese did not match the changes observed in the midwinter survey.

DISCUSSION

All changes in population size result from changes in birth, death, immigration, and/or emigration. The inability to account for observed population changes solely in terms of birth and death rates has led to an increased awareness of the potential importance of movement to population dynamics. Our analyses permit several inferences about movement among and fidelity to wintering areas for Canada Geese. Our results indicated that considerable movement occurred among large-scale regions. The estimated probabilities of returning to the previous wintering ground, used as a measure of site fidelity, were consistently highest for

TABLE 2. Comparison of mean estimated transition products under model MV2 for geese that were either located in region k at time i ($\phi'_{i+1,j,k}P_{i+2,k}$) or not located in region k at time i ($\phi^*_{i+1,j,k}P_{i+2,k}$).

From region j	To region k	$\phi^*_{i+1,j,k}P_{i+2,k}$	
		$\phi^*_{i+1,j,k}P_{i+2,k}$	$\phi'_{i+1,j,k}P_{i+2,k}$
A	A	0.21	0.31
A	B	0.043	0.11
A	C	0.0023	0.0022
B	A	0.026	0.12
B	B	0.22	0.25
B	C	0.0048	0.063
C	A	0.021	0.075
C	B	0.084	0.12
C	C	0.11	0.30

TABLE 3. Number of individuals released from each cohort ($n_{i,j}$), and estimated means (with corresponding estimated standard errors) of the probability of surviving and moving to region k given that the goose was released at time i from region j ($\hat{\phi}_{i,j,k}$, where j and k may be regions A , B , or C); of surviving until $i+1$ given that the goose was alive at time i in region j ($\hat{S}_{i,j}$);* and of being observed during time $i+1$ given that the goose was in region j at that time ($\hat{P}_{i+1,j}$). Means, estimated SES, and approximate 95% confidence intervals, of those estimates are also shown for the three periods combined.

	Transition periods (i to $i + 1$)								
	1984-1985		1985-1986		1986-1987		Three periods combined		
	\hat{x}	SE[\hat{x}]	\hat{x}	SE[\hat{x}]	\hat{x}	SE[\hat{x}]	\hat{x}	SE[\hat{x}]	95% CI
	Mid-Atlantic								
$n_{i,A}$	785		2083		2663				
$\hat{\phi}_{i,A,A}$	0.424	0.035	0.450	0.025	0.363	0.020	0.412	0.016	0.382-0.443
$\hat{\phi}_{i,A,B}$	0.156	0.021	0.161	0.014	0.180	0.013	0.166	0.010	0.147-0.184
$\hat{\phi}_{i,A,C}$	0.000	0.000	0.000	0.000	0.006	0.002	0.002	0.0007	0.0006-0.003
$\hat{S}_{i,A}$	0.580	0.033	0.611	0.024	0.549	0.019	0.580	0.015	0.551-0.609
$\hat{P}_{i+1,A}$	0.715	0.055	0.520	0.030	0.581	0.032	0.605	0.024	0.559-0.652
	Chesapeake								
$n_{i,B}$	2086		3915		4028				
$\hat{\phi}_{i,B,A}$	0.057	0.007	0.079	0.007	0.052	0.005	0.063	0.004	0.055-0.070
$\hat{\phi}_{i,B,B}$	0.647	0.036	0.535	0.024	0.570	0.023	0.584	0.016	0.552-0.616
$\hat{\phi}_{i,B,C}$	0.007	0.003	0.005	0.002	0.018	0.003	0.010	0.002	0.007-0.013
$\hat{S}_{i,B}$	0.711	0.034	0.619	0.023	0.640	0.022	0.656	0.016	0.626-0.687
$\hat{P}_{i+1,B}$	0.452	0.027	0.412	0.020	0.436	0.019	0.433	0.013	0.408-0.458
	Carolinas								
$n_{i,C}$	622		1100		912				
$\hat{\phi}_{i,C,A}$	0.056	0.012	0.026	0.007	0.017	0.006	0.033	0.005	0.023-0.042
$\hat{\phi}_{i,C,B}$	0.185	0.027	0.234	0.022	0.127	0.017	0.182	0.013	0.157-0.207
$\hat{\phi}_{i,C,C}$	0.246	0.034	0.224	0.023	0.362	0.037	0.278	0.019	0.241-0.314
$\hat{S}_{i,C}$	0.488	0.037	0.484	0.025	0.506	0.036	0.493	0.019	0.455-0.530
$\hat{P}_{i+1,C}$	0.437	0.066	0.647	0.064	0.542	0.057	0.542	0.036	0.471-0.613

* Although the $\hat{S}_{i,j}$ are presented for completeness, we prefer the annual survival estimates of Hestbeck and Malecki (1989), which are based on a different method and use more of the available data.

geese in the Chesapeake region, averaging 0.89. Average estimated probabilities of returning to the mid-Atlantic and Carolinas were 0.71 and 0.56, respectively.

The comparison of models MV1 and MV2 also provided information about the role of site fidelity or tradition in wintering ground selection. These tests clearly

rejected the assumption that a first-order Markov chain described movement and provided evidence that wintering ground location in any given year (i) is influenced by wintering ground location not only in the previous year ($i - 1$), but also 2 yr previous ($i - 2$). The comparison of estimated transition products in Table 2 provided evidence that geese located in region k at time

TABLE 4. Estimated annual probability with corresponding standard error of being in region k at time $i+1$ given that the goose is alive at $i+1$ and was released at time i from region j ($\hat{\psi}_{i,j,k}$). Means, estimated SES, and approximate 95% confidence intervals for these estimates are also shown.

	Transition periods (i to $i + 1$)								
	1984-1985		1985-1986		1986-1987		Three periods combined		
	\hat{x}	SE[\hat{x}]	\hat{x}	SE[\hat{x}]	\hat{x}	SE[\hat{x}]	\hat{x}	SE[\hat{x}]	95% CI
	Mid-Atlantic								
$\hat{\psi}_{i,A,A}$	0.731	0.036	0.737	0.023	0.662	0.024	0.710	0.016	0.678-0.742
$\hat{\psi}_{i,A,B}$	0.269	0.036	0.263	0.023	0.328	0.024	0.287	0.016	0.255-0.319
$\hat{\psi}_{i,A,C}$	0.000	0.000	0.000	0.000	0.010	0.004	0.003	0.001	0.001-0.006
	Chesapeake								
$\hat{\psi}_{i,B,A}$	0.080	0.011	0.127	0.012	0.081	0.009	0.096	0.006	0.084-0.109
$\hat{\psi}_{i,B,B}$	0.911	0.012	0.865	0.013	0.891	0.011	0.889	0.007	0.875-0.902
$\hat{\psi}_{i,B,C}$	0.009	0.004	0.009	0.002	0.028	0.005	0.015	0.002	0.010-0.020
	Carolinas								
$\hat{\psi}_{i,C,A}$	0.114	0.024	0.053	0.013	0.033	0.011	0.067	0.010	0.047-0.086
$\hat{\psi}_{i,C,B}$	0.380	0.049	0.484	0.039	0.250	0.034	0.371	0.024	0.324-0.418
$\hat{\psi}_{i,C,C}$	0.506	0.051	0.464	0.039	0.717	0.036	0.562	0.025	0.514-0.611

TABLE 5. Estimated immigration ($\hat{I}_{i,j}$), emigration ($\hat{E}_{i,j}$), net movement ($\hat{M}_{i,j}$) (means and their corresponding SE's) of geese for region j and years i to $i + 1$. * Observed annual changes in the midwinter number of geese as estimated from the midwinter survey are shown for comparison.

	$\hat{I}_{i,j}$	SE ($\hat{I}_{i,j}$)	$\hat{E}_{i,j}$	SE ($\hat{E}_{i,j}$)	$\hat{M}_{i,j}$	SE ($\hat{M}_{i,j}$)	Change in midwinter counts†
Mid-Atlantic							
1984–1985	38 700	5200	27 100	5500	11 600	7600	15 800
1985–1986	58 200	5800	30 000	2900	28 200	6500	8100
1986–1987	35 700	4100	45 300	5000	–9600	6500	29 600
Chesapeake							
1984–1985	36 700	4100	45 300	5000	–4000	6500	–16 400
1985–1986	37 100	3000	61 300	5900	–24 300	6600	68 500
1986–1987	48 300	5000	47 100	4700	1200	6900	–185 200
Carolinas							
1984–1985	4100	1800	11 700	1500	–7600	2300	–11 400
1985–1986	3900	1100	7800	700	–3900	1400	3900
1986–1987	13 400	2400	5000	700	8400	2500	–2800

* Estimates were computed using survival estimates of Hestbeck and Malecki (1989), movement estimates from Table 4, and number of geese counted in the US Fish and Wildlife Service midwinter survey.

† Estimated as $N_{i-1} - N_i$.

i had consistently higher probabilities of being found again in region k at time $i + 2$ than geese not located in region k at time i .

The annual estimates of movement probabilities demonstrate strong site fidelity to the Chesapeake but also support the notion that geese are opportunistic in selecting wintering areas. Estimated probabilities of moving from the mid-Atlantic or the Carolinas to the Chesapeake ranged from 0.26 to 0.48 and were 3 and 25 times as high, respectively, as that of moving from the Chesapeake to the mid-Atlantic or Carolinas. Also, the average estimated probability of geese moving north from the Carolinas was 0.44. The high probability of moving north from the Carolinas provides empirical evidence of "short-stopping" and supports the idea that movement may have contributed to historical declines in southern goose populations. These estimates are also consistent with the idea that the Chesapeake is a region of high habitat suitability (*sensu* Fretwell 1972) and suggest that significant annual variation in habitat suitability occurs in the surrounding regions.

The estimated probabilities of moving varied among years. Although a formal analysis was not possible with estimates for only 3 yr, we found that the annual variation in movement probabilities corresponded to changes in weather. During the winter of 1985–1986, the mid-Atlantic had the fewest days below freezing and the temperature gradient between the mid-Atlantic and Carolinas was the smallest. Estimated movement probabilities during this period indicated that geese were wintering farther north. In the next winter, 1986–1987, the mid-Atlantic had the highest number of days below freezing and the temperature gradient was the largest. Estimated movement probabilities during this period indicated that geese were wintering farther south. These observations are consistent with the idea that fall–winter temperatures play some role in wintering

ground selection by Canada Geese (Humburg et al. 1985). Ponds provide food and refuge for geese (Bellrose 1980), and warm weather keeps ponds ice-free and available for use.

The rejection of the assumption that a first-order Markov chain described movement, the existence of temporal variation in movement probabilities, and the knowledge that survival and reproduction may also influence the regional relative abundance of geese, indicate that our Markov process model is not strictly appropriate for projecting equilibrium regional abundances of geese. However, we note that our use of this model is analogous to the use of Lotka-Leslie demographic projections (e.g., Leslie 1966, Mertz 1971, Nichols et al. 1980, Lande 1988), which assume that survival and reproductive rates vary only with age (not with physiological condition or any other individual attribute) and remain constant over time. Equilibrium behavior of these demographic models is of substantial interest to the study of population dynamics and the evolution of life history characteristics (Charlesworth 1980), despite the realization that the models do not provide strictly accurate descriptions of natural populations. The equilibrium regional relative abundances associated with our average estimated movement probabilities, T , matched the independent estimates of relative abundance based on the midwinter survey.

The estimated numbers of geese emigrating or immigrating annually (Table 5) depend not only on movement probabilities, but also on regional survival rates and abundances of geese. The projected annual changes in regional goose numbers based strictly on survival and movement probability estimates did not correspond to annual changes estimated from the midwinter survey. Changes in regional goose numbers are functions of survival, reproduction, and movement, whereas we estimated only the number of moving survivors.

In addition, we know very little about the accuracy or precision of the midwinter counts.

The changes in relative abundance of wintering Canada Geese during the 1960s may have been caused by differential hunting pressure and by changes in agricultural practices that created favorable goose habitat in the Chesapeake (Crider 1967, Hankla and Rudolph 1967, Addy and Heyland 1968). Changes in relative abundance have continued during the 1980s. The relative abundance of wintering geese has increased in the mid-Atlantic, decreased in the Chesapeake, and remained constant in the Carolinas. The changes in the 1980s do not appear to be caused primarily by movement. The probability of moving favors moving to and remaining in the Chesapeake. Changes in the relative abundance of wintering geese have, however, been related to changes in regional survival rates (Hestbeck and Malecki 1989).

Model MV2 provided an adequate description of our capture-resight data. Models MV1 and MV2 should be useful for other researchers studying among- and within-year probabilities of movement. These models can also be used to study transition probabilities among any strata or subclasses (e.g., age, mass, reproductive condition, territorial class) of interest within a population.

We used a two-step process to estimate movement probabilities, first estimating $\phi_{i,j,k}$ using program SURVIV and then using Appendix A to estimate $\psi_{i,j,k}$. Following suggestions from W. A. Link and from K. H. Pollock, we also attempted to estimate movement probabilities directly by parameterizing our models with $S_{i,j}$ and $\psi_{i,j,k}$ (rather than $\phi_{i,j,k}$) using the constraint that $\sum_{k=1}^3 \psi_{i,j,k} = 1$. Under this model, useful estimates for the Canada Goose data could not be obtained using program SURVIV. However, we believe that this approach holds promise and plan to investigate it further in the future.

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LITERATURE CITED

- Addy, C. E., and J. D. Heyland. 1968. Canada Goose management in Eastern Canada and the Atlantic flyway. Pages 10–23 in R. L. Hine and C. Schoenfeld, editors. Canada Goose management. Dembar Educational Research Services, Madison, Wisconsin, USA.
- Arnason, A. N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* 13:97–113.
- . 1973. The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology* 15:1–8.
- Bellrose, F. C. 1980. Ducks, geese, and swans of North America. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band-recovery data—a handbook. United States Fish and Wildlife Service Resource Publication 156.
- Carothers, A. D. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. *Journal of Animal Ecology* 48:863–869.
- Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge, England.
- Connor, E. F., S. H. Faeth, and D. Simberloff. 1983. Leafminers on oak: the role of immigration and in situ reproductive recruitment. *Ecology* 64:191–204.
- Crider, E. D. 1967. Canada Goose interceptions in the southwestern United States, with special reference to the Florida flock. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 21:145–155.
- Crissey, W. F. 1968. Informational needs for Canada Goose management programs. Pages 141–147 in R. L. Hine and C. Schoenfeld, editors. Canada Goose management. Dembar Educational Research Services, Madison, Wisconsin, USA.
- Diefenbach, D. R., J. D. Nichols, and J. E. Hines. 1988a. Distribution patterns during winter and fidelity to wintering areas of American Black Ducks. *Canadian Journal of Zoology* 66:1506–1513.
- Diefenbach, D. R., J. D. Nichols, and J. E. Hines. 1988b. Distribution patterns of American Black Ducks and Mallard winter band recoveries. *Journal of Wildlife Management* 52:704–710.
- Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey, USA.
- Goodman, L. A. 1960. On the exact variance of products. *American Statistical Association Journal* 55:708–713.
- Hankla, D. J., and R. R. Rudolph. 1967. Changes in the migration and wintering habits of Canada Geese in the lower portion of the Atlantic and Mississippi flyways, with special reference to National Refuges. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 21:133–144.
- Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. *Oikos* 39:157–163.
- . 1986. Multiple regulation states in populations of the California vole, *Microtus californicus*. *Ecological Monographs* 56:161–181.
- . 1988. Population regulation of cyclic mammals: a model of the social fence hypothesis. *Oikos* 52:156–168.
- Hestbeck, J. B., and R. A. Malecki. 1989. Estimated survival rates of Canada Geese within the Atlantic Flyway. *Journal of Wildlife Management* 53:91–96.
- Humburg, D. D., D. A. Graber, and K. M. Babcock. 1985. Factors affecting autumn and winter distribution of Canada Geese. Transactions of the North American Wildlife and Natural Resource Conference 50:525–539.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrics* 52:225–247.
- Koerner, J. W., T. A. Bookhout, and K. E. Bednarik. 1974. Movements of Canada Geese color-marked near southwestern Lake Erie. *Journal of Wildlife Management* 38:275–289.
- Krebs, C. J., M. S. Gaines, B. L. Keller, J. H. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. *Science* 179:35–41.
- Krohn, W. B., and E. G. Bizeau. 1988. Changes in winter distribution of the Rocky Mountain Canada Goose population. *Wildlife Society Bulletin* 16:272–277.

- Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). *Oecologia* (Berlin) **75**: 601–607.
- Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of Guillemots (*Uria aalge* Pont.). *Journal of Animal Ecology* **35**: 291–301.
- Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals. Pages 102–128 in F. B. Golley, K. Petruszewicz, and L. Ryszkowski, editors. Small mammals: their productivity and population dynamics. Cambridge University Press, Cambridge, England.
- Lincoln, F. C. 1935. Migration of North American birds. United States Department of Agriculture Circular Number **363**.
- Mertz, D. B. 1971. The mathematical demography of the California Condor population. *American Naturalist* **105**: 437–453.
- Mood, A. M., F. A. Graybill, and D. C. Boes. 1974. Introduction to the theory of statistics. Third edition. McGraw-Hill, New York, New York, USA.
- Nichols, J. D., G. L. Hensler, and P. W. Sykes, Jr. 1980. Demography of the Everglade Kite: implications for population management. *Ecological Modelling* **9**:215–232.
- Nichols, J. D., K. J. Reinecke, and J. E. Hines. 1983. Factors affecting the distribution of Mallards wintering in the Mississippi alluvial valley. *Auk* **100**:932–946.
- Pienkowski, M. W., and P. R. Evans. 1985. The role of migration in the population dynamics of birds. Pages 331–352 in R. M. Sibly and R. H. Smith, editors. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Science, Oxford, England.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* **107**.
- Pollock, K. H., and D. G. Raveling. 1982. Assumptions of modern band-recovery models with emphasis on heterogeneous survival rates. *Journal of Wildlife Management* **46**: 88–98.
- Pulliam, H. R., and T. A. Parker, III. 1979. Population regulation of sparrows. *Fortschritte der Zoologie* **25**:137–147.
- Quirin, W. L. 1978. Probability and statistics. Harper and Row, New York, New York, USA.
- Raveling, D. 1969. Roost sites and flight patterns of Canada Geese in winter. *Journal of Wildlife Management* **33**:319–330.
- . 1970. Dominance relationships and agnostic behavior of Canada Geese in winter. *Behaviour* **37**:291–319.
- . 1979. Traditional use of migration and winter roost sites by Canada Geese. *Journal of Wildlife Management* **43**:229–235.
- Reeves, H. M., H. H. Dill, and A. S. Hawkins. 1968. A case study in Canada Goose management: the Mississippi valley population. Pages 150–165 in R. L. Hine and C. Schoenfeld, editors. Canada Goose management. Dembar Educational Research Services, Madison, Wisconsin, USA.
- Rusch, D. H., S. R. Craven, R. E. Trost, J. R. Cary, R. L. Drieslein, J. W. Ellis, and J. Wetzel. 1985. Evaluation of efforts to redistribute Canada Geese. *Transactions of the North American Wildlife and Natural Resource Conference* **50**:506–524.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* **52**:249–259.
- . 1982. The estimation of animal abundance and related parameters. Second edition. Griffin, London, England.
- Spaans, A. L. 1977. Are Starlings faithful to their individual winter quarters? *Ardea* **64**:83–87.
- Sulzbach, D., and F. Cooke. 1978. Elements of nonrandomness in mass-captured samples of Snow Geese. *Journal of Wildlife Management* **42**:437–441.
- Szymczak, M. R. 1975. Canada Goose restoration along the foothills of Colorado. Colorado Division of Wildlife Technical Publication Number **31**.
- Terrill, S. B., and R. D. Ohmart. 1984. Facultative extension of fall migration of Yellow-rumped Warblers (*Dendroica coronata*). *Auk* **101**:427–438.
- Trost, R. E., R. A. Malecki, L. J. Hindman, and D. C. Luszcz. 1986. Survival and recovery rates of Canada Geese from Maryland and North Carolina 1963–74. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **40**:454–464.
- Vaught, R. W., and L. M. Kirsch. 1966. Canada Geese of the Eastern Prairie population, with special reference to the Swan Lake flock. Missouri Department of Conservation Technical Bulletin **3**.
- White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* **47**:716–728.

APPENDIX A

The probability of moving, $\hat{\psi}_{i,j,k}$, to region k at time $i + 1$ from region j at time i given that the goose survives from i to $i + 1$ was estimated (Mood et al. 1974) as:

$$\hat{\psi}_{i,j,k} = \frac{\hat{\phi}_{i,j,k}}{\sum_{k=1}^3 \hat{\phi}_{i,j,k}} + \frac{\text{Cov}\left[\hat{\phi}_{i,j,k}, \sum_{k=1}^3 \hat{\phi}_{i,j,k}\right]}{\left(\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right)^2} - \frac{\hat{\phi}_{i,j,k} \text{Var}\left[\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right]}{\left(\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right)^3}$$

The variance for $\hat{\psi}_{i,j,k}$ was estimated as:

$$\text{Var}[\hat{\psi}_{i,j,k}] = (\hat{\psi}_{i,j,k})^2 \left\{ \frac{\text{Var}[\hat{\phi}_{i,j,k}]}{(\hat{\phi}_{i,j,k})^2} + \frac{\text{Var}\left[\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right]}{\left(\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right)^2} - \frac{2 \text{Cov}\left[\hat{\phi}_{i,j,k}, \sum_{k=1}^3 \hat{\phi}_{i,j,k}\right]}{\hat{\phi}_{i,j,k} \left[\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right]} \right\},$$

where

$$\text{Var}\left[\sum_{k=1}^3 \hat{\phi}_{i,j,k}\right] = \sum_{k=1}^3 \text{Var}[\hat{\phi}_{i,j,k}] + 2 \sum_{k=1}^2 \sum_{l=k+1}^3 \text{Cov}[\hat{\phi}_{i,j,k}, \hat{\phi}_{i,j,l}]$$

and

$$\text{Cov}\left[\hat{\phi}_{i,j,k}, \sum_{l=1}^3 \hat{\phi}_{i,j,l}\right] = \text{Var}[\hat{\phi}_{i,j,k}] + \sum_{\substack{l \neq k \\ l=1}}^3 \text{Cov}[\hat{\phi}_{i,j,k}, \hat{\phi}_{i,j,l}].$$