

MOVEMENT, SURVIVAL RATE ESTIMATION, AND POPULATION
MODELLING OF EASTERN TUNDRA SWANS,
CYGNUS COLUMBIANUS COLUMBIANUS

A Dissertation

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MOVEMENT, SURVIVAL RATE ESTIMATION, AND POPULATION
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Khristi Ann Wilkins, Ph.D.

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The Eastern Population (EP) of tundra swans (*Cygnus columbianus columbianus*) winters in the eastern United States and breeds from the North Slope of Alaska to the eastern side of Hudson Bay in Canada. EP swans were marked on the wintering grounds in Maryland, North Carolina, Pennsylvania, and Virginia in order to study movements, habitat use, survival, and population structure. Swans were marked with individually coded neck collars ($n=1,471$), USFWS leg-bands ($n=3,504$), and satellite-tracked radio transmitters ($n=43$) from February 1997–March 2002. Location information was collected from February 1997–March 2003 via ground observers, recapture, recovery of dead birds, or satellite location. Satellite-tracked EP tundra swans spent approximately 7 months each year on breeding or wintering grounds, and about 5 months of each year in migration. Significant time spent in migration highlights the importance of migratory habitats to this population. No sub-populations were identifiable based on the exclusive use of migratory pathways, Bird Conservation Regions, wintering grounds, or breeding grounds. Movement rates between states on the wintering grounds (Maryland, North Carolina, Pennsylvania, and Virginia) ranged from 0.00 to 0.46, but were rarely different from 0.25 ($P<0.05$), which suggested that exchange between states caused significant mixing of the population within and between years. Indirect survival rates of marked adult swans ranged 66–84% depending on analytical method or marker type, but were statistically similar (95% confidence intervals overlapped). Use of neck collars in operational marking program

is not recommended for future studies due to the cost and difficulty of collecting representative data. To investigate the necessity of annual survival rate estimates, I used data from operational monitoring programs (Mid-Winter Index [MWI], winter ground Production Survey, number of hunting permits, retrieved swan harvest) to develop a model of EP tundra swan dynamics. The model provided reasonable and precise predictions of population size, harvest, and survival. The model can help to predict and understand the effects of harvest on population size. Analyses did not detect density-dependence in recruitment and suggested that a population size goal of at least 80,000 swans can be sustained at current or slightly decreased levels of harvest.

BIOGRAPHICAL SKETCH

Khristi A. Wilkins was born in Battle Creek, Michigan, and grew up in northern Illinois and Connecticut. She received a B.A. in biology from Wesleyan University in Middletown, CT, in 1986. She received an M.S. in wildlife biology from Clemson University in Clemson, SC, in 1998. While a graduate student at Clemson, Ms. Wilkins was a cooperative education student with the U.S. Fish and Wildlife Service. She worked at Patuxent Wildlife Research Center and, upon graduation, was hired by the Division of Migratory Bird Management. She has been a wildlife biologist with the Division of Migratory Bird Management in the Population and Habitat Assessment Branch since 1998, and earned her Ph.D. while working for the Division of Migratory Bird Management.

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TABLE OF CONTENTS

BIOGRAPHICAL SKETCH.....	iii
ACKNOWLEDGMENTS.....	iv
TABLE OF CONTENTS.....	vi
LIST OF FIGURES.....	ix
LIST OF TABLES.....	xi
CHAPTER 1.....	1
ABSTRACT.....	1
INTRODUCTION.....	2
METHODS.....	4
Marking.....	4
Annual Cycle.....	7
Habitat Use.....	9
Wintering Ground Movements.....	11
Characterization of Individual Swan Movements.....	11
Characterization of Population Structure.....	12
RESULTS.....	13
Marking.....	13
Annual Cycle.....	14
Spring Migration.....	14
Breeding Grounds.....	15
Fall Migration.....	16
Habitat Use.....	21
Movements on the Wintering Grounds.....	26
Characterization of Individual Swan Movements.....	26
Characterization of Population-Level Movements.....	29
DISCUSSION.....	30
MANAGEMENT IMPLICATIONS.....	35
APPENDIX A. Multi-state modelling of EP movement on the wintering grounds with data from satellite-tracked radio transmitters, neck collars, and leg bands.....	37

REFERENCES	51
CHAPTER 2	54
ABSTRACT	54
INTRODUCTION	55
METHODS	57
Marking	57
Neck-collar retention rates	63
Analyses	64
Estimation with dead recoveries	64
Estimation with dead recoveries and live resightings	66
RESULTS	70
Encounters with leg bands and neck collars	70
Neck-collar retention rates	70
Analyses	71
Survival estimation from dead recoveries	71
Survival estimation from dead recoveries and live resightings	73
DISCUSSION	78
MANAGEMENT IMPLICATIONS	82
APPENDIX B. Very High Frequency Radio Transmitters	85
REFERENCES	90
CHAPTER 3	94
ABSTRACT	94
INTRODUCTION	95
METHODS	96
Databases	96
Mid-winter inventories	96
Production surveys	97
Harvest data	98
Model Development	99
Survival	99

Recruitment	102
Weighting	103
Estimation.....	104
Model Selection.....	106
Sensitivity Analyses	106
Starting conditions.....	106
Weighting	107
Model Validation.....	107
Model Predictions.....	111
RESULTS.....	112
Model development	112
Parameter estimates	112
Survival.....	114
Recruitment	114
Estimation.....	114
Sensitivity Analyses	134
Starting conditions.....	134
Weighting	135
Model Validation.....	136
Survival.....	136
Recruitment	137
Estimation.....	137
Model predictions.....	147
DISCUSSION.....	148
MANAGEMENT IMPLICATIONS	151
APPENDIX C. Data used in Eastern population tundra swan model.	153
REFERENCES.....	157

LIST OF FIGURES

Figure 1.1. Trapping locations of Eastern Population tundra swans in the eastern U.S., winters of 2000–01 and 2001–02.	6
Figure 1.2. Satellite locations of 39 Eastern Population tundra swans during 2001–2003, classified into 3 month periods.	8
Figure 1.3. Bird Conservation Regions in North America used by 46 satellite-tracked Eastern Population tundra swans, 1998–2003.	10
Figure 1.4. Satellite locations of wintering Eastern Population tundra swans classified into 4 states the U.S., winter 1998–2003.	12
Figure 1.5. Fifty-six spring migration pathways of 39 North American Eastern Population tundra swans marked with satellite-tracked radio transmitters, 2001–2003.	16
Figure 1.6. Breeding ground locations of 39 Eastern Population tundra swans 2001–2003, classified by state in which the bird was originally marked during the winter. .	17
Figure 1.7. Twenty-eight fall migration pathways of 23 North American Eastern Population tundra swans marked with satellite-tracked radio transmitters, 2001–2003.	19
Figure 1.8. Seasonal use of important areas in North America by Eastern Population tundra swans, February 1998–March 2003.	24
Figure 1.9. Presence of 21 satellite-tracked Eastern Population tundra swans on the wintering grounds in Maryland, North Carolina, Pennsylvania, and Virginia, U.S., from December 1998–March 2003.	27
Figure 1.10. Movements of 21 satellite-tracked Eastern Population tundra swans between 4 wintering states in the eastern U.S., winter 1998–2003.	28
Figure 1.11. Movement rates (Ψ_{ij}) of 21 satellite-tracked Eastern Population tundra swans between.	30
Figure A.1. Number of days observers located Eastern Population tundra swans marked with neck collars in the eastern U.S., October 2000–March 2003.	39
Figure A.2. Seasonal movement rates of Eastern Population tundra swans between states on the wintering grounds of the eastern U.S. during three 2-month periods, 1997–2003.	46
Figure 2.1. Trapping locations where Eastern Population tundra swans were marked during the winters of 1996–97 through 2002–003 in the eastern U.S.	62

Figure 2.2. Number of days observers located Eastern Population tundra swans marked with neck collars in the eastern U.S., October 2000–March 2003.	63
Figure 3.1. Survival estimates for the linear recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013.	116
Figure 3.2. Survival harvest estimates for the Ricker recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013.	119
Figure 3.3. Recruitment estimates for the linear recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013.	122
Figure 3.4. Recruitment estimates for the Ricker recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013.	125
Figure 3.5. Population and harvest estimates for the linear recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013.	128
Figure 3.6. Population and harvest estimates for the Ricker recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013.	131
Figure 3.7. Survival estimates for North American Western Population tundra swans for 2 recruitment functions with 10-year predictions and 95% confidence intervals, 1949–2013.	138
Figure 3.8. Recruitment estimates for North American Western Population tundra swans for 2 recruitment functions with 10-year predictions and 95% confidence intervals, 1949–2013.	141
Figure 3.9. Population and harvest estimates for WP tundra swans for 2 recruitment functions with 10-year predictions and 95% confidence intervals.	144

LIST OF TABLES

Table 1.1. Seasonal time budget of 39 satellite-tracked Eastern Population tundra swans in North America, December 1998–December 2003.	14
Table 1.2. Arrival dates, departure dates, and number of satellite-tracked Eastern Population (EP) tundra swans in states, provinces, and territories in the U.S. and Canada.	20
Table 1.3. Seasonal use of important areas by 39 satellite-tracked Eastern Population tundra swans in North America, February 1998–March 2003.	22
Table 1.4. Bird Conservation Regions (BCRs) in North America used by 39 Eastern Population tundra swans marked with satellite-tracked radio transmitters during breeding, migration, and wintering periods, and approximate proportion of time spent in each BCR during each season, February 1998–March 2003.	25
Table 1.5. Transition rates ($\Psi_{i,j}$) ¹ and coefficients of variation (CV) of 21 satellite-tracked Eastern Population tundra swans between states of the wintering grounds of the eastern U.S. ² , winters 1998–2003, and projected coefficients of variation (CVs) at 2, 5, and 10 times the sample size in this study.	33
Table A.1. Multi-state capture-recapture model parameterizations investigated for estimation of movement rates of wintering Eastern Population tundra swans.	41
Table A.2. Multi-state capture-recapture model selection results from resighting and recovery records of Eastern Population tundra swans marked with leg bands, neck collars, and satellite-tracked radio transmitters in the eastern U.S., February 1997–March 2003.	45
Table A.3. Estimated movement rates (SE) of Eastern Population tundra swans between 4 states of the wintering grounds in the eastern U.S., February 1997–March 2003.	47
Table A.4. Number and proportion of Eastern Population tundra swans marked and observed >1 during the same winter in Maryland, North Carolina, Pennsylvania, or Virginia by marker type, February 1997–March 2003.	48
Table 2.1. Numbers of EP swans marked with leg bands only, and neck collars and leg bands during the winters of 1996–97 through 2002–03 in their primary wintering range.	59
Table 2.2. Numbers of wintering Eastern Population (EP) tundra swans marked in each state by marker type, February 1997–March 2003, compared to the proportion of EP wintering in that state.	61

Table 2.3. Survival and reporting rate parameterizations investigated in analysis of dead recoveries of leg-banded and neck-collared Eastern Population tundra swans. . .	66
Table 2.4. Neck-collar retention rates of 49 Eastern Population tundra swans in the eastern U.S., winter 1999–00 through 2002–03.	71
Table 2.5. Model selection results, adjusted for model selection uncertainty, from survival rate analyses of recoveries of dead leg-banded and neck-collared Eastern Population tundra swans.	73
Table 2.6. Model selection results, adjusted for model selection uncertainty, from survival rate analyses of resightings, recaptures, and recoveries of leg-banded and neck-collared Eastern Population tundra swans.	75
Table 2.7. Survival, recapture, reporting, resighting, and fidelity rates estimated from encounter histories of Eastern Population tundra swans marked with leg bands and neck collars in the eastern U.S., winter 1996–97 through 2002–03.	76
Table 2.8. Comparison of survival and recovery rates estimated for Eastern Population tundra swans using 2 types of capture-recapture data and analytical methods. Swans marked in the eastern U.S. November 1997–March 2003.	77
Table B.1. Distance in miles of aerial radio transmission at 3 different elevations (1000, 2000, and 3000 m) for two different receiver types (ATS ¹ and CS ²) and 2 different VHF frequencies (151.891 MHz and 151.953 MHz).	87
Table 3.1. Comparison of Mid-Winter Inventory population size [N(t)] and annual growth rates [N(t+1)/N(t)] for Eastern (EP) and Western Population (WP) tundra swans in the U.S., 1956–2003.	108
Table 3.2. Point estimates and 95% confidence intervals for parameter estimates and AIC values for 4 models of Eastern Population tundra swan population dynamics in the U.S., 1956–2003.	113
Table 3.3. Sensitivity of North American Eastern Population tundra swan model parameter estimates to starting conditions, using linear recruitment and unequal data set weighting, 1956–2003.	135
Table 3.4. Comparison of predicted population growth rates (λ^1) and average harvest (\bar{H}^2) of North American Eastern Population tundra swans from a population model with linear recruitment.	136
Table 3.5. Predictions of North American Eastern Population tundra swan population size and harvest in the Atlantic and Central Flyways, using the linear recruitment model with unequal weights, 2004–2013.	147
Table C.1. Data used in population model.	154

CHAPTER 1

Description and analysis of large and small-scale movements of Eastern Population tundra swans (*Cygnus columbianus columbianus*)

ABSTRACT

The Eastern Population (EP) of tundra swans (*Cygnus columbianus columbianus*) winters in the eastern United States and breeds from the North Slope of Alaska to the eastern side of Hudson Bay in Canada. EP swans were marked on the wintering grounds in Maryland, North Carolina, Pennsylvania, and Virginia in order to study movements, habitat use, survival, and population structure. Swans were marked with satellite-tracked radio transmitters ($n=43$) from February 1998–March 2002. Location information was collected from February 1997–March 2003 via satellite location. Complete migration pathways were obtained for 56 swans in spring and 28 in fall. Twenty-one birds were tracked from their return to wintering grounds in late fall or early winter until their departure in spring. Satellite-tracked EP tundra swans spent approximately 7 months each year on breeding or wintering grounds, and about 5 months of each year in migration. Significant time spent in migration highlights the importance of migratory habitats to this population. No sub-populations were identifiable based on the exclusive use of migratory pathways, Bird Conservation Regions, wintering grounds, or breeding grounds. Satellite-marked swans made all possible transitions between the 4 states except for a direct movement from Pennsylvania to North Carolina. While on wintering grounds, birds were more likely to stay in the same region than to move. However, movement rates between regions were still large enough to cause continual mixing of the populations within and between years. Movement rates between states on the wintering grounds (Maryland, North Carolina, Pennsylvania, and Virginia) ranged from 0.00 to 0.46, but were rarely

different from 0.25 ($P < 0.05$), which suggested that exchange between states caused significant mixing of the population within and between years. These movement rates suggest that the EP should be managed as 1 population.

INTRODUCTION

Tundra swans (*Cygnus columbianus columbianus*) wintering in the eastern United States from Pennsylvania to South Carolina number about 100,000 birds and for management purposes are collectively referred to as the Eastern Population (EP). A similar number of tundra swans that winter from southern British Columbia to central California comprise the Western Population (WP). EP tundra swans nest on tundra areas from the Northern Slope of Alaska to the eastern side of Hudson Bay in Canada, while WP swans breed along the west coast of Alaska (Bellrose 1980). There is only slight mixing of the 2 populations (Serie and Bartonek 1991). Over 98% of the EP winters in 3 states: Maryland, North Carolina, and Virginia; with the remainder in Pennsylvania, Delaware, New Jersey, New York, and South Carolina. From the mid-1950's until the early 1970's, 60%–80% of EP swans wintered in the Chesapeake Bay area of Maryland. Currently, most swans ($\approx 70\%$) winter in North Carolina (Serie and Raftovich 2003).

EP tundra swans are managed by the EP tundra swan management plan (hereafter referred to as the Plan, *Ad Hoc* EP Tundra Swan Committee 1998). The Plan includes a population objective of a 3-year average Mid-Winter Inventory (MWI) of 80,000 swans in the Atlantic Flyway. When this population objective is met, the Plan allows sport harvest of 5% of the EP (as indexed by the 3-year average MWI). Harvest, regulated by permit allocation, is distributed equally among production (Alaska, Northwest Territories, Nunavut, Yukon Territories), migration (U.S. Central Flyway states, U.S. Mississippi Flyway states, Saskatchewan, Manitoba, and Ontario),

and wintering zones (U.S. Atlantic Flyway states). Within the migration zone, harvest is equally distributed between the Canadian provinces of Saskatchewan, Manitoba, and Ontario; U.S. Central Flyway States; and U.S. Mississippi Flyway. However, most states, territories, and provinces do not participate in the EP tundra swan hunt. Current permit allocation is about 42% to the migration zone and 58% to the wintering zone: Montana (500 permits), North Dakota (2,000 permits), South Dakota (1,300 permits), North Carolina (5,000 permits), and Virginia (600 permits; *Ad Hoc* EP Tundra Swan Committee 1998).

Knowledge of seasonal movement patterns and habitat use is critical for conservation planning, and may suggest avenues of research should the population decline (Nichols and Kendall 1995). Previous studies have provided some information about the movement and habitat use of EP tundra swans (e.g., Sladen 1973), but our knowledge has been limited by the large scale of annual movements. Recently, detailed information about annual movements of individual EP tundra swans has become available through satellite telemetry (Petrie and Wilcox 2003), but sample sizes were small ($n=12$).

Historically, EP swans have been managed as one population, in the absence of information on subpopulation structure of EP swans. If sub-populations of EP tundra swans exist within the larger population, managers would likely establish separate population goals for each subpopulation and monitor the harvest rates of each (Hilborn 1990). Some managers have speculated that there is a geographically and demographically distinct sub-population of EP tundra swans wintering in Virginia, but this claim has not been supported by strong evidence (Sladen 1991). Knowledge on population structure also provides context for interpreting the changing winter distributions of EP swans. Finally, because biologists in some Mississippi and Atlantic Flyway states have expressed interest in opening tundra swan hunting seasons,

population structure is important for projecting impacts of expansion of harvest into areas that have not had swan-hunting seasons.

I marked 43 swans with satellite-tracked radio transmitters in Maryland, North Carolina, Pennsylvania, and Virginia during the winters of 2000–01 and 2001–02, and analyzed small- and large-scale movements of EP tundra swans using satellite telemetry data. Large-scale movements described migration pathways, important concentration regions, time spent in various locations or ecoregions, and between-year affiliation with breeding and wintering areas. Quality and quantity of movements of individual birds on the wintering grounds were also examined. Although neck-collar resightings, leg-band recoveries, and satellite telemetry have provided anecdotal evidence of wintering swan movements both within and between years (Sladen 1973, Serie and Bartonek 1991, Petrie and Wilcox 2003), movement rates have never been formally estimated. I calculated rates of movement between wintering states for evidence of sub-populations: high rates of movement suggest no sub-population structure, and low rates of movement are evidence of geographically distinct sub-populations (Hilborn 1990, Hanski 1998).

METHODS

Marking

Forty-three female swans were marked with U.S. Fish and Wildlife Service (USFWS) aluminum leg bands and 39-gram battery-powered PTT-100 satellite-tracked radio transmitters made by Microwave Telemetry, Inc., Columbia, Maryland. All but one swan were >1 year old (after-hatch year; AHY). Swans were captured and marked in Maryland ($n=6$), North Carolina ($n=20$), Pennsylvania ($n=10$), and Virginia ($n=7$) during the winter (November–March), from November 2000–March 2002. Allocation of satellite-tracked radio transmitters to the 4 states was based on both the

number of swans wintering in that state and available funding for satellite markers. Swans from Pennsylvania were over-represented in this sample (23% of the satellite-tracked radio transmitters and 1% of the average MWI in 2001 and 2002), while swans from North Carolina were under-represented (47% of the satellite-tracked radio transmitters and 72% of the MWI). Swans in Maryland (14% of the satellite-tracked radio transmitters and 18% of the MWI) and Virginia (16% of the satellite-tracked radio transmitters and 8% of the MWI) were marked in closer proportion to their population size.

Marking effort was spread throughout the winter range and transmitters were distributed among different locations (inland and coastal) and habitat types (fields and wetlands) to obtain the most representative sample possible (Figure 1.1). Most birds were captured by rocket-netting over bait adjacent to wetlands because this method proved to be the most reliable and efficient. We also used rocket-netting over plastic decoys and bait in fields, night-lighting in wetlands, and baited funnel traps in wetlands to sample birds in different habitat types and to minimize the effect of capture method on sample composition (Grand and Fondell 1994, Guyn and Clark 1999). Satellite-tracked radio transmitters were affixed to white collars to minimize hunter selection. Duty cycles were transmission of signals for 8 hours every 4th day during September–May and 8 hours every 8th day during June–August. Expected battery life of satellite radios was 1.5 years, and transmitters provided data from January 2001–April 2003. Location data were sorted for consistency with a routine that compared pairs of consecutive points in time and selected the most likely pair of latitude and longitude coordinates for each point. Biologically impossible locations were deleted (Malecki et al. 2001).

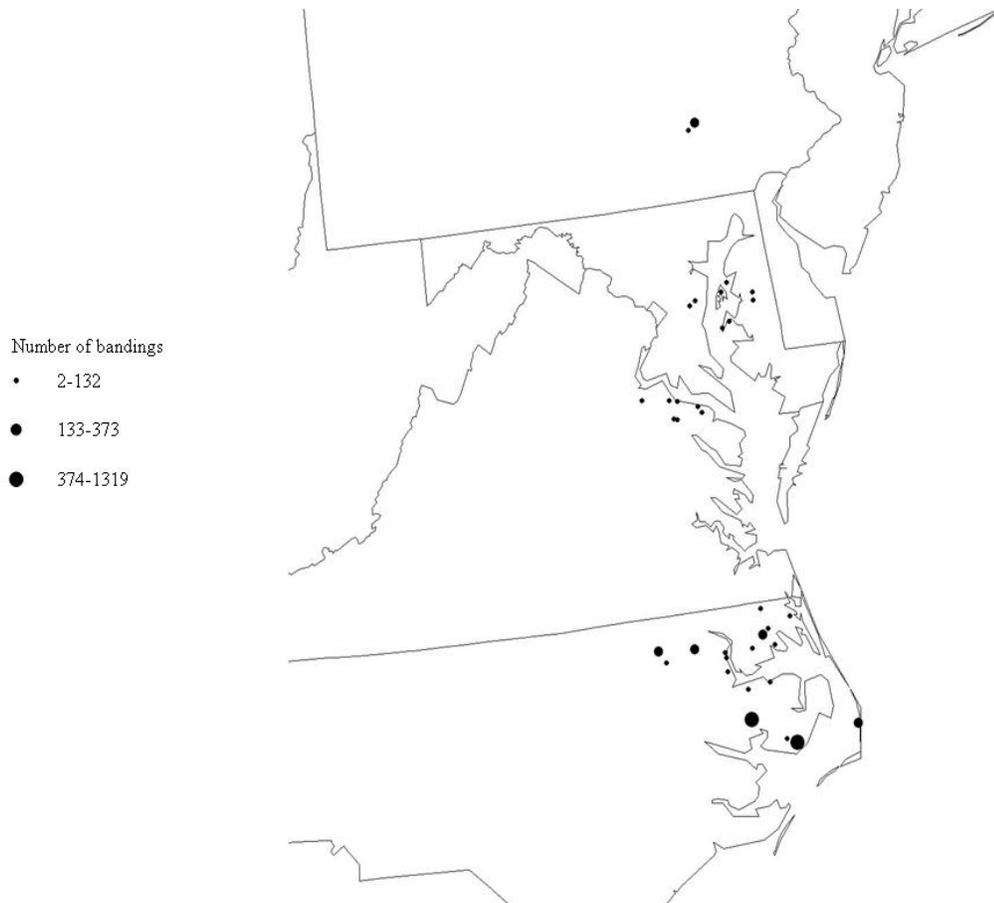


Figure 1.1. Trapping locations of Eastern Population tundra swans in the eastern U.S., winters of 2000–01 and 2001–02.

In an unrelated study of habitat use at an important EP tundra swan migration stopover point, 12 swans were equipped with satellite-tracked radio transmitters during the spring and fall of 1998 and fall of 1999 in Ontario (Petrie and Wilcox 2003), and data from 3 adult female swans were used in these analyses. These transmitters provided location information every 1–3 days from December 1998–September 2000.

Annual Cycle

Timing and geography of annual movements were highly variable among individual birds (Figure 1.2), so I used the following rules to assign each satellite location to a portion of the annual cycle:

(1) *Spring Migration*: Northerly movements outside of North Carolina, Maryland, and Virginia after February were considered spring migration. For example, a movement from North Carolina to Ontario in March was considered the beginning of spring migration for that bird. However, spring movements to Pennsylvania from the south were classified as wintering-ground movements if the bird stayed in Pennsylvania for 30 or more days. If the stopover was for a shorter period and was followed by a move north, it was considered a spring migration movement.

(2) *Breeding*: Satellite locations in the spring and early summer that did not vary by >150 km were all considered breeding ground locations.

(3) *Fall migration*: The first southerly movement in the late-summer or early-fall that was >800 km was considered the beginning of fall migration.

(4) *Winter*: Arrival in North Carolina, Virginia, or Maryland in the late fall or early winter was considered the start of the wintering period. Arrival in Pennsylvania was classified as wintering if the bird stayed for more than 2–3 days. However, if the bird continued south after 2–3 days, the Pennsylvania locations were considered part of fall migration. In a few cases, arrival in Ontario was considered the beginning of wintering, because 2 swans spent the entire winter in Ontario, and one bird stayed in Ontario for almost 2 months before moving to North Carolina in early January.

Satellite-tracked radio transmitters were active only every 4–8 days, so there were gaps of several days when locations were not known. I used the mid-point

between each pair of locations to estimate the number of days a bird spent in each part of the annual cycle. If the gap between locations was an odd number of days, the time spent in the first part of the annual cycle was arbitrarily assigned 1 less day than the subsequent part. I summed the days each bird spent in each phase of the annual cycle and calculated means and standard errors. To provide baseline information for harvest regulation, I tallied arrival dates, departure dates, and number of satellite-transmitter tracked EP tundra swans in each state, province, or territory during the hunting season.

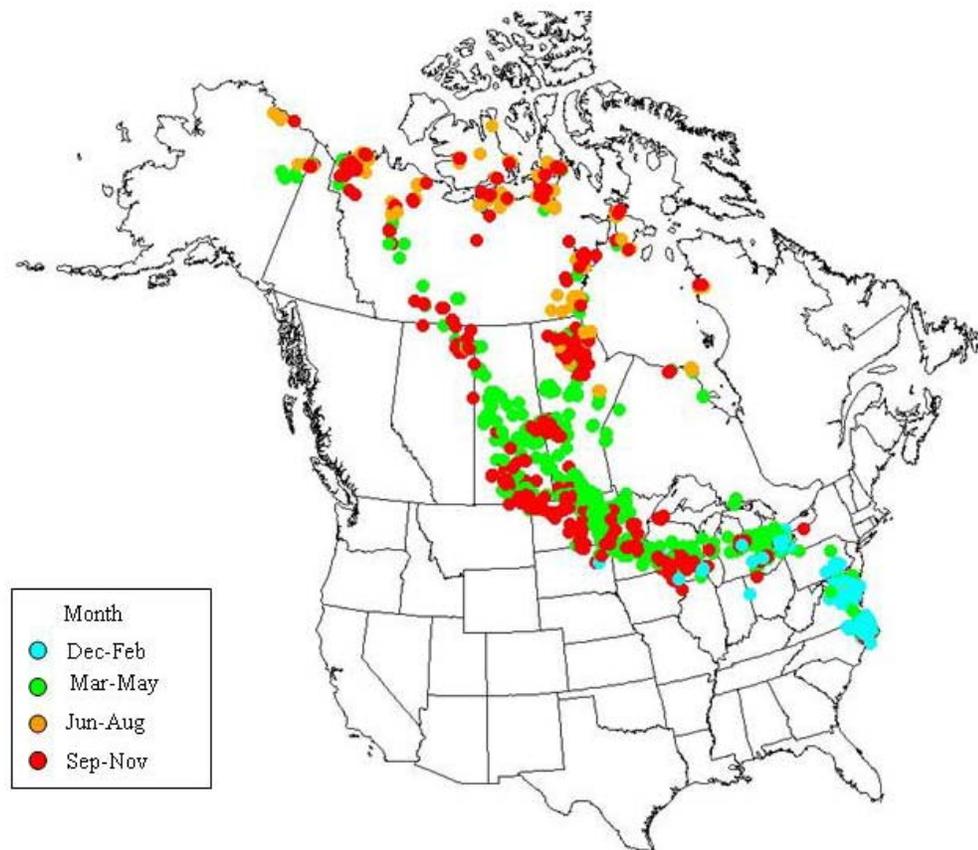


Figure 1.2. Satellite locations of 39 Eastern Population tundra swans during 2001–2003, classified into 3 month periods.

Habitat Use

Important stopover points were identified by the proportion of marked swans using them at different times of the year. For all analyses except the identification of important sites and assessment of harvest pressure, only data from complete seasons were used. Use of data from incomplete seasons can bias estimates of time spent in different regions or parts of the annual cycle if: (1) transmitter attrition causes overestimation of time spent in regions or phases of the annual cycle that occurred earlier in the transmitter's life; (2) transmitter failure is related to geographic location or time of year; (3) the number of active transmitters varied non-randomly (e.g., if the number of transmitters was greatest during the spring, and dropped off as the seasons progressed); and (4) seasonal duty cycles. Number of locations or number of transmitters was not an appropriate metric for habitat use because these effects would cause underestimation of locations in more southern habitats. Data from incomplete seasons were used to identify locations important to EP tundra swans, but these data were adjusted with the approximate number of marked swans during that time (e.g., 9 individuals using a site in the fall represented a larger portion of the population than 9 marked individuals using a site in the spring, because there were fewer active transmitters in the fall). For assessment of potential harvest pressure, all satellite locations were used.

To quantify large-scale habitat use, satellite locations were assigned to Bird Conservation Regions (BCRs), the most current system of ecoregion classification in North America (NABCI Committee 2000). There are 66 BCRs in North America, 15 of which were used by satellite-tracked EP tundra swans in this study (Figure 1.3). BCR use was characterized by the proportion of time spent in each BCR. Calculations were based on days of use by each bird (bird-days) summed across the number of birds for each part of the annual cycle. Assignment of season and BCR was done using

ArcView Geographic Information Systems software. Migration pathways were mapped using the Animal Movement extension to ArcView (Hooge and Eichenlaub 2000).

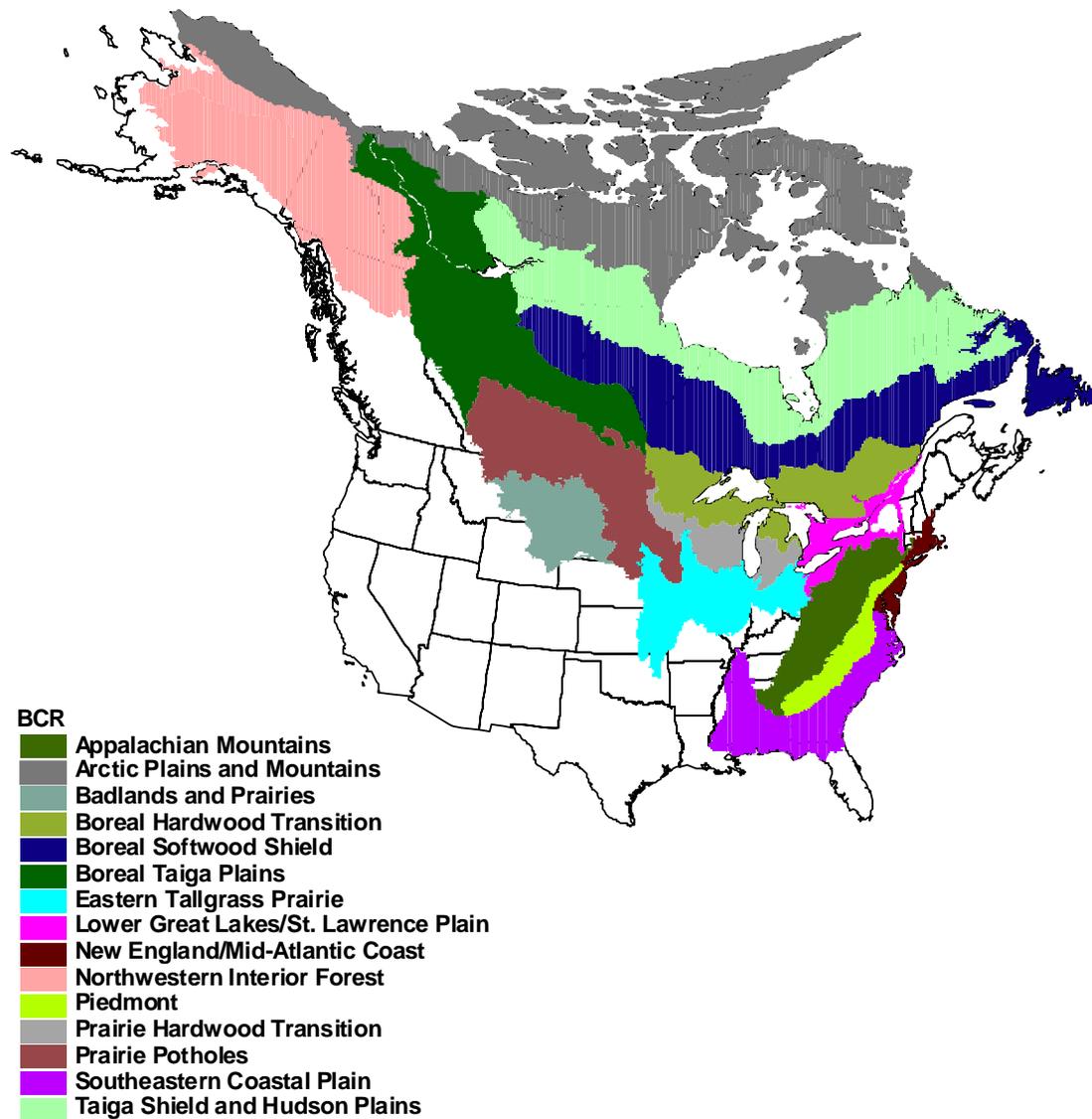


Figure 1.3. Bird Conservation Regions in North America used by 46 satellite-tracked Eastern Population tundra swans, 1998–2003.

Wintering Ground Movements

Characterization of Individual Swan Movements

Timing of swan migration is strongly driven by photoperiod and internal physiological rhythms (Bellrose 1980, Gill 1990) but can fluctuate in response to annual weather conditions (Limpert and Earnst 1994). I attempted to analyze movements separately for each year, to remove the confounding influence of annual weather conditions. However, pooling over years was necessary due to small sample sizes. Location data were grouped into two 15-day periods each month for October–March.

Potential sub-division of EP swan wintering grounds was based on a combination of political boundaries and major habitat features: (1) Pennsylvania, (2) Maryland/Northern Chesapeake Bay (Maryland), (3) Potomac River/Southern Chesapeake Bay (Virginia), and (4) North Carolina/Southeast Virginia (North Carolina; Figure 1.4). Final boundaries were determined by examining patterns of movement of birds in the border areas and choosing boundaries that minimized the effects of small changes in location. Locations were assigned to regions using ArcView software.

When swans were located in >1 state during a single period ($n=16$), locations were assigned to states so that the number of transitions between states was maximized. For example, one bird was located in Maryland, Virginia, and North Carolina during 16–31 December and was located in North Carolina during the subsequent period (1–15 January). In order to maintain the appropriate *number* of transitions, this bird was assigned to Maryland during 1–15 December, Virginia during 16–31 December, and North Carolina during 1–15 January. If assignment of the location did not influence the number of transitions during the winter, the state for that period was the one in which the swan spent most of that 2-week period. When there

were gaps in satellite data, I assumed birds remained in the same state entire time, provided they were relocated in the same state.

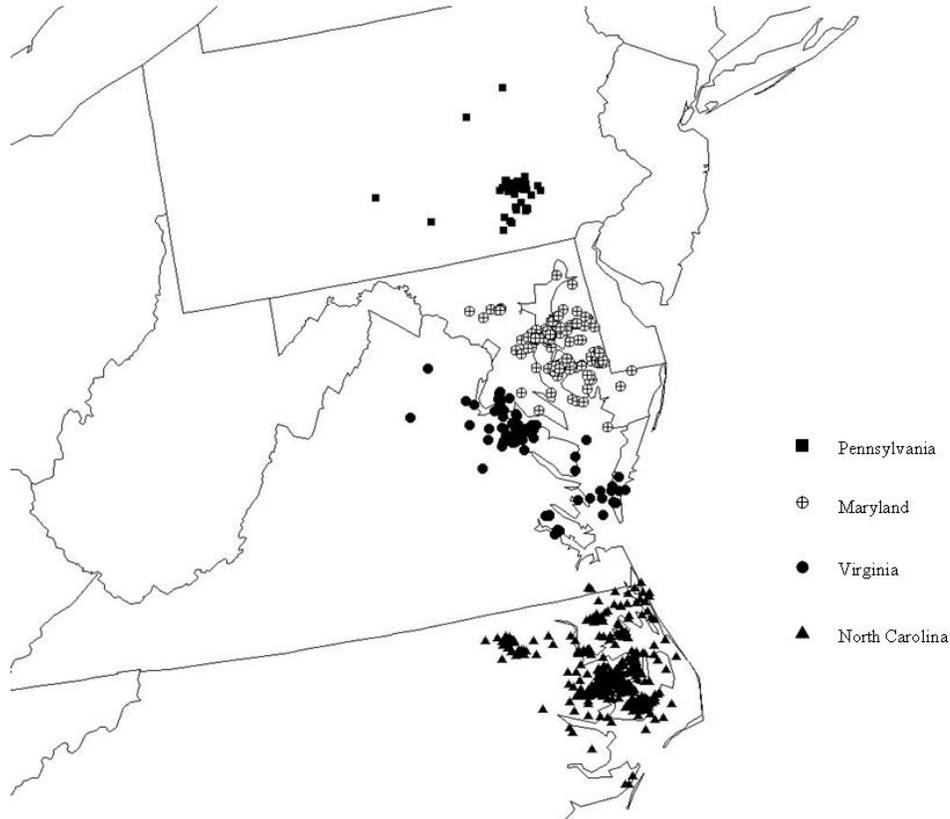


Figure 1.4. Satellite locations of wintering Eastern Population tundra swans classified into 4 states the U.S., winter 1998–2003.

Characterization of Population Structure

I calculated movement probabilities for individual swans, where Ψ_{ij} was the probability of moving from state i to state j , and Ψ_{ii} was the probability of not leaving state i . For example, Ψ_{PM} was the probability of a swan moving from Pennsylvania to Maryland, and Ψ_{NN} was the probability of staying in North Carolina. Free movement between different states (i.e., $\Psi_{ij} = 0.25$) would support the hypothesis of a single homogenous winter population. Conversely, no movement between states (i.e., $\Psi_{ij} = 0$

and $\Psi_{ii} = 1$ for all i, j) supports the alternative hypothesis of discrete sub-populations on the wintering grounds (Hilborn 1990).

Movement rates were calculated as number of transitions from state i to state j divided by the total number of movements from state i :

$$\Psi_{ij} = \frac{Y_{ij}}{N_i}$$

with a standard error of Ψ_{ij} :

$$SE(\Psi_{ij}) = \sqrt{\frac{p_{ij}(1-p_{ij})}{N_i}}$$

where i = state of origin and j = state at time $t+1$.

RESULTS

Marking

Satellite telemetry locations were received from Service Argos for 43 swans from February 1997–December 2003. Satellite-tracked radio transmitters provided location information every 4–21 days. One swan was found dead under a power line in Maryland and was reported to the U.S. Geological Survey’s (USGS) Bird Banding Laboratory (BBL). Of the remaining 42 satellite-tracked radio transmitters, 17 functioned until their batteries died, 5 failed earlier than expected, and 20 eventually transmitted signals from fixed positions. Signals from fixed positions could be caused by death of the bird, a slipped or broken collar, or the radio falling off the collar, and I could not distinguish between these fates, except for the bird found dead. Initial distribution of samples between states was not considered in these analyses for several reasons. First, many swans were banded late in the winter (February and March), when the state of banding may not have been the state in which the bird spent most of

the winter. Second, because of the frequency with which swans moved between states both within and between years, state of banding was often not relevant after the first winter.

Annual Cycle

I used data from 39 satellite-tracked swans to estimate annual time budgets. Swans marked with satellite-tracked radio transmitters spent the largest proportions of time on the breeding and wintering grounds and the remainder of the year in migration (Table 1.1). Satellite-tracked tundra swans spent about 5 months each year migrating in the spring and fall, and about 7 months of each year on the breeding and wintering grounds. The length of spring and fall migration were similar (as determined by overlapping 95% confidence intervals), as was the average time spent on breeding and wintering grounds.

Table 1.1. Seasonal time budget of 39 satellite-tracked Eastern Population tundra swans in North America, December 1998–December 2003. Proportion of year and average number of days per year spent with standard error (SE) and 95% confidence interval (CI) for average.

Season	Proportion of year	Average no. of days/year	SE days/year	95% CI days/year	n ¹
Spring migration	0.22	79	2.6	75–82	56
Breeding	0.30	111	3.4	106–116	39
Fall migration	0.20	73	5.3	66–80	28
Wintering	0.28	102	1.7	91–112	19

¹ Sample size is the number of complete seasons of satellite data, and could be from the same bird for two years if a transmitter lasted >1 year.

Spring Migration

Fifty-six complete spring migrations were obtained from satellite-tracked radio transmitters during the springs of 2001–2003. Twenty-two individual birds provided

data for 1 spring migration, and 17 individual birds provided data for 2 consecutive spring migrations. Most birds left wintering areas during the first half of March, but departure date ranged from 2 February to 28 March. Swans moved northwest to the Great Lakes region of Ontario and Michigan, where they stayed for 15–30 days and then continued west to the prairies in western Minnesota, North Dakota, and the prairie provinces of Canada (Figure 1.5). They stayed there for 30–40 days, usually until mid-April, but as late as early May. Migration paths then diverged; some birds migrated northwest toward the Mackenzie River Valley, the western Arctic Islands, or the North Slope of Alaska; others migrated north or northeast to eastern Nunavut or the Hudson Bay. Swans that went northwest first moved into the boreal forests of Saskatchewan and Manitoba and usually stayed in the Athabasca Delta region for 2–3 weeks, where migration paths again diverged. Some birds continued northwest to the North Slope and the Mackenzie River Valley; others moved northeast to the western Arctic Islands. Birds settled onto breeding ground locations from 4 May to 18 June.

Breeding Grounds

Breeding locations of EP tundra swans were unrelated to the state in which the swan was marked during the winter (Figure 1.6). Swans spent about 3–3.5 months on the breeding grounds and moved little, likely due to nesting and brood-rearing constraints. Small movements on the breeding grounds followed 2 general patterns: (1) a relatively large southerly movement (80–160 km in length) 2–4 weeks after arriving on the breeding grounds, followed by a movement back north to the earlier breeding location; and (2) a small southern movement (15–160 km) from tundra to river delta habitat shortly before fall migration. This pre-migration movement usually occurred in the Mackenzie River/Anderson River Delta area, and was followed by a major movement of 800 km or more to the south at the end of the summer, which was clearly the beginning of fall migration.

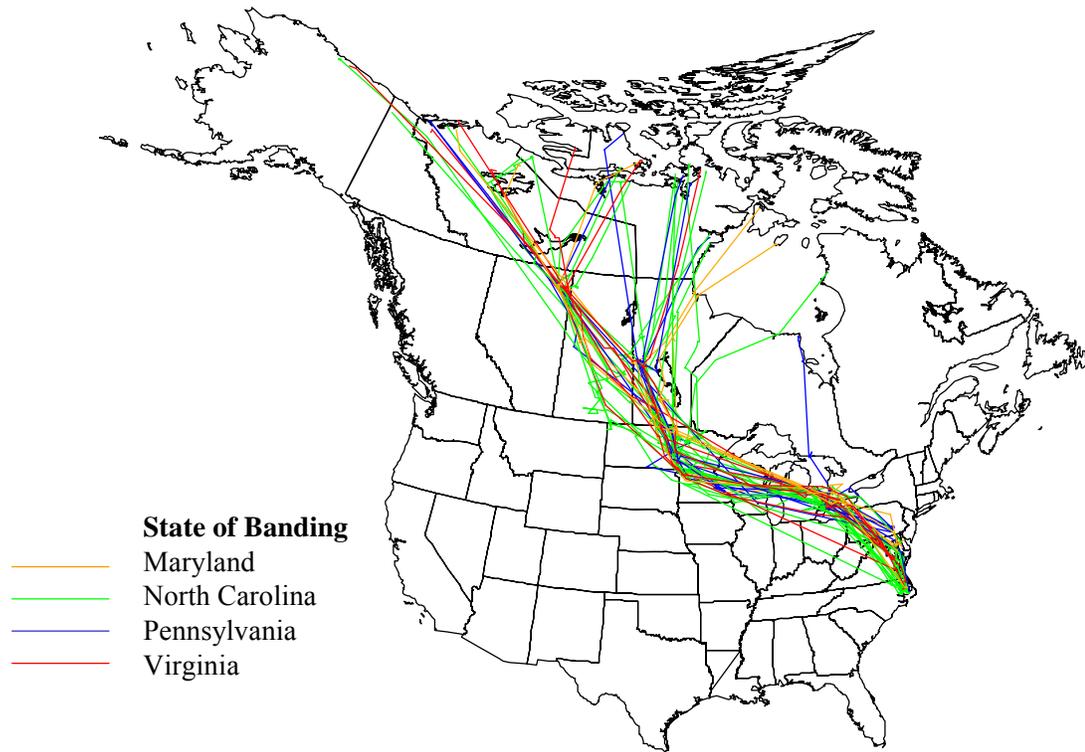


Figure 1.5. Fifty-six spring migration pathways of 39 North American Eastern Population tundra swans marked with satellite-tracked radio transmitters, 2001–2003.

Of the 17 adult females tracked for 2 consecutive years, all but one had the same summer location for both years, within the accuracy of satellite-tracked radio transmitters (<150m). The exception was a bird that spent the first summer on the southern tip of Southampton Island and the next summer on Coats Island, a small island just to the south of Southampton Island.

Fall Migration

I obtained data on 28 complete fall migrations during 2001–2003, 10 of which were consecutive fall migrations by 5 birds. EP tundra swans left breeding grounds from 2 September–7 October, and migrated down through the boreal forests of the Northwest Territories and Nunavut, to northern Saskatchewan and Manitoba (Figure

1.7), where they again spent about 2–3 weeks. They then continued south into southern Saskatchewan and Manitoba, where they typically stayed for several more weeks. Next the birds moved to the prairies of Montana, the Dakotas, and western Minnesota, where they stayed for 20–30 days, then headed east to the Upper Mississippi River region and, from there, to the Great Lakes region, which was the endpoint of migration for the few birds that remained in Ontario for most or all of the winter. However, most birds continued southeast to the wintering grounds of the mid-Atlantic coast, and arrived from 27 October–5 January.

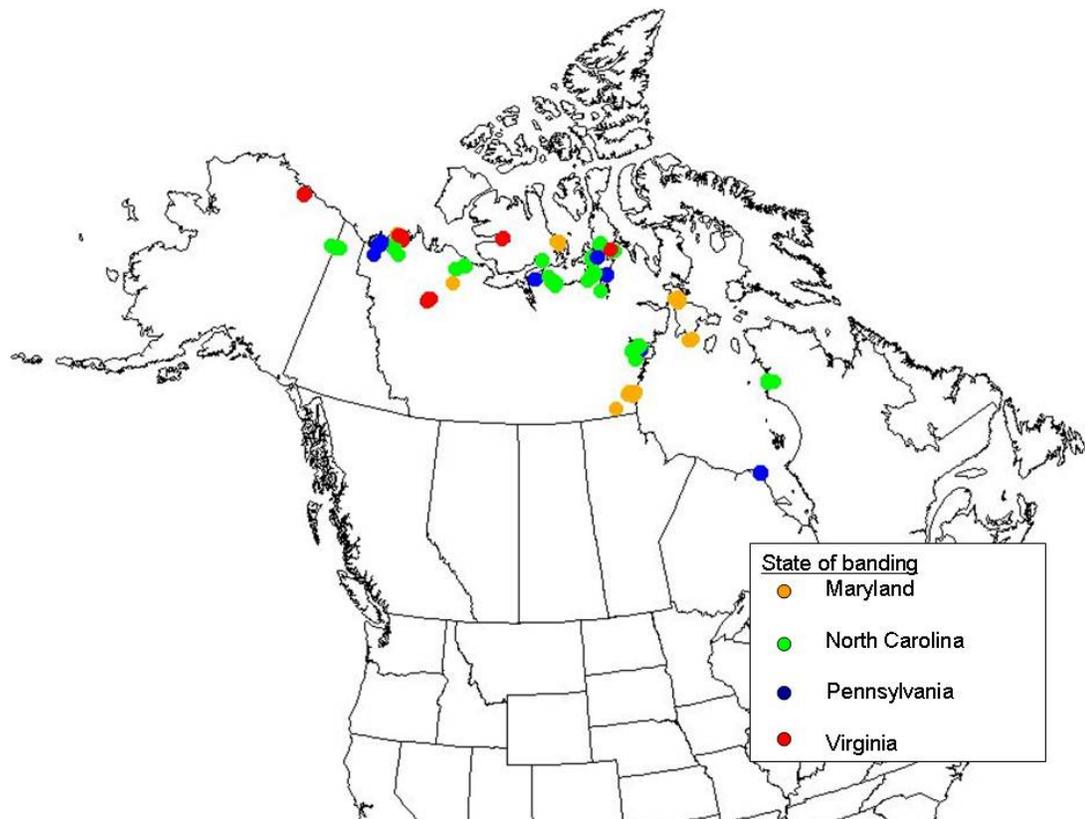


Figure 1.6. Breeding ground locations of 39 Eastern Population tundra swans 2001–2003, classified by state in which the bird was originally marked during the winter.

In all cases in which satellite location data from the same bird were available for 2 consecutive spring ($n=17$) or fall ($n=5$) migration pathways, the general route

was the same each year. Gaps in satellite location data precluded exact comparison of paths between years. Although timing of movements varied, overall movement patterns were consistent between years. Sample sizes were too small to characterize differences between years or even between spring and fall.

Satellite-tracked swans were located during the hunting season in all of the states, provinces, and territories of the production zone (Table 1.2). Satellite-tracked swans departed Alaska by 3 September, but remained in Nunavut until late October. One satellite-tracked radio transmitted tundra swan bred in Quebec, a province not assigned to a Hunt Plan zone. No EP swans migrated south of 52° latitude in Quebec, suggesting that EP swans are not at risk of sport harvest in southern Quebec. During fall migration, the greatest numbers of satellite-tracked radio transmitted swans were located in Alberta, Manitoba, Saskatchewan, North Dakota, Minnesota, and Wisconsin. Alberta was also not included in the EP Hunt Plan, but several of the satellite-tracked radio transmitted swans migrated through the northeastern corner of the province (12 swans in the fall, 18 swans in the spring + fall combined). In the Hunt Plan, Ontario was classified as a migration zone. However, 2 satellite-tracked radio transmitted swans bred in northern Ontario along the Hudson Bay and 1 swan spent the entire winter in southern Ontario (near Long Point). Therefore, timing and location of migration in Ontario was characterized by satellite locations <47 ° latitude. Only 1–3 EP swans visited Indiana, Iowa, and Ohio. Although EP tundra swans winter in New Jersey and South Carolina (Serie and Raftovich 2003), none of the satellite-tracked swans in this study went into these states.

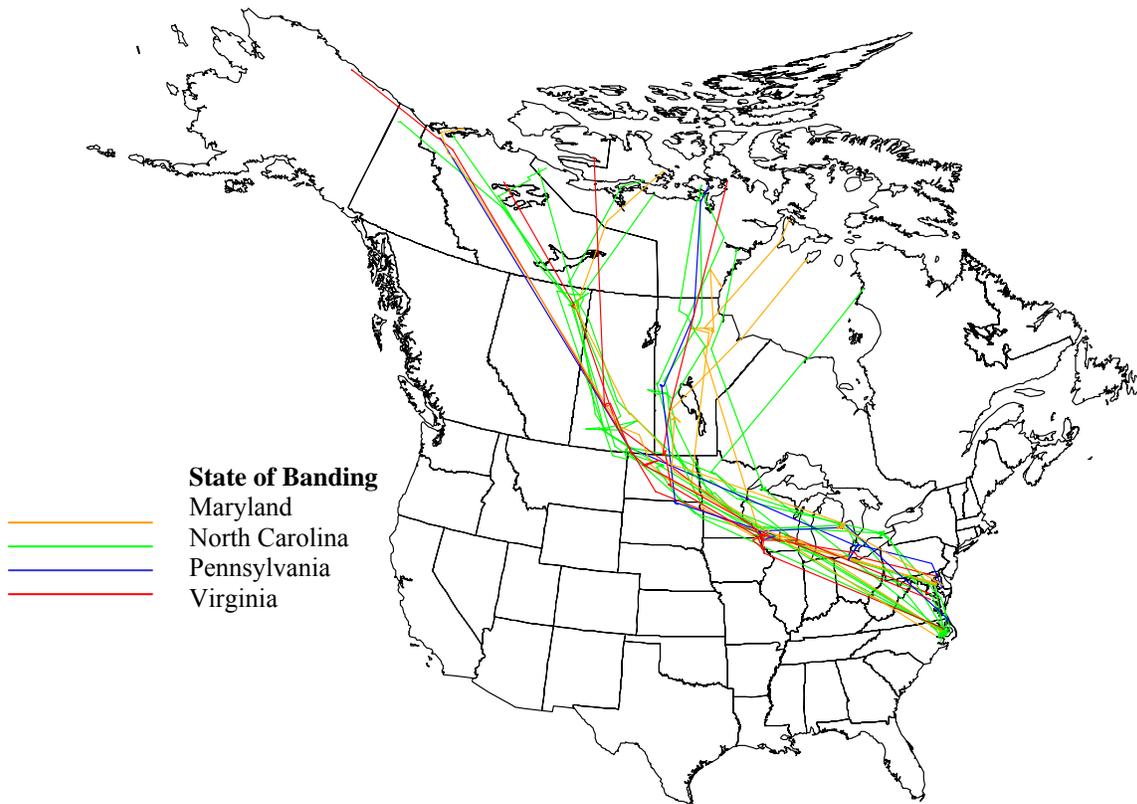


Figure 1.7. Twenty-eight fall migration pathways of 23 North American Eastern Population tundra swans marked with satellite-tracked radio transmitters, 2001–2003.

Table 1.2. Arrival dates, departure dates, and number of satellite-tracked Eastern Population (EP) tundra swans in states, provinces, and territories in the U.S. and Canada. States, provinces and territories are grouped by EP Hunt Plan zone. Swans were marked during the winters of 2000–01 and 2001–02 in Maryland, North Carolina, Pennsylvania, and Virginia.

EP Hunt Plan Zone State/Province/Territory	Arrival date of first fall migrants	Departure date of last fall migrants	Number of satellite transmitters during hunting season ¹	Number of satellite transmitters during year
Production				
Alaska	n/a	3-Sep	2	3
Northwest Territories	n/a	21-Oct	15	17
Nunavut	n/a	27-Oct	25	27
Quebec ²	n/a	21-Sep	1	1
Yukon Territories	n/a	28-Sep	1	1
Migration – Canada				
Alberta ³	24-Sep	21-Oct	12	18
Manitoba	8-Sep	1-Nov	13	27
Ontario ⁴	28-Oct	year-round	9	35
Saskatchewan	21-Sep	27-Nov	16	21
Migration – U.S. Central Flyway				
Montana	25-Sep	5-Nov	3	3
North Dakota	30-Sep	14-Nov	16	28
South Dakota	18-Oct	19-Dec	5	7
Migration – U.S. Mississippi Flyway				
Indiana	13-Dec	13-Dec	1	1
Iowa	6-Nov	13-Dec	3	3
Michigan	13-Oct	24-Dec	6	28
Minnesota	9-Oct	19-Dec	15	33
Ohio	19-Nov	9-Dec	2	3
Wisconsin	19-Oct	27-Dec	15	27
Winter – U.S. Atlantic Flyway				
Delaware	28-Dec	16-Mar	1	4
Maryland	4-Nov	22-Mar	8	22
New Jersey	none	None	0	0
New York ⁵	17-Mar	17-Mar	0	1
North Carolina	29-Oct	22-Mar	14	23
Pennsylvania	5-Dec	25-Mar	1	16
South Carolina	none	none	0	0
Virginia	22-Nov	28-Mar	4	14
Total number of active satellite transmitters			35	42

¹ 1 September–31 January.

² Quebec is not listed in the EP Hunt Plan. EP swans breed in northern Quebec along the Hudson Bay.

³ Alberta is not listed in the EP Hunt Plan. EP swans migrate across the northeast corner of the province.

⁴ Because EP swans breed in northern Ontario along the Hudson Bay, locations <48° latitude were classified as migration.

⁵ Present during spring migration only.

Habitat Use

I analyzed data from 39 satellite-tracked swans for the study of large-scale habitat use (Table 1.3) and I identified 10 sites as important migration stopover or staging areas. In the spring, the Red River Valley (63% of satellite radio-transmitted swans were located here at some time) and the Ontario Peninsula (51%) were the most important migration stopover locations. The Souris River (50%) and Athabasca Delta (46%) were the most important fall migration stopover sites. The Tri-Refuge area of North Carolina and the Chesapeake Bay were the most important wintering sites (53%). Important breeding sites were the Mackenzie and Anderson River Deltas (25%) and Great Bear Lake (19%). All key migration areas were used during both spring and fall (Figure 1.8) but use often varied by season. The Ontario peninsula, Saginaw Bay, and the Red River Valley were more important in spring. The upper Mississippi River and Souris River Valleys received more use by EP swans in the fall than in the spring. The North and South Saskatchewan Rivers and Athabasca Delta were equally important during spring and fall migration. Table 1.3 includes some areas thought to be important to EP tundra swans that were not used by many birds in this study (e.g., the North Slope of Alaska). Although Pennsylvania was classified as a wintering area, it was probably more important as a spring migration stopover point. However, the satellite data were insufficient to separate fall migration, winter, and spring migration in this state; therefore, all birds in Pennsylvania were classified as wintering birds.

Table 1.3. Seasonal use of important areas by 39 satellite-tracked Eastern Population tundra swans in North America, February 1998–March 2003.

Season/Region name	Number of birds	Proportion of birds
Spring migration		
Red River Valley	26	0.63
Ontario Peninsula (includes Long Point and Lake St. Clair/Aylmer)	21	0.51
Lake St. Clair/Aylmer WMA	16	0.39
Long Point	6	0.15
Saginaw Bay	18	0.44
Athabasca Delta	14	0.34
Souris River	14	0.34
Cedar Lake	11	0.27
Churchill/Hayes River	9	0.22
North and Southern Saskatchewan River	9	0.22
Upper Mississippi River, Pools 4–8	6	0.15
Lake Winnebago/Horicon Marsh	5	0.12
Upper Red Lake	4	0.10
Summer		
Mackenzie & Anderson River Deltas	8	0.25
Great Bear Lake	6	0.19
Victoria Island	5	0.16
Adelaide Peninsula	4	0.13
Chesterfield Inlet	4	0.13
Boothia Peninsula	3	0.09
McConnell River/Churchill	3	0.09
King William Island	2	0.06
North Slope	2	0.06
Southampton Island	2	0.06
Island Below Southampton	1	0.03
Old Crow Flats	1	0.03
Ungava Peninsula	1	0.03
Yukon Flats	1	0.03
Fall migration		
Souris River	14	0.50
Athabasca Delta	13	0.46
Upper Mississippi River, Pools 4–8	11	0.39
Churchill/Hayes River	10	0.36

Table 1.3 (Continued).

Season/Region name	Number of birds	Proportion of birds
North and Southern Saskatchewan River	7	0.25
Red River Valley	6	0.21
Cedar Lake	5	0.18
Saginaw Bay	5	0.18
Ontario Peninsula (includes Long Point and Lake St. Clair/Aylmer)	4	0.14
Lake St. Clair/Aylmer WMA	4	0.14
Long Point	1	0.04
Lake Winnebago/Horicon Marsh	3	0.11
Upper Red Lake	2	0.07
Winter		
Chesapeake Bay	20	0.53
TriRefuge Area (Alligator River, Mattamuskeet, and Pocosin Lakes NWRs and surrounding areas)	20	0.53
Middle Creek WMA/Susquehanna River	11	0.29
Potomac River	11	0.29

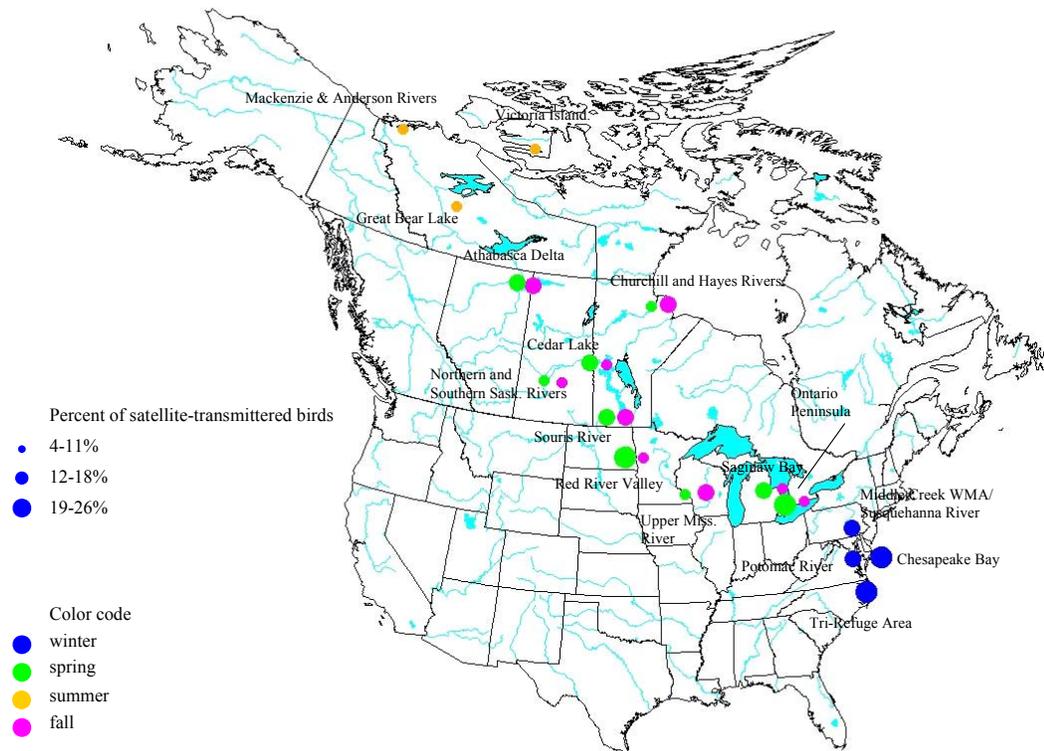


Figure 1.8. Seasonal use of important areas in North America by Eastern Population tundra swans, February 1998–March 2003. Color of marker indicates the season, and size of marker indicates the number of 39 birds marked with satellite-tracked radio transmitters that used the areas.

Satellite radio-transmitted EP swans used 16 BCRs during the year, and several were important during >1 season: 10 BCRs in spring, 12 BCRs in fall, 4 BCRs in summer, and 5 BCRs in winter. The most important were the Prairie Pothole Region and Boreal Taiga Plains in the spring, the Prairie Pothole Region and Prairie Hardwood Transition in the fall, the Arctic Plains and Mountains (including tundra) in the summer, and the Southeastern Coastal Plain and Mid-Atlantic Coast in the winter (Table 1.4). Within each season, individual birds had different patterns of BCR use. Individual swans used 2–8 BCRs during the spring, 2–6 BCRs during the fall, 1–2 BCRs during the summer, and 1–3 BCRs during the winter.

Table 1.4. Bird Conservation Regions (BCRs) in North America used by 39 Eastern Population tundra swans marked with satellite-tracked radio transmitters during breeding, migration, and wintering periods, and approximate proportion of time spent in each BCR during each season, February 1998–March 2003.

Season/BCR	No. of birds	Proportion of days	Minimum no. of days	Maximum no. of days
Spring migration				
Prairie Potholes	51	0.288	4	49
Boreal Taiga Plains	44	0.229	4	41
Lower Great Lakes/St. Lawrence Plain	43	0.173	5	47
Boreal Hardwood Transition	34	0.104	4	40
Prairie Hardwood Transition	33	0.074	2	38
Boreal Softwood Shield	21	0.058	4	25
Taiga Shield and Hudson Plains	22	0.051	4	23
Arctic Plains and Mountains	8	0.010	4	8
Piedmont	3	0.007	5	19
Appalachian Mountains	3	0.005	4	13
Breeding				
Arctic Plains and Mountains	36	0.882	82	136
Northwestern Interior Forest	2	0.067	145	146
Boreal Taiga Plains	5	0.046	7	134
Taiga Shield and Hudson Plains	1	0.004	19	19
Fall migration				
Prairie Potholes	25	0.303	4	40
Prairie Hardwood Transition	20	0.236	4	63
Boreal Taiga Plains	20	0.152	7	25
Lower Great Lakes/St. Lawrence Plain	7	0.084	5	64
Boreal Hardwood Transition	8	0.082	4	57
Taiga Shield and Hudson Plains	13	0.079	4	31
Arctic Plains and Mountains	9	0.028	4	11
Boreal Softwood Shield	4	0.016	4	13
Eastern Tallgrass Prairie	4	0.014	5	9
Badlands and Prairies	1	0.002	5	5
New England/Mid-Atlantic Coast	1	0.002	5	5
Piedmont	1	0.002	5	5
Winter				
Southeastern Coastal Plain	14	0.640	16	151
New England/Mid-Atlantic Coast	14	0.289	4	93
Lower Great Lakes/St. Lawrence Plain	2	0.062	7	113
Piedmont	2	0.007	4	10
Prairie Hardwood Transition	1	0.003	5	5

The BCRs used in the spring and fall were similar, but importance of BCR types varied by season. The Boreal Taiga Plain (tundra) was used more in the spring than in the fall. In contrast, the Prairie Hardwood Transition in the southern Great Lakes region (Minnesota, Michigan, and Wisconsin) was used more in the fall than the spring. Four BCRs were used in either the spring (Appalachian Mountains) or fall (Badlands, New England/Mid-Atlantic Coast, and Eastern Tallgrass Prairie), but this was likely due to the small number of marked birds ($n=42$) and the short amount of time spent in these regions (4–13 days/year).

Movements on the Wintering Grounds

Twenty-one birds were tracked from their return to the wintering grounds in late fall/early winter until their departure in the spring: 2 in 1998–99, 1 in 1999–2000, 4 in 2001–2002, and 14 in 2002–2003. Of the 21 swans for which we had complete winter data, 2 were marked in Pennsylvania (10% of the sample), 5 in Maryland (24%), 3 in Virginia (14%), and 8 in North Carolina (38%). This initial distribution of markers across wintering states was closer to the spatial distribution of the wintering population, although North Carolina was still under-represented in this sample. The remaining 3 swans were marked in Ontario.

Characterization of Individual Swan Movements

EP tundra swans arrived on the wintering ground in a staggered fashion but departures were more closely correlated in time (Figure 1.9). Eleven of the 18 birds marked in the U.S. were first located in the same state in which they were marked the previous winter. Of the remaining 7, 4 eventually returned to the state in which they were banded, and 3 never returned. Arrival dates of individual swans ranged from 29 October–7 January (average 4 December) and departure dates ranged from 30 January–28 March (average 8 March). No birds arrived prior to mid-October, but they

gradually filtered down from the Great Lakes area from mid-October through late December. January was the only month when all birds were present on wintering areas. Swans began moving back to the Great Lakes region as soon as early February, but as late as late March.

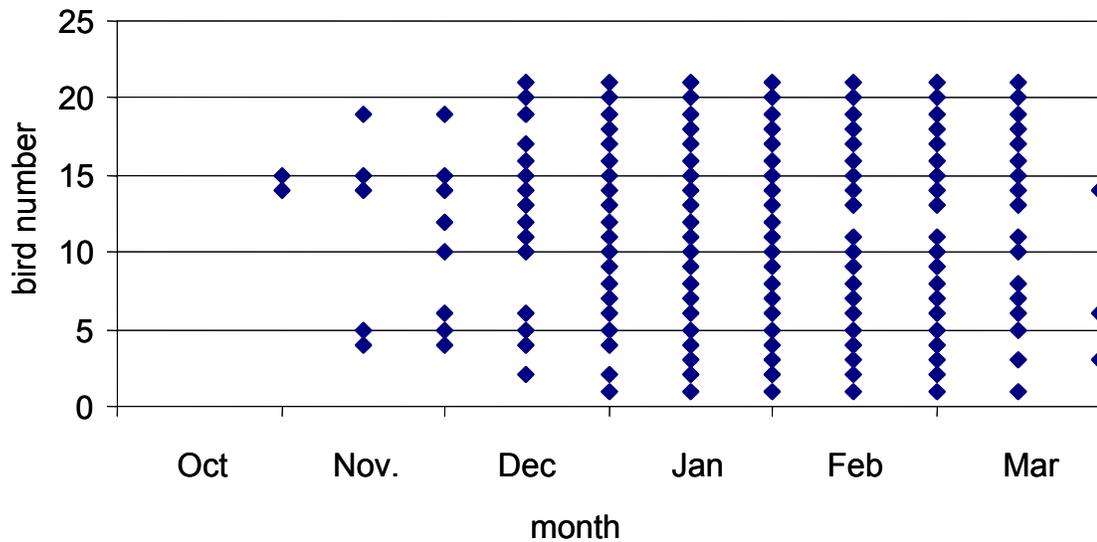


Figure 1.9. Presence of 21 satellite-tracked Eastern Population tundra swans on the wintering grounds in Maryland, North Carolina, Pennsylvania, and Virginia, U.S., from December 1998–March 2003. Each dot indicates the presence of an individual swan.

Once the satellite-tracked swans reached the wintering grounds, most moved among the 4 states. Six birds were in 1 state during the winter, 12 birds were in 2 states, 2 birds were in 3 states, and 1 individual was in all 4 wintering states during a single winter period (Figure 1.10). Swans 30297 and 30298 had identical capture histories, as did swans 33884 and 33893; all other capture histories were unique. However, movement rates could be underestimated because satellite transmitters were not programmed to provide daily locations.

In general, swans tended to move south soon after their arrival on the wintering grounds (unless they first arrived in North Carolina) and to move north later in the winter. Only swan 30420 made a northerly movement in the middle of the winter

before returning south the next period. Although 15 of the 21 birds used more than 1 state, most birds spent the majority of the winter in 1 state; only swans 3722 and 33891 spent significant amounts of time in >1 state.

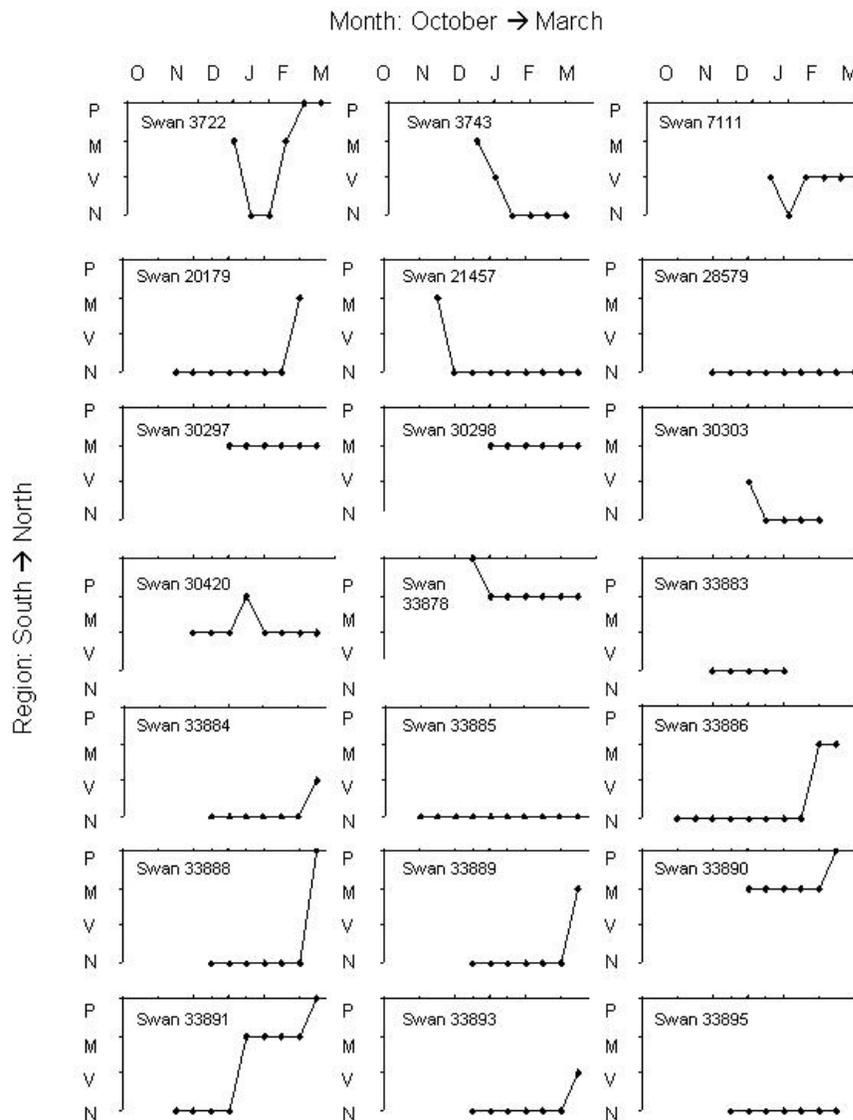


Figure 1.10. Movements of 21 satellite-tracked Eastern Population tundra swans between 4 wintering states in the eastern U.S., winter 1998–2003. On the y-axis, states run from south to north: Pennsylvania (P), Maryland (M), Virginia (V), and North Carolina (N). On the x-axis, time runs from October (O) through March (M).

Characterization of Population-Level Movements

The satellite-tracked EP tundra swans made all possible transitions between the 4 states except for a direct movement from Pennsylvania to North Carolina (Figure 1.11). Within each state, the highest movement probability was the probability of remaining in the same state (Ψ_{ii}). However, the probability of moving to another state was >0.5 for all states except Pennsylvania. Only in Pennsylvania was a swan more likely to remain in the state than to move to one of the other 3 states ($\Psi_{PP} = 0.71$). Six movement rates from states were $\approx \Psi=0.25$: North Carolina to Maryland, North Carolina to Virginia, Maryland to North Carolina, Maryland to Pennsylvania, Virginia to North Carolina, and Virginia to Maryland. Movement rates between states (Ψ_{ij}) were rarely different from 0.25, and only 1 confidence interval for the probability of remaining in the same state (Ψ_{ii}) included 1.0. These results support the hypothesis of a single wintering population. However, almost all of the 16 movement rates have overlapping confidence intervals because of large standard errors associated with the point estimates caused by small sample size, especially in Pennsylvania.

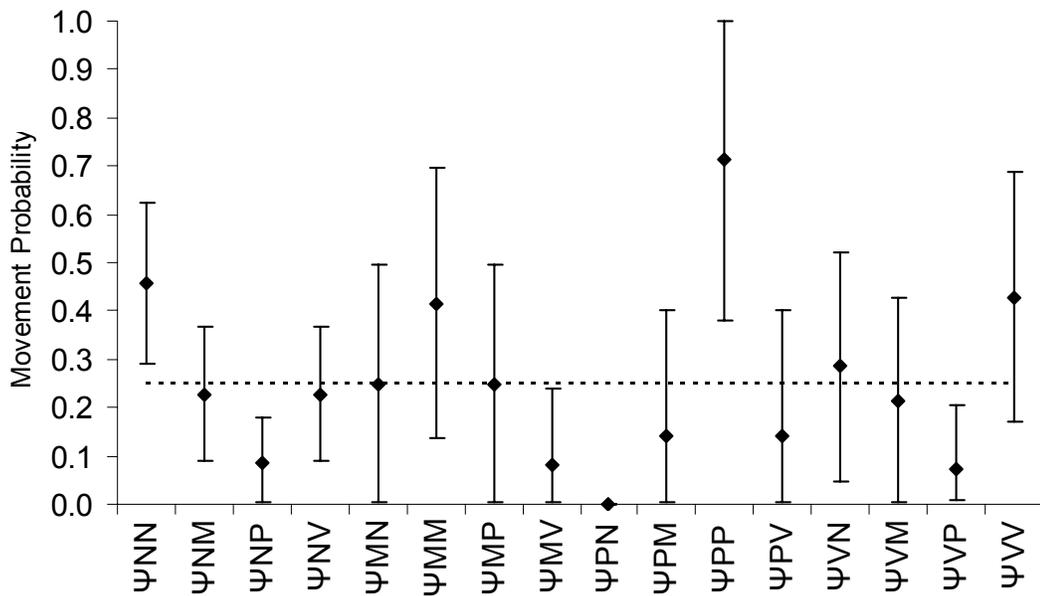


Figure 1.11. Movement rates (Ψ_{ij}) of 21 satellite-tracked Eastern Population tundra swans between Pennsylvania (P), Maryland (M), Virginia (V), and North Carolina (N), December 1998–March 2003. Vertical lines show 95% confidence intervals. A horizontal reference line is at $\Psi = 0.25$.

DISCUSSION

While leg bands and neck collars can provide insights into EP swan movements, only satellite-tracked radio transmitters can provide nearly complete information on migration chronology, important stopover points, and continental-scale habitat use. As found in other studies (e.g., Petrie and Wilcox 2003), satellite-tracked EP tundra swans spent over 7 months each year on the breeding and wintering grounds and the rest of the year in migration. EP swans spend about 5 months each year in migration, so migratory habitats play a key role in the life-cycle of EP tundra swans. Unlike Petrie and Wilcox (2003), who reported that fall migration was 1 month shorter than spring migration, I found no statistical difference between the time spent in fall and spring migrations, likely due to small sample sizes for both studies as well as annual differences in migration chronology due to weather. Timing of annual spring

and fall migration movements and movements on wintering and breeding areas were variable between individuals. However, migration pathways were consistent with those described elsewhere (e.g., Bellrose 1980, Sladen 1973, Petrie and Wilcox 2003) and were also consistent between years.

Traditional stopover sites presumably provide suitable feeding and roosting habitat at appropriate locations along the migration route. Petrie et al. (2002) found that EP tundra swans in Ontario spent more time foraging for submerged aquatic vegetation (SAV) in the fall than the spring. In the spring, swans spent more time foraging in fields for waste grain. Seasonal feeding patterns may be dictated by nutritional needs during the annual cycle (e.g., migration, completion of feather molt, preparation for nesting) and nutritional quality (e.g., SAVs are higher in protein, grains are higher in carbohydrate; Bortner 1985). Therefore, seasonal use patterns in particular sites may reflect food availability. However, food preferences deduced from foraging time may be biased due to seasonal fluctuations in availability, and thus must be interpreted with caution (Petrie et al. 2002).

Although tundra swans were thought to be fairly sedentary during the summer and winter, I found substantial movement within these seasons. Individual swans used up to 2 different BCRs during the summer and winter. Use of multiple BCRs may help EP swans meet different nutritional and habitat needs during the critical nesting, fledging, and molting periods (Baldassarre and Bolen 1994, Grant et al. 1994). Movement by satellite-tracked birds on the breeding grounds may be used to infer breeding outcomes (Petrie and Wilcox 2003; Reed et al. 2003). A relatively large early summer movement suggested either a failed nesting attempt, because an adult could not travel far with young so early in the season (Monda et al. 1994), or a bird that did not breed, because non-breeding females tend to molt earlier and thus can make long-distance moves earlier in the summer (Earnst 1994). On the other hand, a short, early

fall movement suggested a successful breeding female with fledged young (Monda et al. 1994). Most of these movements were to large river deltas, which suggested that those habitats were important to recently fledged young preparing for fall migration. One female did not use the same location each year; not surprisingly, this was the only female that was a young-of-the-year bird when it was marked, because tundra swans do not generally breed until they are 4–5 years old (Bart et al. 1991).

The lack of winter population structure was contrary to the findings of Sladen (1991), who suggested that Virginia tundra swans were a distinct sub-population of the EP. However, the power of these analyses was low because of small sample sizes. Despite a large banding effort, samples from Pennsylvania were particularly lacking because of transmitter failure and the small number of birds wintering in that state. A sample about 10 times larger than that used here would provide a more acceptable level of precision (coefficient of variation [CV] ≈ 0.15 or less for all states except for Pennsylvania; Table 1.5). These sample-size calculations assumed that all transmitters provided data; therefore, actual banded sample sizes would need to be larger to account for transmitter loss and failure. To minimize bias in movement rate estimates, swans should be marked with satellite-tracked radio transmitters as soon as possible after they arrive on the wintering grounds and markers should be distributed in close approximation to wintering distribution: 72% in North Carolina, 18% in Maryland, 8% in Virginia, and 1% in Pennsylvania. Marking swans in stopover locations shortly before arrival on the wintering grounds would not be appropriate because this could result in an unrepresentative sample.

Table 1.5. Transition rates (Ψ_{ij})¹ and coefficients of variation (CV) of 21 satellite-tracked Eastern Population tundra swans between states of the wintering grounds of the eastern U.S.², winters 1998–2003, and projected coefficients of variation (CVs) at 2, 5, and 10 times the sample size in this study. Rates of movement rates for 2-week time periods.

Transition	This study:		Expected CV if sample size increased:		
	Rate	CV	2x	5x	10x
$\Psi_{N,N}$	0.46	0.18	0.13	0.08	0.06
$\Psi_{N,M}$	0.23	0.31	0.22	0.14	0.10
$\Psi_{N,P}$	0.09	0.55	0.39	0.25	0.17
$\Psi_{N,V}$	0.23	0.31	0.22	0.14	0.10
$\Psi_{M,N}$	0.25	0.50	0.35	0.22	0.16
$\Psi_{M,M}$	0.42	0.34	0.24	0.15	0.11
$\Psi_{M,P}$	0.25	0.50	0.35	0.22	0.16
$\Psi_{M,V}$	0.08	0.96	0.68	0.43	0.30
$\Psi_{P,N}$	0.13	0.94	0.66	0.42	0.30
$\Psi_{P,M}$	0.13	0.94	0.66	0.42	0.30
$\Psi_{P,P}$	0.63	0.27	0.19	0.12	0.09
$\Psi_{P,V}$	0.13	0.94	0.66	0.42	0.30
$\Psi_{V,N}$	0.29	0.42	0.30	0.19	0.13
$\Psi_{V,M}$	0.21	0.51	0.36	0.23	0.16
$\Psi_{V,P}$	0.07	0.96	0.68	0.43	0.30
$\Psi_{V,V}$	0.43	0.31	0.22	0.14	0.10

¹ i=from state, j=to state

² M = Maryland, N = North Carolina, P = Pennsylvania, V = Virginia

There are 3 important considerations about these analyses of satellite data. First, all estimates of use and movement were minimum estimates, because time gaps of up to 2 weeks between satellite locations meant that birds could be missed. Second, the *proportion* (not number) of the marked population that traveled through each location was approximate, because the size of the marked sample (number of swans with active transmitters) varied within seasons. I think that proportion of marked birds was less likely biased by non-randomly varying sample size; however, fall and winter sites were more likely to be missed than spring and summer sites because of transmitter attrition over time. Finally, because analyses were from 43 marked females (all were AHY but 1 bird), one must consider the limitations of the data inherent in this small sample size. Because tundra swans mate for life, movements of AHY females should be similar to movements of their male AHY mates (Hawkins 1986). EP swans travel as family groups for at least the first spring migration, so movements of AHY females should also be similar to those of hatch-year (HY) birds (Limpert and Earnst 1994). These analyses of satellite data did not provide information about non-breeding AHY tundra swans, except for data from the 1 swan that was banded as an HY bird. This swan was the only marked bird that did not spend consecutive summers in the same location.

In this study, 21 of 43 satellite-tracked radio transmitters stopped moving within the life of the transmitter. Because most of the transmitters stopped moving in remote regions, the fates of these transmitters were unknown. I suspect that the cause of most sedentary transmitters was the transmitter falling off of the neck collar. It is possible that some of the losses on the breeding grounds were due to subsistence harvest, but this seems unlikely because subsistence harvest of swans is small (Georgette 2000, Walker 2003, Priest and Usher 2004) and most of the collars that stopped moving on the breeding grounds were not near villages. Another possible

cause is the collar fell off the swan. This seems unlikely, given an estimated collar retention rate of 90% per year for similar neck collars (Chapter 2). Also, 2 swans with radio transmitters were recaptured; neither had lost a radio transmitter.

MANAGEMENT IMPLICATIONS

My data lend no support to the hypothesis that EP tundra swans are organized into discrete sub-populations. Furthermore, this mixing on the wintering ground, where pair bonds are formed (Limpert and Earnst 1994), suggests that the formulation of sub-populations is unlikely in EP tundra swans. The inability to identify sub-populations indicates that it is reasonable for biologists conducting marking studies to concentrate their efforts in states of the wintering grounds where swans were easier to catch. However, this sort of opportunistic marking scheme should be used in conjunction with total population counts (MWI) to keep track of the total number of swans in the Flyway. Without large-scale monitoring, small-scale intensive studies could miss large-scale changes in population size and distribution.

Waterfowl managers can use these results to help predict the effects of changes in harvest regulations on the population. The movements exhibited by satellite-tracked birds suggest that the degree to which particular portions of the population are affected by hunting will depend on the timing of the hunting season when hunting takes place in migration stopover areas (i.e., Pennsylvania, the Dakotas, and Montana). However, hunting on the wintering grounds impacts the entire population, especially since swan-hunting seasons on the wintering grounds run from late October (in North Carolina) or December (in Virginia) through the end of January.

The huge range of EP swans means that EP tundra swans do not all rely on one area or habitat type. This may buffer the population from being negatively affected by changes in any one area. Key concentration points used during migration, breeding,

and on the wintering grounds should continue to be emphasized in waterfowl management plans (e.g., *Ad Hoc* EP Tundra Swan Committee 1998), habitat planning (USFWS et al. 1998), and habitat management efforts such as joint ventures (NABCI 2000). These satellite data suggest that within the annual range of EP tundra swans, winter habitats should receive high priority for protection and conservation because: (1) tundra swans are concentrated into the smallest geographic region during the winter; (2) the Atlantic coast of the U.S. is highly impacted by human development and has the highest population densities of the continent (source: U.S. Census Bureau Population Estimates Program); and (3) many other species of migratory birds rely upon some of the same key regions, especially the Chesapeake Bay and northeastern North Carolina.

Despite small sample sizes, data from satellite-tracked swans can be useful for development of harvest management plans. My data suggested several important modifications to the EP swan Hunt Plan. Quebec should be considered as an addition to the production zone, and Alberta (the Central Flyway portion) should be considered as an addition to the Canadian migration zone. Although relatively more important as spring migration stopover locations, the Great Lakes states and Ontario were also important in the fall. Inferences based upon counts of satellite-tracked radio transmittered birds must be interpreted with caution because swans were banded in winter. In particular, because many swans were marked in Pennsylvania, data in Table 1.2 may artificially inflate the importance of Pennsylvania as a spring migration stopover location. However, the satellite data, considered with MWI data, suggest that harvest in Pennsylvania during the regular hunting season (before 1 February) will have the greatest impact on the local population.

APPENDIX A. Multi-state modelling of EP movement on the wintering grounds with data from satellite-tracked radio transmitters, neck collars, and leg bands.

INTRODUCTION

In Chapter 1, movement rates of Eastern Population (EP) swans between states of the wintering ground were calculated using satellite locations from 21 after-hatch-year (AHY) female EP tundra swans marked with satellite-tracked radio transmitters for which I had a complete winter of data. Generalizing movement rates estimated from 21 individual swans to the $\approx 100,000$ EP tundra swans is only appropriate if the satellite-tracked swans exhibited the same patterns of movement as the rest of the population. While there is no reason to suspect this was not true, we cannot know if these movement rates were biased by an unrepresentative sample. Therefore, I augmented the data from 21 AHY female satellite-tracked swans with data from AHY and hatch-year (HY) male and female swans marked with neck collars and leg band, and used multi-state capture-recapture models as an alternative method to estimate movement rates (e.g., Hestbeck et al. 1991).

METHODS

EP swans were marked as a part of a large-scale study of Atlantic Flyway EP tundra swans. Swans were marked with satellite-tracked radio transmitters ($n=43$), coded neck collars ($n=1,471$) and leg-bands ($n=3,504$) from February 1997–March 2003. Observers surveyed for neck-collared swans during the winters of 2000–01, 2001–02, and 2002–03 in Maryland, North Carolina, Pennsylvania, and Virginia. See Chapter 2 for details on marking and observation efforts and distribution of markers over place and age/sex cohorts.

I used multi-state models to estimate movement probabilities between states of the wintering grounds (Brownie et al. 1993, Hestbeck et al. 1991), because they are appropriate when probabilities of resighting (p), survival (S), reporting (r), or movement (Ψ_{ij}) can vary by state (e.g., region, breeding status, disease status). I estimated movement rates from state i to state j , where $i, j =$ Maryland ($i, j = M$), North Carolina ($i, j = N$), Pennsylvania ($i, j = P$), and Virginia ($i, j = V$). Resightings during the winter outside of the study area (e.g., in North Dakota, South Dakota, Montana, Minnesota, Michigan, Wisconsin, Ontario) were not used because they were not relevant to the question of movement on the wintering grounds or to wintering-ground population structure. Thus, 16 different geographic transitions were possible: Ψ_{MM} , Ψ_{MN} , Ψ_{MP} , Ψ_{MV} , Ψ_{NM} , . . . , Ψ_{VV} .

Data were grouped into 2-month time periods for each winter: February-March, October-November, and December-January to create encounter occasions (i.e., February-March 1997, October-November 1997, December 1997-January 1998, February March 1998, . . . , February-March 2003; $n=19$) and transition probabilities ($n=18$). Because data were too sparse to calculate $18 \times 16 = 288$ time-specific movement rates between each encounter occasion for all Ψ_{ijt} , time effects were ignored in movement rates. Instead, movements between 2-month periods from different years were considered equivalent, regardless of the calendar year in which the movement occurred. This grouping allowed me to calculate the following seasonal movement rates: early (movements between regions of the wintering ground in October-November and December-January), late (movements between December-January and February-March), and between-year (movements between February-March and October-November). Observations of 137 swans were recorded in >1 state during a single 2-month time period were dropped from the data. The swan was assigned to the state in which it spent most of the 2-month time period.

Complete sampling was not always possible because of the remote locations of birds and a lack of personnel in some states. Because probability of observing a marked swan is a function of observation effort and observation effort varied regionally, I developed a metric to quantify observation effort. I used the number of days during the winter when at least one marked swan was observed, or the number of *successful* observer days, as a measure of observation effort because observers in some states only recorded observations when marked swans were seen. If *total* number of observer days were used instead, then effort would be underestimated in states where only observations were recorded (i.e., there was no record of survey effort if a marked swan was not seen). Although using successful observer days could underestimate effort in states where swans were sparser or harder to see, I believed this method had the smallest potential for bias. (Figure A.1).

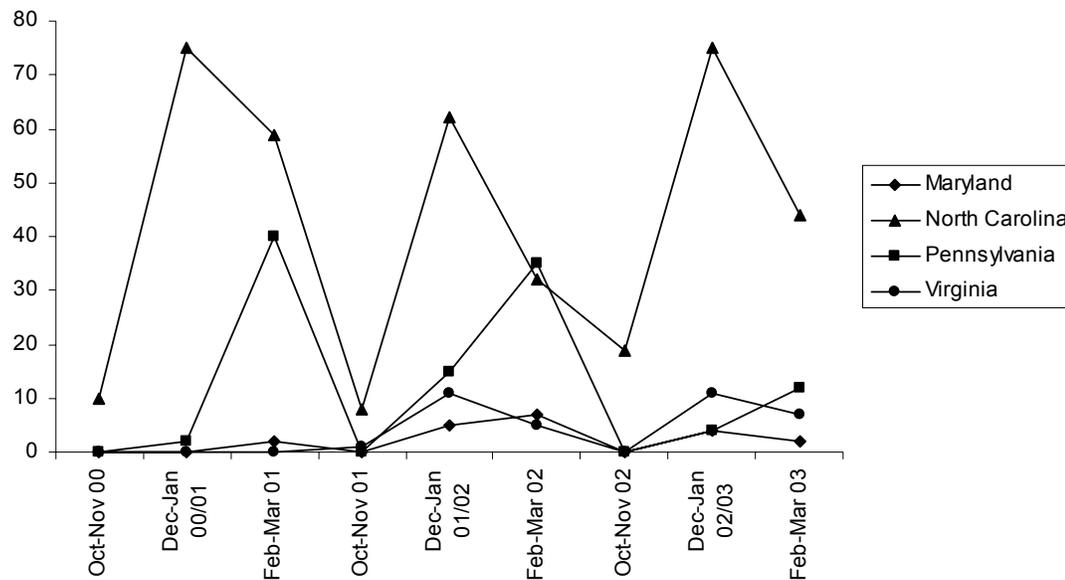


Figure A.1. Number of days observers located Eastern Population tundra swans marked with neck collars in the eastern U.S., October 2000–March 2003.

The multi-state model for live and dead encounters was used in Program MARK (White and Burnham 1999) to calculate maximum likelihood estimates of survival, resighting, and movement rates. I tested models for which survival rate varied by marker type, state, or was held constant. Reporting rates were kept constant. Resighting rates varied by (1) marker type, time, and state; (2) marker type and time; and (3) marker type, time, and state, with neck-collar observation a function of state-specific effort. Movement rates varied by state or by season and state. I also ran models with all movement rates set to 0.25 to simulate random movement between states (Table A.1). Time intervals, or the amount of time between capture occasions, were set equal to 2 or 8 months as appropriate (e.g., October-November → December-January and December-January → February-March were 2-month intervals, February-March → October-November was an 8-month interval). Because satellite data came from live birds (i.e., not from recoveries of dead birds), satellite data were not allowed to influence survival rate estimates.

Table A.1. Multi-state capture-recapture model parameterizations investigated for estimation of movement rates of wintering Eastern Population tundra swans. Notation for models follows in parentheses.

Parameter	Variation type modelled
Survival rate (S)	<ul style="list-style-type: none"> • Marker type (m) • Region (i.e., U.S. state) (r) • Constant (.)
Resighting rate (p)	<ul style="list-style-type: none"> • Marker type*time*region ($m*t*r$) • Marker type*time ($m*t$) • Marker type*time *region*effort, where neck-collar resight was a function of region specific observation effort and satellite and leg-band resight were a function of time ($m*t*r*e$)
Reporting rate (r)	<ul style="list-style-type: none"> • Constant (.)
Movement rate (Ψ)	<ul style="list-style-type: none"> • Region (r) • Region*Season (where season was October-November \rightarrow December-January; December-January \rightarrow February-March; February-March \rightarrow October-November; ($r*s$)) • All 0.25 (to model equal probability of moving between all states)

Program MARK calculates one movement rate with standard error from each of the 4 states to the other 3 states (the Ψ_{ij} 's and $se(\Psi_{ij})$). The probability of not moving was calculated as 1 – the probability of moving to the other 3 states:

$$\Psi_{ii} = 1 - \sum_{i \neq j} \Psi_{ij} .$$

with standard error:

$$SE(\Psi_{ii}) = \sqrt{\sum_{i \neq j} \text{var}(\Psi_{ij}) + \sum_{i \neq j} 2 * \text{cov}(\Psi_{ij}, \Psi_{ij})}.$$

Neck-collar resighting rates were set equal to 0 during the first 8 periods, because no birds with neck collars were released into the population during that time. Because of this distribution of markers in time, year was included in all resighting rate parameterizations. Locations outside of the study area were not included as part of the wintering grounds. When birds were located away from the wintering ground states, this analysis defined their locations as “unknown,” so their resighting rate was not = 1.

Model selection was performed using QAICc in Program MARK (Burnham and Anderson 1998). QAICc is a modification of the standard AIC calculation, adjusted for small sample size and overdispersion:

$$QAICc = - \left[\frac{2 \log L(\hat{\theta})}{\hat{c}} \right] + 2K + \frac{2K(K+1)}{n-K-1}$$

where: K = number of parameters

n = sample size

c-hat = variance inflation factor.

Variance estimates from count data are often negatively biased, or overdispersed, because of lack of independence of samples and use of the same data for model selection and parameter estimation (Burnham and Anderson 1998). The c-hat overdispersion adjustment is estimated as:

$$\hat{c} = \frac{\chi}{df}$$

from the model with the most parameters. C-hat is also multiplied to variance estimates, to inflate them by an appropriate amount. Since this estimate of c-hat is often negatively biased, it is recommended that one calculate c-hat using bootstrap goodness of fit (BSGOF) or median c-hat in Program MARK. C-hat values of 1–4 suggest reasonable model fit (White and Burnham 1999). Because this option is not yet available in the software for multi-state models with individual covariates, I used the c-hat estimate from the most-parameterized model, recognizing that this estimate is probably low.

Relative performance of models was assessed by Delta QAICc (difference between QAICc value of the best model and the particular model being compared), QAICc weights (ratio of $e^{(-0.5*QAICc)}$ of the particular model and the sum of $e^{(-0.5*QAICc)}$ for all models), and the model likelihood (in this context, the ratio of the QAICc weight from the best model and the particular model being compared). Movement rates from the models with Delta QAICc values of <10 were examined for evidence of population structure. Within-state transition probabilities (Ψ_{ii}) near 1.0 suggested sub-population structure along state lines, whereas between-state transitions (Ψ_{ij}) probabilities near 0.25 suggested no sub-populations on the wintering grounds.

RESULTS

Encounter histories for 5,025 individual birds provided usable data for estimation of resighting probability and movement rates between the 4 states. Of those encounter histories, 3,545 were from leg-banded birds, 1,446 were from neck-collared birds, and 34 were from birds with satellite-tracked radio transmitters. Observed c-hat was 9.812, indicating probable lack of fit of this model to the data. The top-ranked model had constant survival rate, resighting rate varying by marker type and time, and movement probabilities varying between states and by season (Table A.2). The 2

highest-ranked models contained 99% of the QAICc weights, suggesting that these were the 2 most appropriate models. These models differed only in the modeling of survival rate (constant or varying by marker type). Both models contained seasonal movement by state, suggesting that movement on the wintering ground within and between years is important to EP tundra swan dynamics. Both models also contained resighting rates that varied by marker type and time; observation effort was not a useful covariate for estimation of resighting rate. Models with $\Psi = 0.25$ ranked lowest, suggesting that equal probability of moving between all states is an unreasonable structure.

Movement rates between regions by season were almost identical in the top 2 models, so I examined the region by season movement rates from the top-ranked model (Figure A.2). This resulted in 3 movement matrices: between October-November and December-January, December-January and February-March, and February-March and October-November. Maps of seasonal movement rates between states suggest that swans were more likely to stay in the same state than to move, except in Pennsylvania. Birds in Pennsylvania are likely to move at the beginning of the season and between years, but those in Pennsylvania in December-January are likely to stay for the rest of the winter. Most movements are southern between October-November → December-January and northern between December-January → February-March.

Table A.2. Multi-state capture-recapture model selection results from resighting and recovery records of Eastern Population tundra swans marked with leg bands, neck collars, and satellite-tracked radio transmitters in the eastern U.S., February 1997–March 2003. Survival, resighting, and reporting rates of swans marked with satellite-tracked radio transmitters were set equal across regions, and reporting rate was constant. Results adjusted for model selection uncertainty with \hat{c} 9.812.¹

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par.
$S(.) p(m^*t) \Psi(r^*s)$	4303.15	0.00	0.7085	1.0000	69
$S(m) p(m^*t) \Psi(r^*s)$	4304.93	1.78	0.2915	0.4114	70
$S(.) p(m^*t) \Psi(r)$	4329.98	26.83	0.0000	0.0000	45
$S(r) p(m^*t) \Psi(r)$	4334.21	31.06	0.0000	0.0000	48
$S(r) p(m^*t) \Psi(r^*s)$	4362.90	59.75	0.0000	0.0000	72
$S(.) p(m^*t^*r^*e) \Psi(r)$	4372.78	69.63	0.0000	0.0000	97
$S(m) p(m^*t^*r^*e) \Psi(r)$	4374.61	71.45	0.0000	0.0000	98
$S(r) p(m^*t^*r^*e) \Psi(r^*s)$	4398.09	94.94	0.0000	0.0000	124
$S(m) p(m^*t^*r) \Psi(r)$	4404.96	101.81	0.0000	0.0000	130
$S(r) p(m^*t^*r) \Psi(r)$	4405.88	102.73	0.0000	0.0000	132
$S(.) p(m^*t^*r) \Psi(r^*s)$	4411.75	108.60	0.0000	0.0000	153
$S(.) p(m^*t^*r) \Psi(r)$	4415.53	112.38	0.0000	0.0000	129
$S(m) p(m^*t^*r) \Psi(r^*s)$	4420.60	117.45	0.0000	0.0000	154
$S(r) p(m^*t^*r^*e) \Psi(r)$	4420.80	117.64	0.0000	0.0000	100
$S(.) p(m^*t^*r^*e) \Psi(r^*s)$	4431.35	128.20	0.0000	0.0000	121
$S(m) p(m^*t^*r^*e) \Psi(r^*s)$	4433.03	129.87	0.0000	0.0000	122
$S(r) p(m^*t^*r) \Psi(r^*s)$	4468.69	165.54	0.0000	0.0000	156
$S(m) p(m^*t) \Psi(r)$	4474.62	171.46	0.0000	0.0000	46
$S(r) p(m^*t^*r^*e) \Psi(0.25)$	4490.99	187.84	0.0000	0.0000	88
$S(.) p(m^*t^*r^*e) \Psi(0.25)$	4494.95	191.79	0.0000	0.0000	85
$S(m) p(m^*t^*r^*e) \Psi(0.25)$	4496.52	193.37	0.0000	0.0000	86
$S(m) p(m^*t^*r) \Psi(0.25)$	4616.62	313.47	0.0000	0.0000	118
$S(.) p(m^*t^*r) \Psi(0.25)$	4672.61	369.46	0.0000	0.0000	121
$S(r) p(m^*t^*r) \Psi(0.25)$	4813.89	510.74	0.0000	0.0000	120
$S(.) p(m^*t) \Psi(0.25)$	4910.98	607.83	0.0000	0.0000	33
$S(m) p(m^*t) \Psi(0.25)$	4912.74	609.58	0.0000	0.0000	34
$S(r) p(m^*t) \Psi(0.25)$	4912.95	609.80	0.0000	0.0000	36

¹ S = survival rate, p = resighting rate, ψ = transition probability. Rates varied by region (r), marker type (m), season (s), observation effort (e), and time (t).

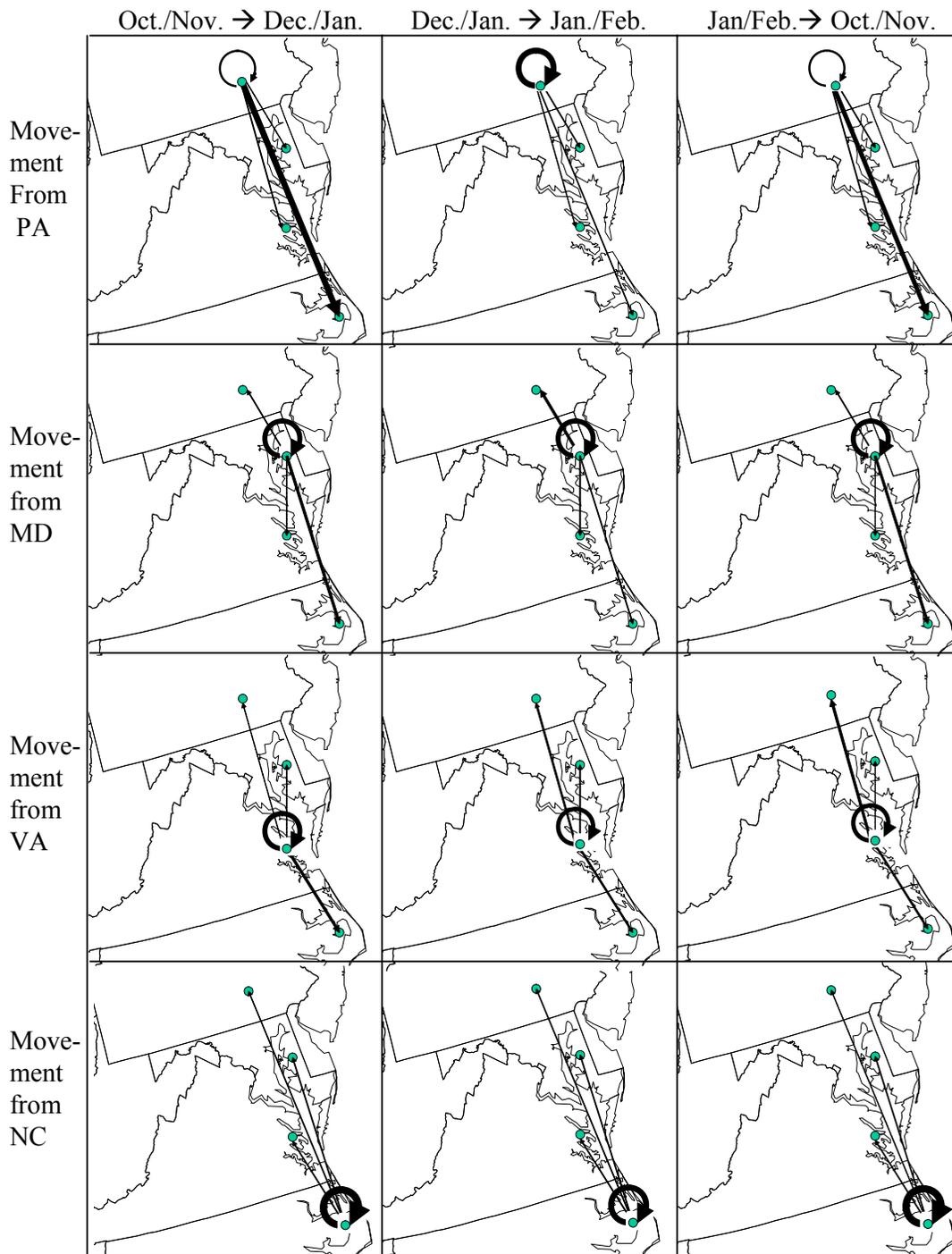


Figure A.2. Seasonal movement rates of Eastern Population tundra swans between states on the wintering grounds of the eastern U.S. during three 2-month periods, 1997–2003. Size of arrow is proportional to rate of movement.

Many of the between-season movement rates in Figure A1.1 had inestimable or large standard errors because they were based on very small sample sizes. Because these point estimates were not meaningful, I re-examined the top-ranked model after eliminating seasonal specificity in movement rates. This was the 3rd-ranked model, with movement rates varying between states and constant survival rate and recapture rate varying by marker type and time (Table A.3). As with seasonal movement rate estimates, the movement rate estimates suggested a low probability of movement out of any state during the winter period, especially for North Carolina ($\Psi = 0.13$). Swans were very unlikely to move between Maryland and Virginia ($\Psi = 0.01$) or to move to either of these states from North Carolina or Virginia ($\Psi = 0.01$ – 0.05). Finally, swans in Pennsylvania were unlikely to move to Maryland or Virginia.

Table A.3. Estimated movement rates (SE) of Eastern Population tundra swans between 4 states of the wintering grounds in the eastern U.S., February 1997–March 2003. Rates estimated from encounter histories of birds marked with leg bands, neck collars, and satellite-tracked radio transmitters.

Destination	Point of Origin			
	NC	MD	PA	VA
NC	0.87 (0.06)	0.13 (0.15)	0.52 (0.14)	0.19 (0.03)
MD	0.02 (0.01)	0.48 (0.01)	0.05 (0.06)	0.01 (0.03)
PA	0.09 (0.03)	0.38 (0.22)	0.40 (0.01)	0.13 (0.11)
VA	0.01 (0.01)	0.01 (0.04)	0.02 (0.04)	0.67 (0.01)

Movement rates were dissimilar to movement patterns in swans marked with satellite-tracked radio transmitters (Chapter 1), so I suspected that the estimates were biased by the addition of data from leg-banded and neck-collared swans. To assess possible bias in movement rate due to marker type, I compared the number of states in which a swan was recorded during a single winter *in addition to the state of banding*.

Very little within-year movement between states was recorded for leg-banded and neck-collared birds, whereas substantial within-year movement was apparent in satellite-tracked birds (Table A.4). If movement rates of the 21 AF swans marked with satellite-tracked radio transmitters were representative of the EP, this disparity in observed movement rates between different marker types suggested that including neck-collar and leg-band data to estimate movement rates may bias movement rate estimates.

Table A.4. Number and proportion of Eastern Population tundra swans marked and observed >1 during the same winter in Maryland, North Carolina, Pennsylvania, or Virginia by marker type, February 1997–March 2003.

Marker type	<i>n</i>	Proportion of swans observed in:		
		1 state	2 states	3 states
Leg band	315	0.997	0.003	0.000
Neck collar	838	0.920	0.076	0.004
Satellite transmitter	34	0.412	0.471	0.118

DISCUSSION

I used multi-state models (Brownie et al. 1993) and data from satellite-transmitters, neck collars, and standard leg bands to estimate survival and movement rates of EP tundra swans within their primary wintering range. After conducting these analyses, I conclude that their models were ineffective at estimating movement rates. My conclusion was based on three observations: (1) suspected bias in movement rates, (2) large standard errors on many parameter estimates, and (3) poor overall model fit, as evidenced by the c-hat statistic exceeding 4.0 (Burnham and Anderson 1998). Therefore, in Chapter 2 of this thesis, survival rates for EP swans were estimated using data from swans marked with neck collars and leg bands only (not satellite transmitters) and using simpler models.

Compared with rates of movement calculated from satellite-tracked swans, rates of movement from multi-state models were lower for states with lower observation effort, more remote habitat, and sparser swan distribution. This suggested that recovery and resighting rates were confounded with state in the multi-state models. In particular, neck-collared swans in the agricultural habitats prevalent in North Carolina and Pennsylvania were more readily observable than swans in the remote wetland habitats more typical of Maryland and Virginia (e.g., Chesapeake Bay, Tappahannock River, Potomac River). Hunting in North Carolina and Virginia increased recovery rates for leg-banded and neck-collared swans in these states. The larger scale of banding operations in North Carolina made it likely that recaptures of previously leg-banded birds would occur only in this state. Because movement rates to Maryland and Virginia were much lower when estimated with the multi-state method than with satellite data, this suggests that recapture, metrics of observation effort, and observation data were not sufficient to account for these confounding differences in resighting probability.

Other assumptions of multi-state and general capture-recapture models were violated as well. Short sampling periods did not exist in this study. Instead, sampling (both marking and observation) occurred continuously throughout the winter period. Independence of fates was unlikely with some birds, because birds were marked as family groups (Williams et al. 2002). The correlation between adult and young movement would likely decline after the first winter, but if both members of an adult pair were marked, it was likely that both would have a similar resighting probability since these birds have strong pair bonds (Baldassarre and Bolen 1994, Sladen 1973). In fact, a few male-female pairs were seen together several years in a row.

Finally, examination of satellite data (Chapter 1) suggested that 2-month time periods were too long to accurately characterize individual EP swan movement rates,

because EP swans can visit several regions during that time. Half-month periods more accurately accounted for the frequency of movement on the wintering grounds, but these data were too sparse to support that level of detail. Therefore, I believe that movement rates calculated from the 21 satellite-tracked swans were more accurate than movement rates estimated from the multi-state model. This assumes that the satellite-tracked swans exhibited the same movement patterns as unmarked swans, but that assumption is less problematic than the assumption that resighting rates were accurately measured in this analysis.

MANAGEMENT IMPLICATIONS

Rates of movement could only be well-measured using satellite-tracked radio transmitters because this method ensures that location is known at frequent intervals (≈ 4 days). Unless resighting rates are accurately estimated, use of markers such as neck collars with resighting rates of < 1 will result in overestimation of the use of easily accessible habitats (e.g., agricultural fields) and underestimation of the use of more remote habitats (e.g., Chesapeake Bay, Potomac River). Because swans stay at some locations very briefly, they could be easily missed in field searches for neck collared birds. This was most evident for migratory stopover points, such as Pennsylvania in the spring, where satellite transmitters revealed that stays often lasted only a few days. More robust models might be explored with the method of Hilborn (1990). The multi-state modeling approach I evaluated has the advantage of pre-existing software (Program MARK), which was an important consideration in my study and other similar studies (White and Lubow 2003).

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CHAPTER 2

Survival rate estimation of Eastern Population tundra swans (*Cygnus columbianus columbianus*) from capture-recapture data

ABSTRACT

The Eastern Population (EP) of tundra swans (*Cygnus columbianus columbianus*) winters in the eastern United States and breeds from the North Slope of Alaska to the eastern side of Hudson Bay in Canada. In order to estimate annual survival rates, EP swans were marked with individually coded neck collars ($n=1,471$) and USFWS leg-bands ($n=3,504$) on their wintering grounds in Maryland, North Carolina, Pennsylvania, and Virginia. Swans were marked from February 1997–March 2002. Locations were collected from February 1997–March 2003 during which 2,915 encounters for 4,974 marked birds were recorded: 1,856 neck-collar resightings by project personnel, 530 neck-collar resightings reported to the Bird Banding Laboratory, 327 recoveries of dead birds, and 202 recaptures of marked birds. Collar retention rates of marked swans ($n=49$) averaged 0.90 (95% CI = 0.86–0.94) per year for the first 3 years after collaring. Survival and recovery rates estimated from recovery data were similar to rates estimated from recovery data supplemented with resightings. Direct survival rates (survival rates for the 1st year following banding) estimated for HY birds may be unreliable as they ranged from 0.29 to 0.88. Indirect survival rates (survival rates for all years except the 1st year following banding) of AHY birds ranged for a low of 0.66 for collared birds to a high of 0.84 of leg-banded birds, but 95% confidence intervals of the point estimates overlapped. Wide confidence intervals did not allow for detection of differences in survival rates due to marker types, but the pattern of point estimates and other ancillary information suggest

that neck collars may reduce survival rates, and use of neck collars in an operational marking program is not recommended for future studies of EP swan survival rates.

INTRODUCTION

The Eastern Population (EP) of tundra swans (*Cygnus columbianus columbianus*) breeds across the North American tundra, from the North Slope of Alaska to the eastern side of the Hudson Bay, and winters from New York to South Carolina (Bellrose 1980, Serie and Raftovich 2003). EP swans are hunted in the fall in the Central and Atlantic Flyways, and reported harvest totals about 3,500 birds per year (Kruse and Sharp 2003). They also are hunted on the breeding grounds by subsistence hunters, but the size of this harvest is thought to be small (<500 birds; Serie and Bartonek 1991, Georgette 2000, Walker 2003, Priest and Usher 2004).

EP tundra swans are currently managed under a plan developed by U.S. and Canadian biologists from the 4 administrative flyways (*Ad hoc* EP Tundra swan committee 1998). The plan objectives are to maintain desired population levels, manage harvest, and improve understanding of the biology of EP tundra swans, which included estimates of EP survival rates (“Management Plan for the Eastern Population of Tundra swans,” p. 11). Improved precision and accuracy on survival rates would aid the monitoring of their population status and improve the performance of a population model (EPSWAN, Sheaffer 1996) used to simulate the effects of different harvest management strategies on the size of the subsequent wintering population. This model was appropriately sensitive to the annual estimate of survival rate imputed, since swans have delayed breeding, low productivity rates, and are long-lived (Gill 1990, Heppell et al. 2000).

Survival rates of harvested migratory birds are most conveniently estimated by analyzing recovery of leg bands from dead birds (e.g., Brownie et al. 1985). However,

a previous analysis found that recovery rates of EP swans were too low to provide precise annual estimates of survival rates because of small banded samples and low annual harvest rates (Sheaffer 1996). At typical levels of EP swan banding ($\approx 200 - 500/\text{year}$) and recovery ($\approx 10 - 20/\text{year}$), precise survival rates could only be estimated when data were pooled over 3-year periods (Sheaffer 1996). Sheaffer (1996) calculated that at least 2,000 EP swans must be banded each year to estimate precise annual survival rates at typical leg-band recovery rates, an effort not possible given the resources typically available to wildlife management agencies.

Neck collars have been used extensively on geese and swans for the estimation of annual survival rates (e.g., Hestbeck et al. 1991, Nichols et al. 1992). Neck collars are appropriate when: (1) leg band recovery rates are low, (2) the population of interest is distributed in an area that is accessible from vehicles, and (3) the birds themselves are conspicuous from ground vehicles. Because EP tundra swans met these criteria, we explored the use of neck collars as a source of capture-recapture data for survival rate estimation. Data from observation of live birds and reports from hunters of harvested birds can be used simultaneously to estimate survival rates with greater precision using the Barker (1997) model.

Emperor and Canada geese (*Chen caniga* and *Branta canadensis*) marked with neck collars have lower survival rates than geese marked with leg bands (Schmutz and Morse 2000, Castelli and Trost 1996), and bird death due to neck-collar icing has also been documented (Zicus et al. 1983). Furthermore, there is anecdotal evidence that hunters selectively harvest swans with neck-collars (P. Padding, U.S. Fish and Wildlife Service [USFWS], personal communication). As part of this evaluation, I examined survival rates for evidence of the negative impacts of neck collars.

My objectives were to: (1) estimate recent survival rates for EP tundra swans, (2) compare results obtained from different types of encounters (dead recovery, dead

recovery + live resighting), and (3) compare results from different types of markers (neck collars and leg bands), and (4) evaluate the potential of using marked swans to monitor annual survival rates. I compared my results with EP swan survival rates estimated by Nichols et al. (1992), who used data from observations and recaptures of neck-collared tundra swans to estimate survival rates from 1966–1990.

METHODS

Marking

A total of 4,975 swans were captured and marked with leg bands and neck collars from February 1997–March 2003, in Maryland, North Carolina, Pennsylvania, and Virginia by state wildlife agency and USFWS employees and project personnel. Swans in all 4 age- and sex-groups were marked with aluminum USFWS leg bands (Table 2.1). During the winters of 1999–00 through 2002–03, 1,471 leg-banded swans were marked with a second auxiliary marker: gray plastic neck collars with unique black alpha-numeric codes. Swans were marked in rough proportion to their population size in each state, although swans from North Carolina and Pennsylvania were slightly over-represented and swans from Maryland were under-represented in the sample (Table 2.2). Marking effort was spread throughout the winter range to obtain the most representative sample possible (Figure 2.1). Markers were distributed among different locations (inland and coastal) and habitat types (fields and wetlands) used by swans within each state. Most birds were captured by rocket netting over bait adjacent to wetlands because this method proved to be the most reliable and efficient (Grand and Fondell 1994). Rocket netting over plastic decoys and bait in fields, nightlighting in wetlands, and baited funnel traps in wetlands were also used to sample birds in different habitat types and to minimize the effect of capture method on sample composition (Grand and Fondell 1994, Guyn and Clark 1999). Birds with gray

plumage were classified as hatch-year (HY); those with white plumage were classified as after-hatch-year (AHY; Limpert and Earnst 1994).

Observers surveyed for neck-collared swans during the winters of 2000–01, 2001–02, and 2002–03 in Maryland, North Carolina, Pennsylvania, and Virginia. Observers in vehicles or on the ground used spotting scopes to identify individual neck-collared birds and used hand-held Global Positioning System (GPS) units to obtain location information. Observations were recorded on field forms and included date, time, location description, location latitude and longitude, collar code, flock size, and number of birds examined. Observers attempted to survey the entire known wintering region in each state twice each month for the entire winter period of 2000–01, 2001–02, and 2002–03. Swans were surveyed opportunistically by volunteers in New Jersey, Delaware, and South Carolina.

Complete sampling was not always possible because of the remote locations of birds and a lack of personnel in some states. Probability of observing a marked swan is a function of observation effort, which varied regionally, so I developed a metric to quantify observation effort. I used the number of days during the winter when at least one marked swan was observed, or the number of *successful* observer days, as a measure of observation effort because observers in some states only recorded observations when marked swans were seen. If *total* number of observer days were used instead, then effort would be underestimated in states where only observations were recorded (i.e., there was no record of survey effort if a marked swan was not seen). Although using successful observer days could underestimate effort in states where swans were sparsely distributed or difficult to see, I believed this method had the smallest potential for bias. (Figure 2.2).

Table 2.1. Numbers of EP swans marked with leg bands only, and neck collars and leg bands during the winters of 1996–97 through 2002–03 in their primary wintering range.

State	Winter	Leg band only					Neck collar and leg band					Both Methods	
		Female		Male		Total	Female		Male		Total	Total	
		HY ¹	AHY ¹	HY	AHY		HY	AHY	HY	AHY			
MD	1996–97												
	1997–98	5	24	2	25							56	
	1998–99												
	1999–00												
	2000–01							27		28	55	55	
	2001–02		2			2						2	
	2002–03												
	All years	5	26	2	25	58							113
NC	1996–97	95	466	34	262	857							857
	1997–98	111	292	32	278	713							713
	1998–99	172	391	128	338	1029	1				1		1030
	1999–00		1		1	2	107	298	37	234	676		678
	2000–01	2	16	2	22	42	33	190	19	285	527		569
	2001–02	42	26	25	132	225	1			16	17		242
	2002–03	24	61	13	58	156		2			2		156
	All years	446	1253	234	1091	3024	142	490	56	535	1223		4247
PA	1996–97	1	7	2	9	19							19
	1997–98	4	2	1	4	11							11
	1998–99	16	25	3	27	71							71
	1999–00						12	22	7	19	60		60
	2000–01							15	2	15	32		32
	2001–02	21	9	16	38	84	4				4		88
	2002–03												
	All years	42	43	22	78	185	16	37	9	34	96		281

¹HY=Hatch Year.

²AHY=After Hatch Year.

Table 2.1 (Continued).

State	Winter	Leg band only					Neck collar and leg band					Both	
		Female		Male		Total	Female		Male		Total	Methods	
		HY ¹	AHY ¹	HY	AHY			HY	AHY	HY		AHY	
VA	1996-97	16	17	4	35	72						72	
	1997-98	4	12	1	7	24						24	
	1998-99	10	37	6	54	107						107	
	1999-00												
	2000-01				1	1	1	35		9	52	97	98
	2001-02	4	1	5	23	33							33
	2002-03												
	All years		34	67	16	120	237						334
All States	1996-97	112	490	40	306	948						948	
	1997-98	124	330	36	314	804						804	
	1998-99	198	453	137		1207	1				1	1208	
	1999-00		1		1	2	119	320	44	253	736	738	
	2000-01	2	16	2	23	43	34	267	30	380	711	754	
	2001-02	67	38	46	193	344	5			16	21	365	
	2002-03	24	61	13	58	156		2				156	
	All years		527	1389	274	1314	3504	159	589	74	649	1471	4975

¹HY=Hatch Year.²AHY=After Hatch Year.

Table 2.2. Numbers of wintering Eastern Population (EP) tundra swans marked in each state by marker type, February 1997–March 2003, compared to the proportion of EP wintering in that state.

State	Marker Type		Total	Proportion of winter population in state ¹
	Neck collar	Leg band only		
Maryland	55 (0.04) ²	58 (0.02)	113	0.17
North Carolina	1,223 (0.83)	3,024 (0.86)	4,247	0.72
Pennsylvania	96 (0.07)	185 (0.05)	281	0.01
Virginia	97 (0.07)	237 (0.07)	334	0.08
All states	1471 (1.00)	3504 (1.00)	4975	0.98 ³

¹ Average of 1997–2003 Mid-Winter Index for EP tundra swans.

² Proportion of markers placed in each state.

³ Does not =1.00 because ≈2% of EP tundra swans winter outside of the study area.

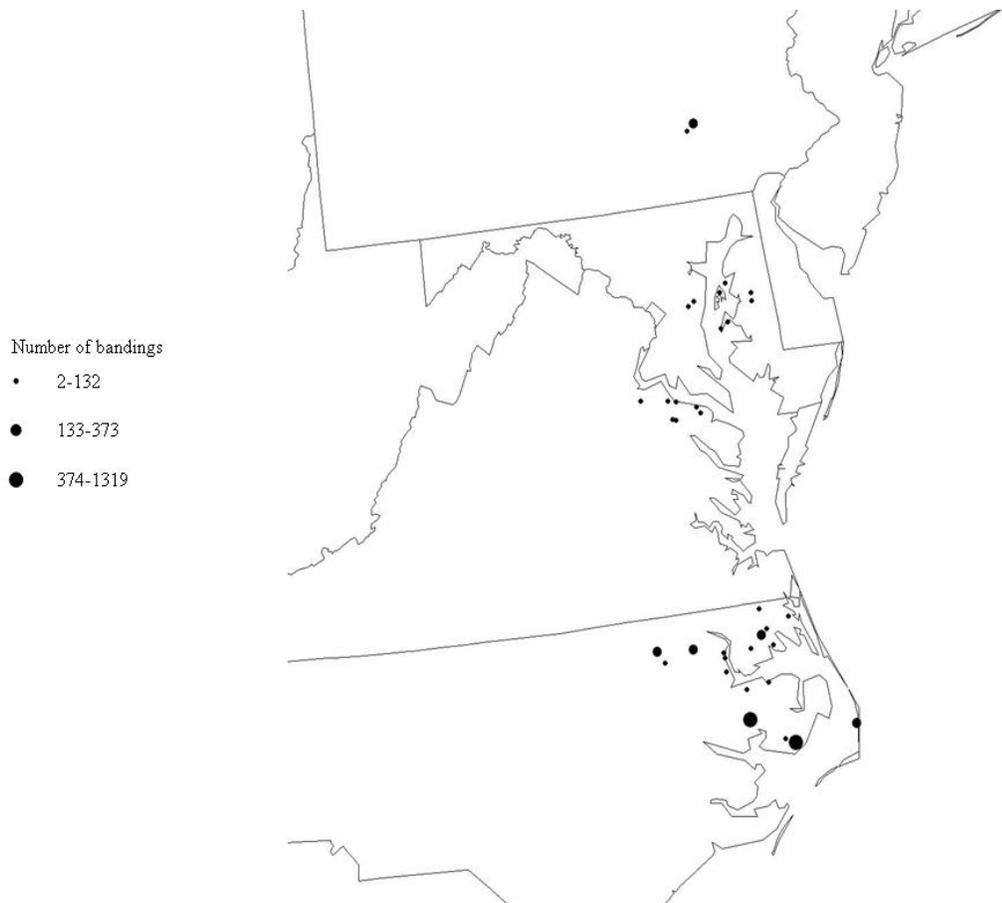


Figure 2.1. Trapping locations where Eastern Population tundra swans were marked during the winters of 1996–97 through 2002–003 in the eastern U.S.

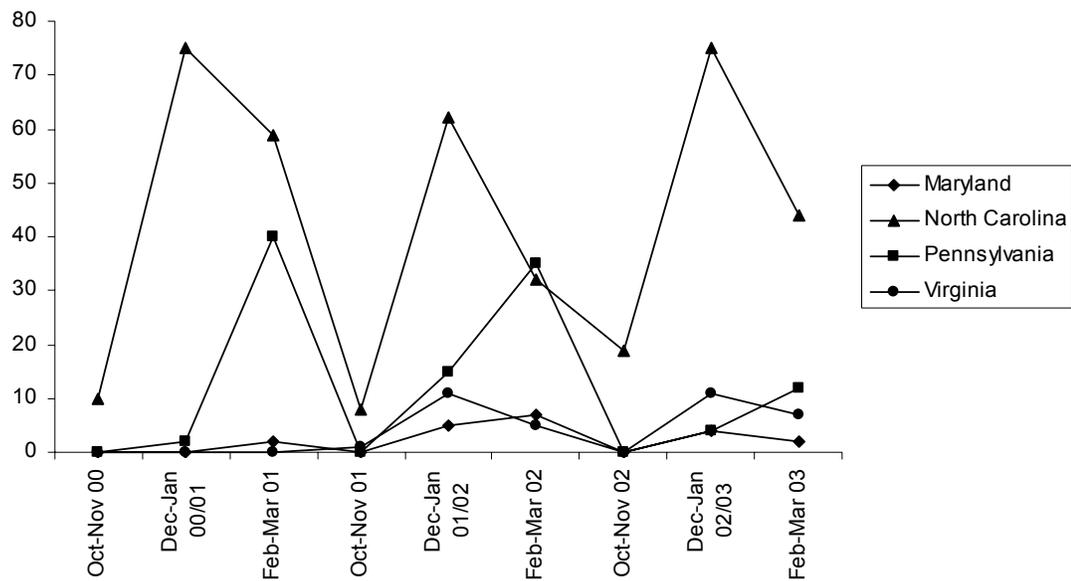


Figure 2.2. Number of days observers located Eastern Population tundra swans marked with neck collars in the eastern U.S., October 2000–March 2003.

Neck-collar retention rates

Survival rates estimated from capture-recapture data are negatively biased if there is no accounting for marker loss (Arnason and Mills 1981, Samuel et al. 1990, Hestbeck et al. 1991, Coluccy et al. 2002). We used records of neck-collared EP swans recaptured during the 1999/2000–2002/2003 banding operations to estimate neck-collar retention rates. Whenever a marked bird was recaptured, presence of neck collar and leg band was noted. Banding records were used to determine whether any recaptured birds had lost neck collars. We used program SURVIV to estimate retention rates, considering age of the collar as a possible explanatory covariate (White 1983, Nichols et al. 1992).

Analyses

Estimation with dead recoveries

Records of birds recovered dead were analyzed using capture-recapture recovery models, with survival and reporting rates modelled as a multinomial probability (Williams et al. 2002) using the “recoveries only” parameterization in program MARK (Seber 1970). Model parameters were:

S_i = survival rate, the probability that a marked swan survives from the end of the marking period i to the beginning of marking period $i+1$, and
 r_i = reporting rate, the probability that a mark was retrieved and reported during reporting period i , given that a swan died.

This model parameterization is a re-formulation of the traditional Brownie recovery models structure (Brownie et al. 1985), and was necessary to account to allow the use of individual covariates in the modeling process.

Study years spanned from 1 November to 31 October, and birds were marked late-November–mid-March. The 4–5-month marking period violated the assumption of instantaneous marking. To account for long banding periods, survival rates were modelled as either direct (S^* ; survival rate for the remainder of the study year following banding) or indirect (S ; survival rate for all subsequent years; Brownie et al. 1985). Because most banding occurred in January-February and S^* covered the time period from date of banding to 31 October, S^* included a time period of <1 year. Therefore, direct survival rates were standardized to cover a 12-month period by calculating a monthly survival rate (n th root of S^* , where n = average number of months from the time a swan was banded until 1 November) and taking the result to the 12th power.

Survival and reporting rate modelling was further complicated for winter-banded EP tundra swans because hunting seasons in North Carolina and Virginia run

from November or December through the end of January. This partial overlap of hunting and marking periods likely induced heterogeneity in S^* and direct reporting rate (r^*). S^* should be larger for a bird marked later in the time period because these birds have a shorter period to survive until the following marking period. The opposite is true of r^* , which should decrease for swans marked later in the marking period because exposure time to hunting is less than for birds marked earlier. Furthermore, probability for direct recovery of swans banded after the hunting season closed on 31 January was close to 0. To model these sources of heterogeneity, S^* was modelled as a function of the number of days since banding, and 2 r^* 's were estimated: one for swans banded during the hunting season and one for swans banded after the hunting season by creating an individual covariate based on banding date (1 November–31 March, a period of 151 days) scaled from 0–1 (Cooch and White 2005).

I developed an *a priori* model set based on swan behavior and life history to reduce the likelihood of spurious results (Burnham and Anderson 1998). All models included S^* adjusted for time since banding (Table 2.3). I also allowed S and S^* to vary by marker type and swan age, and reporting rate (r) varied by marker type, swan age, time, or banding period. Banding period was treated as a categorical variable: swans were banded either during the hunting season (before 1 February) or after the hunting season (1 February or later). I did not test for sex specificity in survival or reporting rates because: (1) survival rates of adult male and female swans were not statistically different in an earlier study (Nichols et al. 1992), (2) adults of both sexes sit on the nest and care for young (Hawkins 1986) so predation risks are similar during the breeding season, and (3) sexes are monomorphic and cannot be distinguished by hunters.

Table 2.3. Survival and reporting rate parameterizations investigated in analysis of dead recoveries of leg-banded and neck-collared Eastern Population tundra swans.

Parameter	Variation type modelled
Direct survival rate (S^*)	<ul style="list-style-type: none"> • Time since banding (b) • Age of swan (a) • Marker type (m) • Constant (.)
Indirect survival rate (S)	<ul style="list-style-type: none"> • Age of swan (a) • Marker type (m) • Constant (.)
Reporting rate (r)	<ul style="list-style-type: none"> • Age of swan (a) • Marker type (m) • Banding period (p) • Year (t)

Estimation with dead recoveries and live resightings

I used the Barker (1997) model to estimate survival rates and other parameters from multiple sources of marking data: recoveries of dead birds, recaptures of live birds during banding operations, and observations of live marked birds (from White and Burnham 1999):

S_i = survival rate, the probability that a marked swan alive at the end of banding occasion i was still alive at banding occasion $i + 1$,

p_i = recapture rate, the probability that a marked swan at risk of capture during banding period i was captured during i ,

r_i = reporting rate, the probability that a marked swan that dies in the interval between period i and $i + 1$ was found dead and the marker was reported,

R_i = resighting rate 1, the probability that a marked swan that survives from period i to $i + 1$ was resighted (alive) some time between period i and $i + 1$,

R'_i = resighting rate 2, the probability that a marked swan that dies in the interval between period i and $i + 1$ without being found dead was resighted alive in the interval between period i and $i + 1$ before it died,

F_i = direct fidelity rate, the probability that a marked swan at risk of capture on the wintering grounds at period i was at risk of capture at period $i + 1$, and

F'_i = indirect fidelity rate, the probability that a marked swan not at risk of capture on the wintering grounds at period i was at risk of capture at period $i + 1$.

Survival rate was the only parameter of interest; the others were nuisance parameters necessary for its estimation. For wintering EP swans, fidelity rates should be nearly equal to 1.0, because most swans return to the Atlantic Flyway each year. The few that do not either remain in regions to the north or winter in the Western U.S., but these numbers are small (Bart et al. 1991).

Banding, recovery, and resighting data from EP swans marked with neck collars and leg bands were used from November 1997–March 2003. For this analysis, I defined the banding period as January–February, when most banding occurred, and the recovery period as March–December. The Barker model assumes that only sightings occurred during the banding periods (i.e., no dead birds were recovered during January-February), and that banding periods were relatively short (i.e., there was no natural or harvest mortality during the banding period). Data from this study did not meet these assumptions, due to hunting during January and a 4–5 month banding period. Rather than omit banding data outside of January–February and

recovery data during January–February, I performed a *post hoc* reclassification the dates of some banding and recovery data to fit the Barker model structure. Specifically, recoveries that occurred during the January–February banding period were reassigned to the previous March–December period, bandings during March were reassigned to the previous February, and bandings during November and December were reassigned to the following January. When a swan was resighted alive and then later recovered dead within a single marking period, only the last observation was used.

As with recovery models, all models included S^* modelled as a function of the individual covariate time since banding. I allowed S and S^* to vary by marker type and swan age. Reporting rate (r) varied by marker type, swan age, time, and banding period (during or after hunting season). Resighting (R and R'') and recapture (p) probabilities varied by marker type. In addition, neck-collar resighting probabilities were modelled as a function of observation effort. Data were insufficient to include time dependence in reporting, recapture, or resighting rates. Direct fidelity (F) and indirect fidelity rate (F'') were set equal, to model random emigration to and from the wintering ground. Reporting probability of neck collars was set to 0 for the winters of 1996–97 through 1998–99 because 1999–00 was the first winter of neck collars were used.

For both analyses, I assessed model goodness of fit by estimating the median variance inflation factor, or c-hat:

$$\hat{c} = \frac{\text{deviance}}{df} \approx \frac{\chi^2}{df}$$

where *deviance* = difference in log likelihood of the saturated model and the most parameterized model in the set; and *df* = degrees of freedom (White and Burnham 1999). Thus, when c-hat = 1.0, the model fits the data perfectly. C-hat values of 1–4

suggest reasonable model fit. Because count data often do not meet multinomial distribution assumptions, variances can be negatively biased (overdispersed). C-hat was also used to adjust the variance appropriately. Corrected variance estimates can change model selection results by increasing the support on less-parameterized models relative to more-parameterized models. Median c-hat was used to adjust for model selection uncertainty.

Model selection was performed using a modified form of AIC, adjusted for small sample size and overdispersion, called QAICc. The model with the lowest QAICc (highest rank) was considered the model that best approximated the data. Other metrics were used to assess the support for other models relative to the best model. These were Δ QAICc, QAICc weights, and model likelihoods:

$$QAICc = \frac{-2\text{Log}L}{\hat{c}} + 2K + \frac{2K(K+1)}{(n-K-1)}$$

$$\Delta QAICc(i) = QAICc(best) - QAICc(i)$$

$$QAICc \text{ weight}(i) = \frac{e^{-0.5*\Delta QAICc(i)}}{\sum_i e^{-0.5*\Delta QAICc(i)}}$$

$$Likelihood = \frac{QAICc \text{ weight}(i)}{QAICc \text{ weight}(best)}$$

where K = number of parameters and n = sample size.

Significant differences between survival and recovery rates were determined by overlap of 95% confidence intervals.

RESULTS

Encounters with leg bands and neck collars

Locations were collected from February 1997–March 2003, during which 2,915 encounters for 4,974 marked birds were recorded: 1,856 neck-collar resightings by project personnel, 530 neck-collar resightings reported to the Bird Banding Laboratory, 327 recoveries of dead birds reported to the Bird Banding Laboratory (151 leg bands, and 176 neck collars, and 202 recaptures of marked birds during banding operations (143 leg bands and 59 neck collars). Many birds were encountered >1 time/year.

Neck-collar retention rates

Point estimates of neck-collar retention rates declined with collar age (Table 2.4), but high variance around these estimates led me to use an average neck-collar retention rate of 0.90 per year to adjust survival rates estimated from neck-collared birds (Arnason and Mills 1981):

$$S_{adjusted} = \frac{S_{apparent}}{\theta}$$

where θ = neck collar retention rate, with standard error calculated by the delta method (Nichols et al. 1992):

$$se(S_{adjusted}) = \sqrt{(S_{adjusted})^2 * \left(\frac{\text{var}(S_{apparent})}{(S_{apparent})^2} + \frac{\text{var}(\theta)}{(\theta)^2} \right)}$$

Table 2.4. Neck-collar retention rates of 49 Eastern Population tundra swans in the eastern U.S., winter 1999–00 through 2002–03.

Years after banding	Retention rate estimate	<i>n</i>	SE ¹	95% Confidence interval
1	0.94	34	0.040	(0.86, 1.00)
2	0.89	12	0.120	(0.65, 1.00)
3	0.80	3	0.343	(0.13, 1.00)
All	0.90	49	0.020	(0.86, 0.94)

¹ Standard error

Analyses

Survival estimation from dead recoveries

Recoveries of 176 neck-collared birds (37 juveniles and 139 adults) and 151 leg-banded birds (42 juveniles and 109 adults) were reported to the BBL. The value of the individual covariate “time since banding” ranged from 0.19–0.90, or 30 October–17 March. The average covariate value was 0.70, or 14 February. Therefore, the average S^* covered the period from 14 February–31 October, or 8.5 months. This length of time was used to convert direct survival rates that covered 8.5 months (on average) to annual survival rates.

The median \hat{c} from 1,000 simulations was 1.1159, which suggested reasonable model fit. Model ranks did not change after adjustment by \hat{c} . The top 11-ranked models were within 10 QAICc units of each other (Table 2.5). The top 7-ranked models had model likelihood values >0.24 and $\Delta\text{QAICc} <3.0$, which indicated model selection uncertainty. All parameterizations of survival rate (i.e., constant, swan age, marker type, swan age, and marker type) were included in the 7 top-ranked models. Reporting rates in the top-ranked models were modelled as a function of swan age and marker type or marker type only. Effects of time, swan age, and banding

period (before or after 1 February) on reporting rate were small relative to these effects.

Results did not provide conclusive evidence that survival rate was dependent up *either* marker type *or* swan age. When one of these effects was in the model, the other did not add sufficient explanatory power to merit consideration. I chose a model with survival rate that varied by marker type and swan age because: (1) 2 models with this survival rate parameterization were within 10 QAICc units of the top-ranked model; (2) I did not think that survival rate estimates pooled over marker type would be representative of the population, due to the potential effects of neck collars; and (3) swan age was a more important predictor of survival rate than marker type. Recovery rates of HY birds were unreasonable when the model included swan age and marker type effects on both survival and reporting rates, due to sparse and a more complicated survival-rate model. Data could not support a model with both survival and reporting rate estimates varying by marker type and swan age. Therefore, I chose a model that contained survival rate varying marker type and swan age, and reporting rate varying by marker type.

Direct survival rate (S^* ; standardized to cover a 12-month period) was 0.84 (standard error = 0.05) for leg-banded young birds, and 0.89 (0.03) for leg-banded adults. Direct survival rate (standardized to cover a 12-month period and adjusted for collar loss) was 0.88 (0.06) for collared HY birds, and 0.96 (0.04) for collared AHY swans. Indirect survival rate was 0.73 (0.05) for leg-banded AHY and 0.66 (0.09) for collared AHY birds (adjusted for collar loss). Direct survival rates were much larger than indirect survival rates, even after standardization to a 12-month period. Reporting rates were 0.15 (0.02) for collared birds and 0.06 (0.01) for leg-banded birds.

Table 2.5. Model selection results, adjusted for model selection uncertainty, from survival rate analyses of recoveries of dead leg-banded and neck-collared Eastern Population tundra swans. Swans marked in the eastern U.S. during the winter 1996–97 through 2002–03.

Survival Rate Model	Reporting Rate Model	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	Number of Parameters
constant	age and marker type	2762.58	0.00	0.28	1.00	6
marker type	age and marker type	2763.16	0.58	0.21	0.75	7
age	age and marker type	2763.88	1.30	0.15	0.52	7
constant	marker type	2764.50	1.91	0.11	0.38	5
age	marker type	2764.87	2.29	0.09	0.32	6
age and marker type	age and marker type	2765.01	2.43	0.08	0.30	10
marker type	marker type	2765.42	2.84	0.07	0.24	6
age and marker type	marker type ¹	2769.72	7.14	0.01	0.03	10
constant	marker type and time	2771.24	8.65	0.00	0.01	11
age	marker type and time	2771.72	9.14	0.00	0.01	12
marker type	marker type and time	2772.37	9.79	0.00	0.01	12
age and marker type	marker type and time	2775.93	13.34	0.00	0.00	16
age and marker type	age	2776.29	13.71	0.00	0.00	9
age and marker type	time	2779.45	16.87	0.00	0.00	15
marker type	age	2779.77	17.19	0.00	0.00	6
age and marker type	banding period	2779.80	17.22	0.00	0.00	11
marker type	time	2781.41	18.83	0.00	0.00	11
marker type	banding period	2783.23	20.65	0.00	0.00	7
constant	time	2823.11	60.52	0.00	0.00	10
age	time	2824.66	62.08	0.00	0.00	11
age	banding period	2853.44	90.86	0.00	0.00	7
constant	banding period	2854.35	91.76	0.00	0.00	6
age	age	2859.90	97.32	0.00	0.00	6
constant	age	2860.69	98.11	0.00	0.00	5

¹ Model that I believe best describes the data and population dynamics of EP tundra swans.

Survival estimation from dead recoveries and live resightings

Encounter histories were available for 225 juvenile and 1,206 adult swans marked with neck collars (1,431 total), and 133 juvenile and 348 adult swans marked with leg bands (481 total). This includes 2,257 bandings and observations during marking periods, 718 observations between marking periods, and 169 recoveries. The median c-hat was 1.1228, suggesting reasonable fit. Model ranks did not change after adjustment by c-hat. The number of successful of observer days was consistently higher in North Carolina and Pennsylvania. However, models using observation effort

as a covariate for resighting probability did not converge. Separation between the top models was greater in this analysis. I concluded that the model with survival rate varying by marker type and swan age, and reporting rate varying by marker type best described the data and population dynamics of EP tundra swans. This model was highest ranked, was 7 times better supported by the data than the next best model. It was similar to the other top 4 ranked models in that all 4 of these models included both marker type and swan age to explain survival rate.

Direct survival rate (S^* ; standardized to cover a 12-month period) was 0.52 (0.08) for leg-banded HY birds, and 0.68 (0.05) for leg-banded AHY birds (Table 2.7). Direct survival rate (standardized to cover a 12-month period and adjusted for neck collar retention rate) was 0.29 (0.03) for collared young birds, and 0.61 (0.03) for collared adult swans. Indirect survival rate was 0.84 (0.04) for leg-banded adults and 0.72 (0.03) for collared adults (adjusted for collar loss). Reporting rates (the probability of being reported, given that a bird died and was retrieved) were 0.14 (0.01) for collared birds and 0.07 (0.01) for leg-banded birds.

Table 2.6. Model selection results, adjusted for model selection uncertainty, from survival rate analyses of resightings, recaptures, and recoveries of leg-banded and neck-collared Eastern Population tundra swans. Swans marked in the eastern U.S. during the winter 1996–97 through 2002–03. Recapture, recovery, and resighting rates varied by marker type in all models.

Survival Rate	Recovery Rate	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	Number of Parameters
swan age and marker type	marker type ¹	10131.83	0.00	0.81	1.00	17
swan age and marker type	swan age and marker type	10135.83	4.00	0.11	0.14	19
swan age and marker type	banding period	10137.09	5.26	0.06	0.07	18
swan age and marker type	swan age	10139.37	7.55	0.02	0.02	17
swan age	marker type	10147.66	15.83	0.00	0.00	13
swan age	swan age and marker type	10151.38	19.55	0.00	0.00	15
marker type	marker type	10158.69	26.86	0.00	0.00	14
marker type	swan age and marker type	10159.35	27.53	0.00	0.00	16
marker type	swan age	10162.56	30.74	0.00	0.00	14
marker type	banding period	10164.07	32.24	0.00	0.00	15
swan age and marker type	banding period	10164.07	32.24	0.00	0.00	15
constant	marker type	10174.58	42.75	0.00	0.00	12
constant	swan age and marker type	10177.02	45.19	0.00	0.00	14
swan age	banding period	10216.37	84.54	0.00	0.00	14
swan age	swan age	10217.31	85.49	0.00	0.00	13
constant	swan age	10242.44	110.62	0.00	0.00	12
constant	banding period	10242.68	110.85	0.00	0.00	13

¹ Model that I believe best describes the data and population dynamics of EP tundra swans.

Table 2.7. Survival, recapture, reporting, resighting, and fidelity rates estimated from encounter histories of Eastern Population tundra swans marked with leg bands and neck collars in the eastern U.S., winter 1996–97 through 2002–03. Encounter histories used data from recaptures and recoveries of neck-collared and leg-banded swans and resightings of neck-collared swans.

Rate	Estimate	SE ¹	LCI ²	UCI ³
Direct survival rate, HY neck-collared birds ^{4,5}	0.29	0.03	0.23	0.36
Indirect survival rate, AHY neck-collared birds	0.72	0.03	0.66	0.78
Direct survival rate, AHY neck-collared birds	0.61	0.03	0.55	0.66
Direct survival rate, HY leg-banded birds	0.52	0.08	0.37	0.67
Indirect survival rate, AHY leg-banded birds	0.84	0.04	0.75	0.90
Direct survival rate, AHY leg-banded birds	0.68	0.05	0.58	0.77
Recapture rate, neck-collared birds	0.93	2.97	0.00	1.00
Recapture rate, leg-banded birds	0.02	0.07	0.00	0.16
Reporting rate, neck-collared birds	0.14	0.01	0.12	0.17
Reporting rate, leg-banded birds	0.07	0.01	0.05	0.09
Resighting rate 1, neck-collared birds	0.33	0.01	0.30	0.36
Resighting rate 1, leg-banded birds	0.00	0.00	0.00	0.01
Resighting rate 2, neck-collared birds	0.14	0.03	0.10	0.20
Resighting rate 2, leg-banded birds	0.00	0.00	0.00	0.00
Wintering ground fidelity rate	0.40	1.27	0.00	1.00

¹ Standard error.

² Lower 95% confidence interval.

³ Upper 95% confidence interval.

⁴ Direct survival rates standardized to cover 1 year.

⁵ Survival rates of neck collared birds adjusted for neck collar loss.

Model estimates were sensitive to starting values. Some estimates were unreliable even after experimentation with a range of starting values. Resighting rates for leg-banded birds had estimated standard errors = 0, indicating poor-quality estimates. The recapture rate of neck-collared birds and the fidelity rate had unacceptably large standard errors. Wintering ground fidelity rate (0.40) seemed unreasonably low, based on rare observations of EP tundra swans in the West. During this study, 10 EP birds were observed or recovered in the range of the WP of tundra swans: 3 were shot in Utah and 1 in Nevada, 2 were found dead in California and 1 in Idaho, and 1 each was seen alive in British Columbia, Oklahoma, and California (out of 5,321 banded birds and 927 recoveries reported to the BBL). Half of these were

male birds and half were female, and all were marked as adults. However, when wintering ground fidelity rate was set to 1.0, models would not converge to results.

Survival and recovery rates from both analyses are summarized in Table 2.8.

Table 2.8. Comparison of survival and recovery rates estimated for Eastern Population tundra swans using 2 types of capture-recapture data and analytical methods. Swans marked in the eastern U.S. November 1997–March 2003.

Parameter ¹	Marker type	Estimate using recovery data from dead birds (SE ²)	Estimate using recovery from dead birds and observation and recapture data from live birds (SE)	95% confidence interval overlap?
<i>S*</i> HY ³	leg band	0.84 (0.05)	0.52 (0.08)	no
<i>S*</i> HY	neck collar ⁴	0.88 (0.06)	0.29 (0.03)	no
<i>S*</i> AHY	leg band	0.89 (0.03)	0.68 (0.05)	no
<i>S*</i> AHY	neck collar	0.96 (0.04)	0.61 (0.03)	no
<i>S</i> AHY	leg band	0.73 (0.05)	0.84 (0.04)	yes
<i>S</i> AHY	neck collar	0.66 (0.09)	0.72 (0.03)	yes
<i>r</i>	leg band	0.06 (0.01)	0.07 (0.07)	yes
<i>r</i>	neck collar	0.16 (0.02)	0.14 (0.01)	yes

¹ *S** = survival rate first year after marking, *S* = survival rate >1 year after marking, HY = hatch-year, AHY = after-hatch-year, and *r* = probability that a marked bird is retrieved and reported;

² SE = standard error.

³ Direct survival rates standardized to cover a 12-month period.

⁴ Neck-collar survival rates adjusted for collar loss.

DISCUSSION

Small differences between QAICc for competing models values suggested that recovery data were insufficient to allow structure to be identified during the estimation procedure. When data from observations of live birds were combined with recovery data, more complex model structures were supported and there was greater separation of QAICc values between the various models.

When only recovery data were used, annual indirect survival rate of adult EP swans was 0.66 (95% CI 0.48–0.84) for birds marked with neck collars and 0.73 (0.63–0.83) for birds marked with leg bands. When recovery data were supplemented with recapture and live observation data, annual (indirect) survival rates were 0.72 (0.66–0.78) for adults swans marked with neck collars and 0.84 for adults marked with leg bands (0.76–0.91). Indirect survival rate estimates of AHY birds were statistically similar, regardless of marker type or data analytical method. However, direct survival estimated from 2 different methods were variable. In general, S^* estimates of comparable parameters were similar within analyses, but not across analyses of different data types (i.e., the following 95% confidence intervals overlap or nearly overlap: S^* HY leg band $\approx S^*$ HY neck collar $\approx S^*$ AHY leg band $\approx S^*$ AHY neck collar from recovery data *or* from the Barker analysis). When recovery data were analyzed, survival rates of HY birds (direct) were 0.88 (0.75–1.0) for birds marked with neck collars and 0.84 (0.75–0.94) for birds marked with leg bands. When recovery data were supplemented with recapture and observation data, direct survival rates were 0.29 (0.23–0.36) for HY swans marked with neck collars and 0.52 for HY swans marked with leg bands (0.37–0.67).

Survival rate estimates from the Barker model were more precise than those from the recoveries-only model, as shown by a smaller coefficient of variation (7–14% for analysis of recovery data versus 4–5% for analysis of recovery, observation, and

recapture data). Greater precision was an expected result of using the additional information provided by observations and recaptures of live birds to supplement records of recovery of dead marked birds. The HY S^* estimates from the Barker model were very low (0.29–0.52), and were significantly lower than HY S^* estimated with recovery data alone (0.84–0.88). Survival rates should be the same from both analyses, suggesting unreliable results from one or both of these analyses. Other unexpected results included: (1) analyses of recovery data produced larger point estimates of S^* for collared birds (0.88 for HY birds and 0.96 for AHY birds) than for leg-banded birds (0.84 for HY birds and 0.89 for AHY birds), although these estimates had (nearly) overlapping 95% confidence intervals; and (2) analyses of recovery, observation, and recapture data produced very low estimates of S^* for HY birds. Other than these anomalies, the expected pattern in point estimates of survival rates was seen. Survival rates were higher for leg-banded birds than neck-collared birds; and for AHY than HY birds. Estimates of r were similar for both analyses by marker type, although reporting rates of leg-banded birds (0.06–0.09) were lower than reporting rates of neck-collared birds (0.14–0.16). Because “ r is not the probability of a hunter reporting the mark, but rather the probability that a mark is reported given that the marked animal died. Cause of death can be from either natural causes, or because of harvest, and thus cause of death affects the probability that a mark is reported” (White and Burnham 1999). The mechanism for the difference in reporting rate of leg-banded and neck-collared birds has not been identified, but could be due to hunter selection of collared birds and a higher probability that a hunter will see and report a neck collar than leg band.

An individual covariate on direct survival rate was important to prevent positive bias in survival rate estimates due to long banding periods when recovery data were analyzed, but models that simply allowed for direct and indirect survival rates

were sufficient when both recovery and observation data were used. Direct survival rates were higher than indirect survival rates, because direct survival rates cover <1 full year. The pooled value was usually closer to the direct than to the indirect survival rate. This suggested that direct survival rates have a stronger influence on the pooled estimate. For example, when I compared the survival rate estimate from a model without direct survival rates with those from the same parameterization but including direct survival rate (i.e., $S(\text{age}) r(\text{marker type})$ vs. $S^*(\text{age}) S(\text{age}) r(\text{marker type})$), the pooled survival rate ($S=0.909$) estimate was between S^* and S ($S^*=0.911$ and $S=0.745$). The pooled survival rate is similar to that estimated by Nichols et al. (1992).

Point estimates of collar retention rates decreased with collar age, but this change was not statistically significant, as determined by overlapping 95% confidence intervals. However, sample sizes were small, making it unlikely that any effect of collar age could be detected, if it existed (Williams et al. 2002). While collar retention rates may have varied by family group status (Badzinski 2003), the sample of recaptured birds was too small to investigate this difference, and family-group status often could not be determined. Estimates of neck-collar retention rates are crucial to meaningful interpretation of parameters estimated from neck collars (e.g., Samuel et al. 1990, Nichols et al. 1992, Coluccy et al. 2002). Opportunistic sampling (recaptures of marked birds during banding operations) likely did not provide a large enough sample of previously marked EP swans for neck-collar retention rate estimation.

Lack of model fit could be a problem in these analyses because of failure to meet some model assumptions: (1) independence of fates (family groups were marked); (2) multinomial modelling (concurrency of marking and recovery periods); (3) adequacy of model to prevent bias in estimates (leg bands and neck collars were used during different years, but small sample size prevented me from modeling year effects). The latter seems the most important because it required much *post hoc* data

manipulation to force data into the model structure, and there were many recoveries during the observation period. However, another violation that could be equally problematic, that all marked individuals in the same cohort have the same survival rate, was accounted for by use of individual covariates.

Except for the estimate of survival rate for leg-banded adults, adult survival rate estimates from these analyses were lower than the 0.92 (95% CI 0.85–0.99) estimated by Nichols et al. (1992). I did not consider differences in survival rate by sex, making it more difficult to compare estimates of immature survival rates, because Nichols et al. (1992) found that immature males had higher survival rates (0.81, 95% CI 0.64–0.99) than immature females (0.52, 95% CI 0.41–0.64). Possible explanations for lower adult survival rates in this study include (1) negative bias in survival rates from the Barker analysis due to reclassification of January–February recoveries into the previous March–December period; (2) positive bias in the Nichols et al. (1992) study, which did not account for extended January–March banding periods in its analyses; (3) hunter selection for collared birds; (4) decreasing trend in survival rate over time, combined with greater use of neck collars during the later part of the study; and (5) increase in hunting permits between the 2 study periods. After 1990, the number of permits issued to hunters increased from about 7,000 to 8,000–10,000, and reported EP tundra swan harvest increased by about 500–1,000 birds (15–30%).

Age and marker type both had an effect on survival and recovery rates, as assessed by model selection procedures. I suspect that survival rates estimated from leg-banded birds are more representative of the EP population than those estimated from collared birds, because of the potential negative effects of neck collars on survival (e.g., Zicus et al. 1983, Schmutz and Morse 2000), unsatisfactory collar retention rate adjustment, and hunter behavior. Hunters could be selecting collared birds either consciously (anecdotal evidence suggested that some did) or

unconsciously (i.e., something different about the marked bird attracting hunter attention). Therefore, I think the best estimate of an annual survival rate for adult EP swans comes from analysis of leg-banded birds and ranges from 0.73–0.84.

MANAGEMENT IMPLICATIONS

These survival rates seem low when placed in the context of what is known about the life history of tundra swans (Bellrose 1980, Baldassarre and Bolen 1994) and current estimates of population size, productivity, and harvest (Serie and Raftovich 2003, Kruse and Sharp 2003, K. Wilkins, USFWS, unpublished data). However, results from these analyses should be interpreted with caution because estimates could be biased from lack of model fit, inefficient adjustment of neck-collar retention rate, and *post hoc* data reclassification. I suspect that although capture-recapture models are robust to some model assumption violations (Williams et al. 2002), the assumption violations in these data may have been too egregious for unbiased parameter estimation. This was probably most true of birds marked with neck collars because of the potential for negative effects of neck collars on survival rate (increased natural and harvest mortality; e.g., Sheaffer et al. 2004). Wide confidence intervals did not allow for detection of differences in survival rate due to marker types, but the pattern in point estimates (lower annual survival and higher annual reporting rate for swans marked with neck collars than for swans marked with leg bands) supported the hypothesis that neck collars may reduce survival rates. Therefore, I think that survival rates estimated from leg bands are more representative of the EP.

Despite the use of leg bands imprinted with a toll-free phone number for reporting starting in 1999, EP tundra swan recovery rates are still only about 1–3% annually. Therefore, sample size requirements for precise annual survival rate

estimation (>2,000/year for 5 years; Sheaffer 1996) were unchanged. This number of bandings is still too large to be practical. Estimation of EP swan survival rates from neck collars proved problematic because of the difficulty of estimating accurate neck-collar retention rates and possible negative effects of neck collars on survival rate. Use of neck collars in an operational marking program will be limited by these 2 constraints, as well as by the amount of effort required to mark and observe swans, and therefore is not recommended for future EP tundra swan survival rate studies. Results from a marking program for EP swans would be improved by shortening the marking period and by not marking swans until after the hunting season. This would remove the need for covariate models, limit within-marking-period mortality, and possibly improve fit of model to the data. A reasonable goal would be to band swans only during the month of February, after the hunting seasons in North Carolina and Virginia have closed.

The use of DNA as a source of capture-recapture data may be useful for estimating survival rates in the future (Lukacs and Burnham 2003). Individuals can be identified using DNA samples from feathers or feces collected on the wintering grounds. Successive identification of individual birds can be thought of as an individual's capture history. Survival rates can then be estimated from these data using capture-recapture methods. However, a basic genetic library of tundra swans first needs to be completed and analyzed for suitable levels of genetic variation (Waits et al. 2001, Lukacs and Burnham 2003), the cost of sample analysis needs to decrease significantly (Waits et al. 2001), and a suitable sampling scheme must be developed (Lukacs and Burnham 2003). These constraints render the method better suited to the study of rare and endangered species (Taberlet et al. 1999). However, the genetic library of trumpeter swans (*C. buccinator*) is currently being developed and possibly could be used on tundra swans as well (S. Oyler McCance, U.S.G.S. Denver, CO

personal. communication.); therefore, this technique should be considered for future use. Excepting cost, a DNA capture-recapture method would be the most desirable of all methods for survival rate estimation because no external marker is attached, disturbance caused by sampling is minimal, and data can often be collected easily.

Finally, EP swan managers must decide whether survival rate estimates are needed for EP swan management programs, given the difficulty of collecting suitable data for survival rate analysis and the generally decreasing funding for wildlife monitoring programs in general and game species monitoring programs in particular (Christensen 2004). Precise annual survival rates would be useful in a model such as EPSWAN (Sheaffer 1996), but the extra information they add to a monitoring program must be substantial to justify the expense of marking and observation time required for current techniques.

APPENDIX B. Very High Frequency Radio Transmitters

INTRODUCTION

The feasibility of using Very High Frequency (VHF; 30–300 megahertz per second) radios for movement and survival rate estimation was explored as part of this study. VHF radios typically have several advantages over coded neck collars. These advantages include higher relocation probabilities, quicker and more accurate data collection, and the ability to collect data from a greater distance (White and Garrott 1990).

METHODS

A sample of 269 leg-banded swans was marked with very high frequency (VHF) transmitters during the winters of 2000–01 (139 birds) and 2001–02 (130 birds). VHF radios were distributed among 4 states: Maryland (26), North Carolina (164), Pennsylvania (47), and Virginia (32). VHF radio transmitters weighing 14 grams were made by High Tech Services, Camillus, NY. Transmitters had a frequency range of 148.000–152.999 MHz, and a distance range of 0.8–4.5 km. Radios had a battery life of 1.5 years, allowing swans to be tracked over 2 consecutive winters. Transmitters were riveted to white collars with 11-inch vertical antennas. White collars were used to minimize selection of collared birds by hunters.

During the winter of 2001–02, several swans that had been marked the previous winter were observed with broken antennas. The antennas were broken at the base, probably as a result of having been chewed off. Therefore, the method of attaching transmitters to collars was modified in 2001–02 by gluing the antennas in an “S-shape” around the collars. Because of the relatively small number of VHF transmitters, my initial goal was to mark only adult female swans. However, I was not

able to capture sufficient numbers of swans in this cohort, so I placed 31 VHF transmitters on swans in the other 3 age/sex classes. Locations of marked swans were determined by observers in vehicles using roof-mounted antennas or on the ground using hand-held antennas. Observers surveyed for VHF radios while surveying for coded neck collars (see Chapter 2). To monitor VHF failure rate, 50 VHF transmitters were mounted outside for 24 months, and tested monthly.

RESULTS

Over a 3-year period, 1,254 encounters of 166 individual birds were collected. Of these encounters, 18 were recoveries of dead birds reported to the BBL, 1,222 were VHF transmitter relocations collected by project personnel, and 14 were recaptures of marked birds by project personnel during marking operations. Of the 139 VHF radio transmitters active during the winter of 2000–01, 106 were relocated at least once during that same winter. However, only 26 of those transmitters were relocated on the wintering grounds during the winter of 2001–02, a 19% relocation rate after 1 year for the first set of transmitters. In contrast, 60 of the 130 VHF transmitters put out in the winter of 2001–02 were relocated later that same winter, but only 40 of them were relocated on the wintering grounds during the winter of 2002–03, a 31% relocation rate after 1 year for the second set of transmitters. The increase in relocation rate was probably due to alteration of the radio-mounting technique, but relocation rate was still lower than expected.

Only 1 of 50 control transmitters failed before 18 months, so transmitter failure was likely not a cause of low relocation rates. No lost or broken transmitters were found during recaptures of tundra swans originally marked with VHF transmitters (9 recaptures of 6 different birds). Therefore, I suspect that low encounter rates of VHF transmitters were probably due to the short range of the radio signal and to broken

transmitter antennas. To investigate the feasibility of tracking of the VHF transmitters from the air, I flew with Karen Bollinger (pilot biologist, Branch of Waterfowl Population Surveys, U.S. Fish and Wildlife Service [USFWS]) on 24 October 2000. We placed 2 VHF radio transmitters (151.891 MHz and 151.953 MHz) on the ground at several heights. We used 2 radio receivers: a typical bag-type Advanced Telemetry Systems (ATS) receiver and a smaller hand-held Communications Specialists (CS) receiver. The observed ranges are in the table B.1 below. Transmitter 151.953 had a shorter range than transmitter 151.891, so ranges for both transmitters are given.

Table B.1. Distance in miles of aerial radio transmission at 3 different elevations (1000, 2000, and 3000 m) for two different receiver types (ATS ¹ and CS ²) and 2 different VHF frequencies (151.891 MHz and 151.953 MHz).

elevation (m)	151.891 MHz		151.953 MHz	
	ATS receiver	CS receiver	ATS receiver	CS receiver
1000	5–5.5 mi	2–3 mi	4–5 mi	<2–3 mi
2000	7 mi	5 mi	6 mi	3.5 mi
3000	11 mi	8 mi	<11 mi	6.5 mi

¹ Advanced Telemetry Systems bag receiver.

² Communications Specialists hand-held receiver.

The estimated range of these radios was much smaller than has been found with other studies. For example, McAuley et al. (1993) had a range of 14–20 mi at 1000 m with an ATS receiver using the same antennas. However, the radios we tested here had a much longer battery life (1.5 years) than their radios (4 months). Our range may have been underestimated for 3 reasons. First, there is a lot of interference in this geographic area (near Baltimore and Washington D.C.); one may be able to distinguish fainter signals in other regions of the country with less electronic interference. Second, our test radios were on the ground. When radios are on swans, they might have longer range for 2 reasons: (1) they are up higher off the ground, and (2) the body of the animal can act as antenna (J. Goldsberry, USFWS retired, personal communication.).

Adding to the questionable quality of the VHF data, several observers reported false signals. Signals were known to be false because they were from birds known to be dead or were too close in time yet too far apart to be possible (e.g., a bird located on the same day in Pennsylvania and Maryland). Because the relocation rate was not close to 1 and relocation rate was not estimable because of the occurrence of false signals, I did not use VHF data in these analyses.

DISCUSSION

VHF transmitters did not provide usable data in this study. Only 19–31% of VHF transmitters were encountered after 1 year, which seems unacceptably low for long-lived birds such as tundra swans (Nichols et al. 1992) if the transmitters had an encounter rate close to 1. Using VHF transmitter data requires an encounter rate either close to 1 or at least estimable (Pollock et al. 1995). In the radio transmitter failure rate test, only 1 of 50 transmitters failed before 18 months, so radio transmitter failure was likely not a cause of low relocation rates. VHF radios mounted on neck collars were expensive and had low encounter rates due to short radio range, remote winter habitat, and antenna breakage.

MANAGEMENT IMPLICATIONS

We did not collect usable data from swans marked with VHF transmitters. Failure of the method was due to the method of VHF radio attachment and the short range of the VHF radio transmitters. We were unable to use the data because we could not correct for a relocation probability of <1 . Future VHF work should use radios with a longer range and stronger signal and should explore other attachment methods. Use of high-quality VHF radio transmitters attached to swans with harnesses is being explored in North Carolina (R. Malecki, NY Cooperative Fish and Wildlife Research

Unit, personal communication). During this study, radio signals will be collected from the air in conjunction with aerial surveys, so the cost for aerial surveying should be minimal. This method has the potential to provide precise survival rates because of high encounter rates and more reliable marker attachment. However, precision of estimates will be limited by transmitter battery life and mass (Caccamise and Hedin 1985). Although it is theoretically possible to obtain survival rate estimates from a study of 2–3 years in length, at least 3–5 years would be preferable to improve precision and to allow investigation of temporal variation in survival and recapture rates (Williams et al. 2002).

Furthermore, a study of EP tundra swans by Petrie and Wilcox (2003) found that satellite-tracked radio transmitters attached to collars had a lower failure rate than transmitters attached to harnesses. Other studies have found evidence that transmitter harnesses may change breeding behavior (Paquette et al. 1997, Garrettson and Rohwer 1998, Garrettson et al. 2000). Finally, given the difficulty of capturing, marking, and tracking sufficient numbers of tundra swans, the expense of radio transmitters, and limited personnel, I do not recommend a transmitter study for operational monitoring purposes.

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CHAPTER 3

Harvest management model for Eastern Population tundra swans

ABSTRACT

The Eastern Population (EP) of tundra swans (*Cygnus columbianus columbianus*) winters in the eastern United States and breeds from the North Slope of Alaska to the eastern side of Hudson Bay in Canada. Using data from operational monitoring programs (Mid-Winter Index, wintering ground Production Survey, and harvest data), I developed a model of EP tundra swan population dynamics that provided reasonable and precise predictions of population size, harvest, and survival. I investigated model performance under various conditions including: relative weight applied to data sets, starting values, and form of recruitment (i.e., density dependent or density independent). Model results were relatively insensitive to starting values and to the form of the recruitment function. The model appears useful for predicting and understanding the effects of changes in harvest on subsequent population size. The model suggests that density-dependent impacts are not currently controlling the population, population dynamics are sensitive to harvest, and that a wintering population size goal of at least 80,000 swans can be sustained at current or slightly smaller levels of harvest. Modeling results indicated that precise annual estimate of survival rates is not necessary for effective management of EP swans. Model validation with data from Western Population (WP) tundra swans suggested that data for WP are not as stable as data for EP, because results were more sensitive to form of recruitment function. This analytical technique may be useful for other waterfowl populations for which there are operational surveys but limited information on annual survival rates.

INTRODUCTION

Population models are important tools for managing wild populations. Sheaffer (1996) developed a stochastic simulation model (EPSWAN) for management of Eastern Population (EP) tundra swans (*Cygnus columbianus columbianus*). This model included a high degree of biological realism, provided reasonable harvest and population size predictions, and proved to be an excellent exploratory tool. However, some of the productivity parameters included in the model came from small-scale, short-term studies. These parameters included proportion of adults in nesting pairs, brood success, and young per adult. Because many of the vital rate estimates used in the EPSWAN model were derived from individual studies that are not part of an operational monitoring program, annually updated estimates are not available. Furthermore, some of the study areas were geographically small and may not have been representative of the entire EP (e.g., Bart et al. 1991, Monda et al. 1994). As a result, the annual and regional variation in the parameters could not be included in the analysis beyond sensitivity analyses.

EPSWAN model simulations indicated that results were highly sensitive to the survival rate estimate. This was not surprising given the strong influence of adult survival rate on population dynamics for species like tundra swans (i.e., long-lived, delayed breeding, and low productivity rates; Gill 1990, Heppell et al. 2000). However, updated estimates of survival rates were not available. Model simulations highlighted the need for precise annual survival rates for EP swan management. To meet this need, the Atlantic Flyway organized a large-scale study of EP tundra swans. One of the goals of this study was to investigate markers with higher resighting rates to improve estimates of survival rates. These markers included VHF radio transmitters and neck collars. However, neither type of marker worked well because of limitations outlined in Chapter 2 and Appendix B.

Therefore, I considered an alternative approach to modelling EP tundra swans that used data from annually conducted operational surveys only and that did not require estimates of annual survival rate. This method used data from several different sources: Mid-Winter Inventories (MWI), productivity surveys, and harvest surveys. Data were fit simultaneously using a model fitting procedure that provided the best overall fit of the model to the observed data (White and Lubow 2003) and included only those aspects of population dynamics that were critical to system behavior (Williams et al. 2002). Because this model used data from operational surveys, it was much simpler in structure than the EPSWAN model. However, I wanted to assess the ability to manage EP tundra swans using data that was on hand, and this necessitated a simpler model structure.

My objective was to develop a population model for EP tundra swan management from operational monitoring programs. Available EP tundra swan data sets were examined and a balance equation model was developed. Sensitivity analyses were conducted to investigate the model's robustness, and the model was validated using data from Western Population (WP) tundra swans. Finally, model results, harvest predictions, and the utility of this model for EP swan management were examined.

METHODS

Databases

Mid-winter inventories

The mid-winter inventory (MWI) is an aerial survey performed annually during early January to count wintering waterfowl in major concentration regions of the U.S. Aerial crews attempt to make complete counts of all waterfowl within pre-defined survey areas. Although some believe the survey is unreliable for most species

(Eggeman and Johnson 1989, Heusmann 1999), EP tundra swan counts are believed to be fairly accurate for several reasons: (1) survey coverage has been fairly consistent in the Atlantic Flyway since 1955; (2) these large white birds are easily seen from the air; and (3) biologists believe they know most of the places that swans occupy during the winter (J. Goldsberry, U.S. Fish and Wildlife Service [USFWS] retired, personal communication.). MWI counts of tundra swans in the Atlantic Flyway have increased from about 40,000 in the 1950s to \approx 100,000 in recent years (Serie and Raftovich 2004). Data from 1956–2003 were used in this analysis.

Production surveys

The gray plumage of young (hatch-year or HY) swans makes them easily distinguishable from older birds that have white plumage (after-hatch-year or AHY; Bellrose 1980). Therefore, the proportion of gray birds in the winter population is an index of the previous summer's production. Observers on the ground conduct production surveys each November and December across the entire wintering range. They sample wintering flocks and record the numbers of gray and white birds (USFWS 1977, Serie and Bartonek 1991a). On average, more than 10,000 birds were examined each year from 1961 to 2003. Therefore, percent young on the wintering ground (PY) was used as an index of recruitment into the fall flight. Data from 1961–2003 were used in this analysis.

PY is not a direct measure of annual production, because it does not account for young birds lost on the breeding grounds or during fall migration. However, a benefit of using PY as an annual production index is that one does not have to account for breeding population age structure (swans do not breed until they are 3–5 years of age) or model the recruitment process (e.g., clutch size, nest success, etc.). Using this integrated index of production and breeding status directly rather than attempting to

partition individuals into age classes when data are unavailable (e.g., Link et al. 2003) was more practical.

Harvest data

EP tundra swans have been hunted by sport-hunters during September–December in the Central Flyway states of Montana, North Dakota, and South Dakota since 1983. They also have been hunted during October–January in North Carolina and Virginia since 1984. EP tundra swan harvests have been managed by a permit system (Serie and Bartonek 1991*b*). A set, known number of permits were issued each year, and each permitted hunter is allowed to harvest 1 swan. At the end of the hunting season, state biologists send a reporting questionnaire to each permitted hunter. Hunters are asked to report whether they shot and retrieved a swan, and if so, the plumage color for harvest age information. They are also asked how many swans they crippled, if any. Reporting was mandatory regardless of hunter success. About 70–90% of EP swan hunters respond to hunter questionnaires (Fuller 2002, Costanzo 2002, Hansen 2004, Johnson 2000, and Vaa 2004), and non-respondents are assumed to have the same success rates as respondents. Thus, survey results can be considered close to a complete count of total harvest. Reported harvest was about 3,500 swans per year, resulting in a crude harvest rate of 3–5% from 1996–2002. Although age ratio in the harvest is often used as an index of duck production (Munro and Kimball 1982), this is not appropriate for EP tundra swans because (1) banding data are insufficient to adjust harvest age ratios for differential vulnerability between age classes, (2) harvest age ratios for tundra swans are likely more a reflection of hunter preference than relative abundance (M. Johnson, North Dakota Game and Fish Department, personal communication; K. Wilkins, USFWS, unpublished data, and (3) EP swans are not harvested in all wintering states.

EP tundra swans are also hunted by subsistence hunters on the breeding grounds. The magnitude of subsistence is difficult to assess because of the remote and diffuse distribution of breeding EP swans (Serie and Bartonek 1991*b*). However, subsistence harvest surveys in Alaska and Nunavut suggest that harvest was very low (≈ 500 birds; Georgette 2000, Walker 2003, Priest and Usher 2004); therefore, it was ignored in this analysis.

Model Development

The basic population model was a simple balance equation:

$$N(t + 1) = S(t) * N(t) + R(t) \quad (1)$$

where $N(t)$ = population size at in January of year t ,

$S(t)$ = survival rate from January of year t to January of year $t+1$, and

$R(t)$ = number of recruits added during year t .

This model assumes that the wintering EP is a closed population; an assumption supported by data from satellite-tracked radio transmitters, observations of marked birds, and recoveries of dead marked birds (Chapters 1 and 2, this thesis). The actual values of these state variables are unknown. Instead, we used indices from MWI, harvest, and productivity surveys to estimate the state variables. $N(t)$ was estimated from the MWI of year t , $S(t)$ was modelled as a function of Central Flyway and Atlantic Flyway harvest data of hunting season $t - t+1$ (e.g., 2001–2002; hereafter referred to hunting season t), and $R(t)$ was modelled as a function of the PY counted in the fall of year t .

Survival

Annual survival rate was modelled as the product of survival rates for 3 sub-periods:

$$S(t) = S_{nh}(\cdot) * S_{CF}(t) * S_{AF}(t) \quad (2)$$

where $S_{nh}(\cdot)$ = non-hunting season survival rate from February to October,

$S_{CF}(t)$ = survival during Central Flyway hunting season t , and

$S_{AF}(t)$ = survival during Atlantic Flyway hunting season t .

The notation for non-hunting survival rate indicates that non-hunting survival rate was estimated as an average non-hunting survival rate over all years.

This separation of survival rates was appropriate because bird movements from the breeding grounds, through the Central Flyway, to the Atlantic Flyway, are fairly distinct in place and time. Central Flyway and Atlantic Flyway harvest processes were kept separate in accordance with the EP Tundra Swan Hunt Plan, where the number of available hunting permits was divided almost equally between breeding, migration, and wintering states (*Ad Hoc* EP Tundra Swan Committee 1998). This modelling assumes that all Atlantic Flyway harvest in year t occurs before the MWI in year $t+1$. This is not true, because about 30–40% of North Carolina's and Virginia's swan harvest occurs after the MWI (J. Fuller, North Carolina Wildlife Resources Commission, personal communication; T. Bidrowski, Virginia Department of Game and Inland Fisheries, personal communication). However, mortality after the MWI is not problematic if the proportion and timing of the January harvest stays about the same from year to year. Then, harvest taken after the MWI is simply lagged by one year.

This survival rate structure superficially assumes that non-hunting mortality occurs only from February to the start of the hunting season. Non-hunting mortality during the October–January period, due to sources such as contaminants and accidents, was not explicitly modelled here. However, the estimation of non-hunting survival rate includes these losses in the estimate, regardless of when they actually occurred.

I modelled annual hunting season survival rates as a function of hunting effort and the risk that swans faced, i.e., their vulnerability (q), while they were in the Central Flyway (q_1) and Atlantic Flyway (q_2):

$$S_{CF}(t) = e^{-q_1 * CFE_t}, \text{ and} \quad (3)$$

$$S_{AF}(t) = e^{-q_2 * AFE_t} \quad (4)$$

where CFE_t = number of permits issued in the Central Flyway in year t , and

AFE_t = number of permits issued in the Atlantic Flyway in year t .

This model provides a direct functional connection between hunting season survival rate and hunting regulations, and therefore allows exploration of effects of different hunting regulations on survival rate, and in turn, on population size and harvest. The “risk” or “vulnerability” coefficient was the equivalent of “catchability” parameters used in many fish population models (Quinn and Deriso 1999). In this model, increases in either vulnerability or effort result in decreased hunting season survival rate.

Flyway-specific survival rates were modelled because there may be differences in vulnerability per unit of hunting effort (permit) between the 2 flyways. Harvest per hunting permit issued might be greater in the Atlantic Flyway, where birds are essentially resident for 2–4 months, than in the Central Flyway, where birds are transient. If such differences in vulnerability exist, they will be reflected in estimates of q_1 and q_2 . Effort was normalized between the 2 flyways by dividing each annual value of effort by the mean effort for that flyway. This makes vulnerability coefficients q_1 and q_2 comparable between flyways, even though there are about twice as many hunting permits issued in the Atlantic Flyway as there are in the Central Flyway.

Recruitment

PY was an index of the recruitment rate each year and not a direct measure of $R(t)$, or recruitment amount. Therefore, $R(t)$ was modelled as a function of PY. I investigated 2 models of recruitment: a linear model that simulates density-independent recruitment, and the Ricker model, which simulates density-dependent recruitment (Quinn and Deriso 1999).

In linear recruitment, the number of new recruits added to the population each year was a proportion (α) of the number of adults in the population:

$$\text{linear recruitment} \quad R(t) = \alpha * N(t) \quad (5)$$

Thus the number of recruits each year was independent of population density (Quinn and Deriso 1999). Density-independent recruitment might be considered the most logical model for EP tundra swans, because their density across the breeding grounds was generally extremely low (e.g., <0.0016 nests per km² in North Central Alaska, Wilk 1993), except in a few concentration spots (e.g., 0.11 nests per km² in the Mackenzie River Delta area, Swystun et al. 2005).

However, a density-dependent model of recruitment may be appropriate if density-dependent effects occur at any life history stage (Quinn and Deriso 1999). For example, density-dependent effects might occur on the wintering grounds or at key migration stopover points, when the birds are concentrated into small areas. Therefore, I also considered a Ricker recruitment model, in which annual recruitment is linear up to some point, and above a population size threshold recruitment declines:

$$\text{Ricker recruitment} \quad R(t) = \alpha * N(t) * e^{-\beta * N(t)} \quad (6)$$

where α = recruits per breeding adult at small population sizes, and

β = describes how quickly the recruits per breeding adult drops as population size increases (Hilborn and Walters 1992).

The threshold population size was a function of both α and β (Quinn and Deriso 1999), and many density-dependent relationships can be captured by various combinations of the 2 parameters.

One should consider models of both density-independent and density-dependent recruitment because they can result in different population size predictions. Density-dependent models assume that population losses due to harvest are compensated for by concurrent decreases in other sources of mortality (Williams et al. 2002). If the population is above some threshold size, a density-dependent model will allow for greater harvest than a density-independent model. Substitution of survival models (equations 2–4) and recruitment models (equations 5–6) into the original balance equation (equation 1) yields 2 final population models:

linear recruitment:

$$N(t+1) = S_{nh}(\cdot) * e^{-q_1 * CFE(t)} * e^{-q_2 * AFE(t)} * N(t) + \alpha * N(t) \quad (7)$$

Ricker recruitment:

$$N(t+1) = S_{nh}(\cdot) * e^{-q_1 * CFE(t)} * e^{-q_2 * AFE(t)} * N(t) + \alpha * N(t) * e^{-\beta * N(t)}. \quad (8)$$

Weighting

The influence of individual data sets on model results can be weighted by the degree of confidence one has in that particular data set (Quinn and Deriso 1999). Greater weight on a particular observation or data set was appropriate when more information was contained in that data component. I investigated several sets of weights, but I present results from only 2 sets: (1) all data sets weighted equally, and (2) population survey data and productivity data weighted ten times more than the harvest data in the objective function. I did not put high weight on harvest data because harvest regulations have not been strongly influenced by population size, so harvest has little correlation with population size. Furthermore, the size of the EP tundra swan harvest is small relative to population size. For example, sport harvest has

remained relatively constant in recent years, while population size has been increasing. Thus, the harvest data have less informative value for the population model than do the population survey and productivity data. Other sets of weights were also investigated for sensitivity analyses.

Estimation

Five or 6 parameters were estimated for each model depending on the recruitment model: initial population size ($N(1956)$), non-hunting survival rate ($S_{nh}(\cdot)$), vulnerability of swans in the Atlantic Flyway ($q1$) and the Central Flyway ($q2$), and either 1 or 2 recruitment coefficients. The linear recruitment model required estimation of α , whereas the Ricker model required estimation of both α and β . Parameters were estimated by non-linear least squares weighted by state variable (winter population size, Atlantic Flyway harvest, Central Flyway harvest, and PY; Seber and Wild 2003). Thus, the final objective function (f) included the minimized sum of squares difference between expected and observed values for each state variable and a weighting factor for each state variable. Data values were log-transformed to make variables on different scales (e.g., population size and PY) more comparable (Seber and Wild 2003).

$$\begin{aligned}
 f = & w_1 * \frac{n_1 - 1}{2} * \log \sum_{t=1956}^{2003} (\log(N \exp(t) / Nobs(t)))^2 + \\
 & w_2 * \frac{n_2 - 1}{2} * \log \sum_{t=1956}^{2003} (\log(H \exp_{CF}(t) / Hobs_{CF}(t)))^2 + \\
 & w_3 * \frac{n_3 - 1}{2} * \log \sum_{t=1956}^{2003} (\log(H \exp_{AF}(t) / Hobs_{AF}(t)))^2 + \\
 & w_4 * \frac{n_4 - 1}{2} * \log \sum_{t=1961}^{2003} (\log(PY \exp(t) / PYobs(t)))^2
 \end{aligned} \tag{9}$$

where $N \exp(t)$ = expected value of winter population size at time t ,

$N obs(t)$ = observed value of winter population size at time t ,

$H exp_{CF}(t)$ = expected value of Central Flyway harvest at time t ,

$H obs_{CF}(t)$ = observed value of Central Flyway harvest at time t ,

$H exp_{AF}(t)$ = expected value of Atlantic Flyway harvest at time t ,

$H obs_{AF}(t)$ = observed value of Atlantic Flyway harvest at time t ,

$PY exp(t)$ = expected value of percent young at time t ,

$PY obs(t)$ = observed value of percent young at time t ,

w_1 = weight on MWI data,

w_2 = weight on Central Flyway harvest data,

w_3 = weight on Atlantic Flyway harvest data,

w_4 = weight on productivity survey data,

n_1 = number of observations in the MWI data,

n_2 = number of observations in Central Flyway harvest data,

n_3 = number of observations in the Atlantic Flyway harvest data, and

n_4 = number of observations in the productivity survey data.

I estimated expected harvests in each flyway as the product of survival probabilities for the previous time periods, the probability of *not* surviving that particular time period, and the population size:

$$H exp_{CF}(t) = S_{nh}(\cdot) * (1 - S_{CF}(t)) * N exp(t) \text{ and}$$

$$H exp_{AF}(t) = S_{nh}(\cdot) * S_{CF}(t) * (1 - S_{AF}(t)) * N exp(t)$$

Recruitment was not directly estimated in any survey; therefore, I calculated “observed” recruitment as observed population size times observed PY:

$$R(t) = PYobs(t) * Nobs(t).$$

I used AD Model Builder software (Fournier 2001) to generate the estimates and associated variances. This software fits non-linear models precisely and quickly

by calculating derivatives directly, instead of numerically as do most non-linear estimation procedures (Fournier 2001). Direct calculation of derivatives has been found to perform better than other algorithms in several aspects, including providing improved accuracy of variance and covariance estimates (Seber and Wild 2003). The AD Model Builder software, while not as user-friendly as a spreadsheet application, is much more powerful and provides more robust solutions to non-linear estimation problems (Fournier 2001).

Model Selection

I used a combination of AIC and visual assessment of plots of predicted versus observed values and residuals. AIC was calculated as follows:

$$AIC = -2*f + 2n$$

where $n = 5$ for model with linear recruitment and $n = 6$ for model with Ricker recruitment. I examined the estimated values of winter population size, harvest, recruitment, PY, and survival rate that were generated using equations 1–6 and the parameter estimates from equation 9. I compared model fit visually for different recruitment functions and data set weights. I compared correspondence between observed and expected values of population size, harvest, and PY. Known values of survival rate were unavailable, but model-based survival rate estimates were compared to survival rate estimates from other studies (Nichols et al. 1992, Chapter 2 of this dissertation).

Sensitivity Analyses

Starting conditions

In non-linear estimation, setting starting values for estimated parameters helps the software find reasonable results (Fournier 2001). Starting values were estimated from the data when possible and were suitably transformed. The following starting

values were used: $N(1956) = 1956$ MWI; $\alpha =$ average PY from 1961–2003; $S_{nhm}(\cdot) = 0.82$; and $q1$ and $q2 = 0.007$. An appropriate value for β was found by trial and error. To investigate sensitivity of non-linear estimation to the starting values, I compared results from 5 different starting values: the starting value calculated directly from data and the calculated starting value multiplied by 0.1, 0.5, 2, and 10 (Seber and Wild 2003).

Weighting

Results can also be sensitive to data set weights, especially if each data set does not exhibit the same trends. Therefore, I explored data set weights of 1, 5, 10, and 100 in several combinations: (1) MWI and PY data weighted higher, (2) Atlantic Flyway and Central Flyway harvest weighted higher, (3) MWI data weighted higher, and (4) PY data weighted higher. Although I did not expect higher weighting on harvest data to provide useful results, as explained above, I explored it simply for illustrative purposes.

Model Validation

One way to evaluate a model is to test it with data other than those used to build the model (Shenk and Franklin 2001). A model that reasonably predicts parameters for similar systems demonstrates robustness and provides some assurance that results are not spurious (Burnham and Anderson 1998; Williams et al. 2002). I validated my model with data from WP tundra swans. WP swans breed in western and northwestern Alaska, and winter in the western U.S. and coastal British Columbia in the Pacific Flyway (Pacific Flyway Waterfowl Council 2001). The EP and WP overlap somewhat in breeding distribution but have distinct wintering grounds with little cross-over between populations (Bellrose 1980). I chose the WP for model validation because those data were not used in model development, WP swans have population

dynamics similar to those of EP tundra swans (Bart et al. 1991), and the same data (MWI, PY, and harvest data) were available and collected in the same manner for both swan populations.

There are several pertinent differences between the EP and WP and their monitoring data. Biological differences include: (1) WP swans have shorter migrations; (2) WP swans breed at lower latitudes than EP birds and thus often have milder weather on the breeding ground, which can increase cygnet survival (Bart et al. 1991); and (3) significant subsistence hunting occurs on WP breeding grounds (Aldrich et al. 2004). Differences in monitoring data include a longer time series, higher PY, and greater variability in MWI counts (Table 3.1) for WP tundra swans. The greater degree of variation in WP MWI counts was due to “annual differences in weather-related phenology of late migration, prevalence of ice and snow, and the abundance of water in January” (Pacific Flyway Waterfowl Council 2001). These variations lead to less consistent wintering distributions and, as a result, greater annual variation in MWI coverage of the WP.

Table 3.1. Comparison of Mid-Winter Inventory population size [N(t)] and annual growth rates [N(t+1)/N(t)] for Eastern (EP) and Western Population (WP) tundra swans in the U.S., 1956–2003.

	EP		WP	
	N(t)	N(t+1)/N(t)	N(t)	N(t+1)/N(t)
mean	73,108 (21,624 ¹)	1.04 (0.21)	51,456 (22,977)	1.11 (0.48)
minimum	27,717	0.63	31,000	0.41
maximum	109,788	1.56	122,521	3.19

¹ Standard error.

Harvest dynamics also differ between the 2 swan populations. Although both populations are hunted by sport-hunters during fall and winter, WP swan hunting began in 1962, and subsistence harvest in Alaska has been estimated to be 2–5 times

the Pacific Flyway sport harvest (Aldrich et al. 2004). For model validation purposes, subsistence harvest in Alaska was treated like Central Flyway sport harvest, and Pacific Flyway sport harvest was treated like Atlantic Flyway sport harvest. That is, subsistence harvest by Alaskan natives was assumed to occur before Pacific Flyway sport harvest:

$$S(t) = S_{nh}(\cdot) * S_{AK}(t) * S_{PF}(t),$$

where $S_{AK}(t)$ = survival during the Alaska subsistence hunting season, and $S_{PF}(t)$ = survival during the Pacific Flyway hunting season.

Expected harvests in Alaska and the Pacific Flyway were estimated as:

$$H_{AK}(t) = S_{nh}(\cdot) * (1 - S_{AK}(t)) * N(t) \text{ and}$$

$$H_{PF}(t) = S_{nh}(\cdot) * S_{AK}(t) * (1 - S_{PF}(t)) * N(t)$$

where $H_{AK}(t)$ = subsistence harvest amount at time t in Alaska, and $H_{PF}(t)$ = sport harvest amount at time t in the Pacific Flyway.

Timing of non-hunting mortality was problematic when modelling WP tundra swans. The subsistence-hunting period can run from 1 March–31 August, but most harvest takes place in the spring (Wentworth 2004, Wentworth and Seim 1996, Paige et al. 1996). A more biologically appropriate series of survival events for WP swans might be

$$S(t) = S_{nh1}(\cdot) * S_{AK}(t) * S_{nh2}(\cdot) * S_{PF}(t),$$

with 2 non-hunting survival periods, one before and one after the main subsistence hunting period, but data were insufficient to estimate non-hunting survival rates for 2

distinct time periods. However, this model accounts for all non-hunting mortality in a single estimate of non-hunting survival. Therefore, splitting non-hunting survival into 2 time periods, although more biologically correct, was unnecessary for model purposes.

Estimates of subsistence harvest for WP swans were available from 3 regions in Alaska for several years: Yukon-Kuskokwim Delta (1985–2003 except 1988, Wentworth and Seim 1996), Bering Straits (2002; C. Wentworth, USFWS, unpublished report), and Bristol Bay (1995–2001; C. Wentworth, USFWS, unpublished report). I added the mean annual Yukon-Kuskokwim Delta harvest (1985–2003), the mean annual Bristol Bay harvest (1995–2001), and the Bering Straits point estimate for 2002 to estimate the average total annual harvest from 1985–2003. I used this average of 6,116 swans as the value of subsistence harvest for 1949–1984 and 1988. For 1985–1987 and 1989–1994, I added the annual estimate for the Yukon-Kuskokwim Delta, the Bristol Bay average, and the Bering Straits 2002 figure to estimate year-specific harvest. For 1995–2003, I added the 2002 Bering Straits estimate to the year-specific figures for the other 2 regions. Permits are not issued for subsistence harvest, so I could not model survival rate directly as a function of effort. Instead, I used a dummy value for hunter effort of 1,000 units, which enabled me to estimate vulnerability (q_1) as a nuisance parameter.

Productivity survey data from Utah were used for model validation. Productivity surveys are also performed in northern Washington, but Washington surveys have been conducted only since 1980, and data from the different surveys have not been combined (Pacific Flyway Waterfowl Council 2001). Bias can arise if the Utah sample was not representative of the entire WP, because not all of the wintering ground was sampled. This was unlike the EP data, for which productivity surveys are conducted in all wintering states.

Model Predictions

The population objective of the EP hunt plan is 80,000 swans based on a 3-year average population index from the MWI (*Ad Hoc* EP Tundra Swan Committee 1998). Therefore, I generated predictions of 3-year average future population size (\bar{N}) and population growth rate after 10 years (λ_{10}):

$$\bar{N} = \frac{N \exp(2011) + N \exp(2012) + N \exp(2013)}{3}, \text{ and}$$

$$\lambda_{10} = \frac{N \exp(2013)}{N \exp(2003)}.$$

I also explored effects of changes in future harvest regulations using several harvest regimes. I predicted harvest for 10 years using 6 different harvest regimes: (1) no harvest, (2) harvest at half of its current level, (3) harvest at its current level, (4) harvest at its current level plus 300 additional permits in the Central Flyway, (5) harvest at its current level plus 300 additional permits in the Atlantic Flyway, and (6) harvest at its current level plus 300 additional permits each in both the Central and Atlantic Flyways. The number of permits issued in the Central Flyway has changed slightly each year; therefore, I used 3,500 permits as the current value. In the Atlantic Flyway, this value was 5,600 permits, the number issued annually since 1996. I then calculated the predicted average future harvest (\bar{H}) and the % change in predicted harvest over 10 years (ΔH):

$$\bar{H} = \frac{\sum_{t=2004}^{2013} [H \exp_{AF}(t) + H \exp_{CF}(t)]}{10}, \text{ and}$$

$$\Delta H = \frac{\bar{H} - [H \exp_{AF}(2003) + H \exp_{CF}(2003)]}{H \exp_{AF}(2003) + H \exp_{CF}(2003)} \times 100.$$

RESULTS

Model development

Parameter estimates

Parameter estimates from all models were remarkably consistent (Table 3.2). However, upper confidence limits were not estimable for the additional density-dependent parameter, β . This suggests that either the data were insufficient to fit the more-parameterized Ricker model or there was no pattern of density dependence in the recruitment data.

The estimated proportion of young produced each year (α) was about 12%, regardless of weighting factor or recruitment model. Vulnerability coefficients suggest that swans are about 4 times more vulnerable in the Atlantic Flyway than in the Central Flyway. Non-hunting survival rate was 0.92 for all 4 models.

Vulnerability coefficients were consistently lower in the Central Flyway than in the Atlantic Flyway, and are essentially identical from the 4 models. These coefficients indicated that one unit of effort in the Atlantic Flyway can be expected to harvest 3–4 times more swans than one unit of effort in the Central Flyway. However, vulnerability was very low in both flyways. Analysis of residuals indicated that observed harvest in the Central Flyway tended to be greater than that expected, while there was no such pattern associated with the Atlantic Flyway harvest.

Table 3.2. Point estimates and 95% confidence intervals for parameter estimates and AIC values for 4 models of Eastern Population tundra swan population dynamics in the U.S., 1956–2003.

Parameter	Model			
	Linear recruitment model		Ricker recruitment model	
	equal weights	unequal weights	equal weights	unequal weights
$N(1956)$	34,098 (31,247–,37,210)	36,316 (35,319, 37,340)	34,098 (31,247, 37,210)	36,316 (35,319, 37,340)
α	0.119 (0.103, 0.136)	0.119 (0.114, 0.124)	0.119 (0.103, 0.136)	0.119 (0.114, 0.124)
β	-	-	1.838e-17 (0, ∞)	1.426e-17 (0, ∞)
q_1	0.003 (0.003, 0.004)	0.003 (0.003, 0.004)	0.003 (0.003, 0.004)	0.003 (0.003, 0.004)
q_2	0.012 (0.011, 0.013)	0.012 (0.012, 0.013)	0.012 (0.011, 0.013)	0.012 (0.012, 0.013)
$S_{nh}(\cdot)$	0.918 (0.900, 0.933)	0.915 (0.909, 0.920)	0.918 (0.900, 0.933)	0.915 (0.909, 0.920)
AIC	-90.068	-992.199	-88.068	-990.199

Survival

Survival rate estimates were similar between both sets of recruitment models and data-set weights, except that estimates derived from unequal weighting were more precise (Figures 3.1 and 3.2). Hunting season survival rates were estimated at 1.0 until commencement of sport-hunting in 1983. After that, hunting season survival rates ranged from 0.95–0.99 from the 4 models. Survival rate estimates were higher during the Central Flyway hunting season than during the Atlantic Flyway hunting season, as expected, because of the larger harvest in the Atlantic Flyway. The estimate of non-hunting survival rate can be seen in the annual survival rate graph as the survival rate before hunting commences. Annual survival rate estimates varied from 0.87–0.92 from the 4 models from 1956–2003. These estimates of survival rate are consistent with survival rates estimated from mark-recapture data (Nichols et al. 1992).

Recruitment

Recruitment data did not show any evidence of density dependence, as determined by examination of the plot of number of cygnets versus population size (Figures 3.3 and 3.4). If density dependence were operating, one would expect the number of recruits to decrease as population size increased. As with survival rate estimates, data-set weighting had little effect on recruitment estimates except for reducing variance. Recruitment predictions were also relatively unaffected by recruitment model. All models predicted about 10,000–12,000 recruits for each of the past 10 years and for 10-year predictions, and a constant PY of 0.12.

Estimation

Population size estimates were slightly sensitive to data-set weighting and relatively insensitive to recruitment model (Figures 3.5 and 3.6). Results from models

with higher weights on population and production survey data were almost identical regardless of recruitment function. Predictions of population size over 10 years from the 4 models ranged from about 91,000–103,000. Each model/weight combination predicted that population size will remain similar to current predicted population size, with both equal-weighted models projecting a slight increase and both unequal-weighted models projecting a slight decrease in population size.

Reported harvest was estimated at 0 in both flyways until the seasons were opened, and thereafter harvest varied positively with number of permits. While some illegal harvest probably occurred prior to the first regulated sport-hunting season, these losses were included in the non-harvest mortality estimates, along with subsistence harvest. Central Flyway harvest was predicted less precisely by number of permits than was Atlantic Flyway harvest, probably because of the greater variability in harvest due to the influence of weather and migration chronology on hunting success along migration routes. Predictions of harvest levels mirrored those for population size (i.e., both equal-weighted models projecting a slight increase and both unequal-weighted models projecting a slight decrease in population size).

Parameter estimates were reasonably precise, with coefficients of variation (cv's) of ranging from 0.007 to 0.192 annually. However, some estimates at the beginning of the time series were fairly imprecise, especially from the Ricker model with equal weights. Annual survival estimates generally had the smallest cv's, followed by Atlantic Flyway harvest. Population size and Central Flyway harvest had relatively larger cv's.

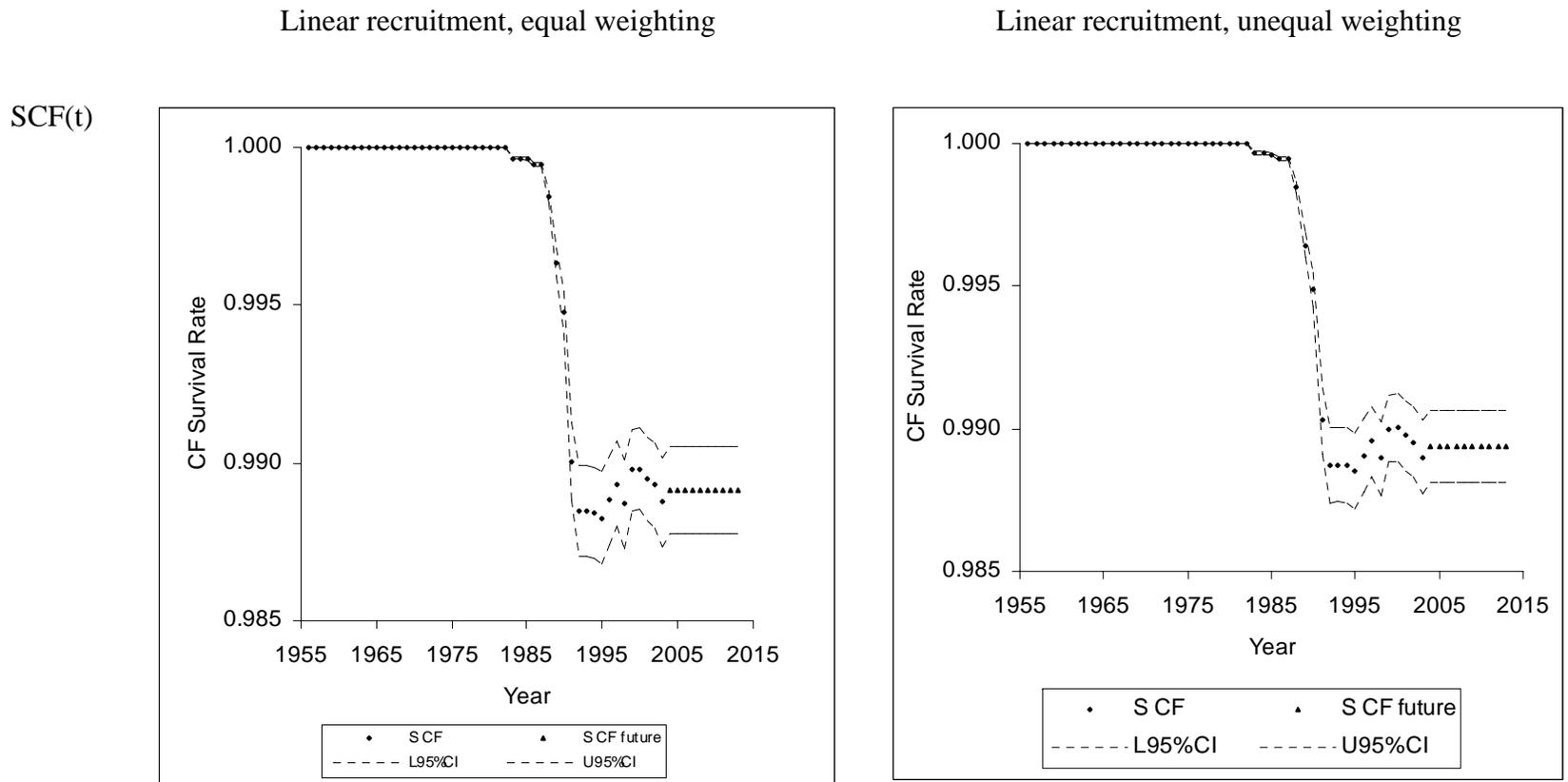


Figure 3.1. Survival estimates for the linear recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013. Predictions assumed that harvest continued at its current level.

Figure 3.1 (Continued).

Linear recruitment, equal weighting

Linear recruitment, unequal weighting

SAF(t)

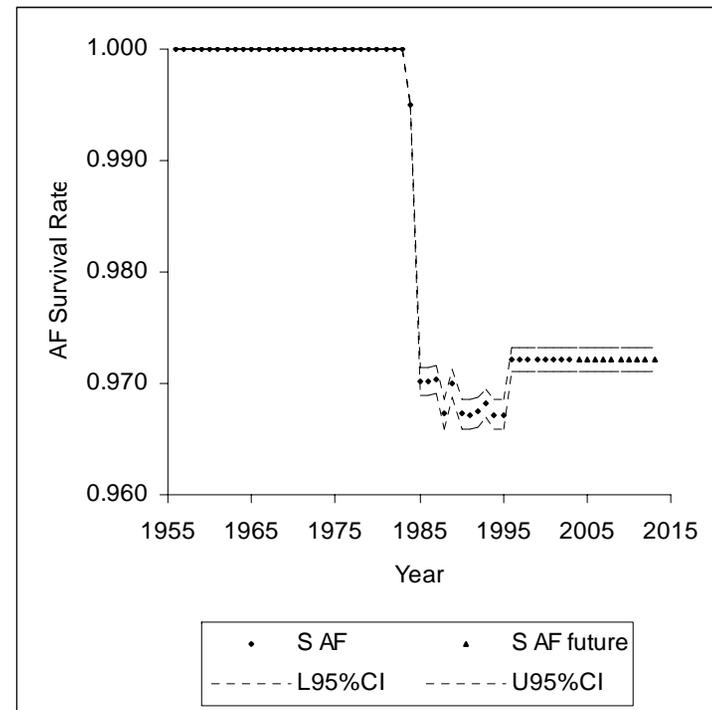
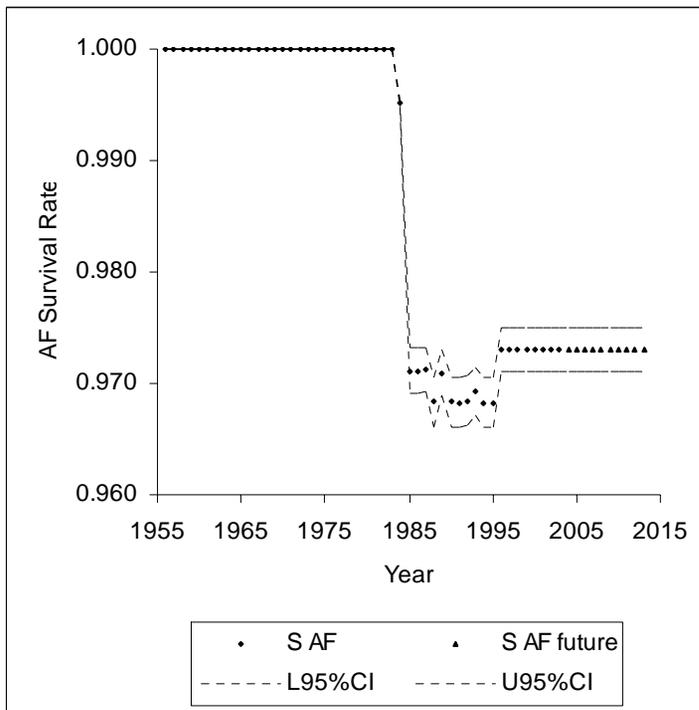
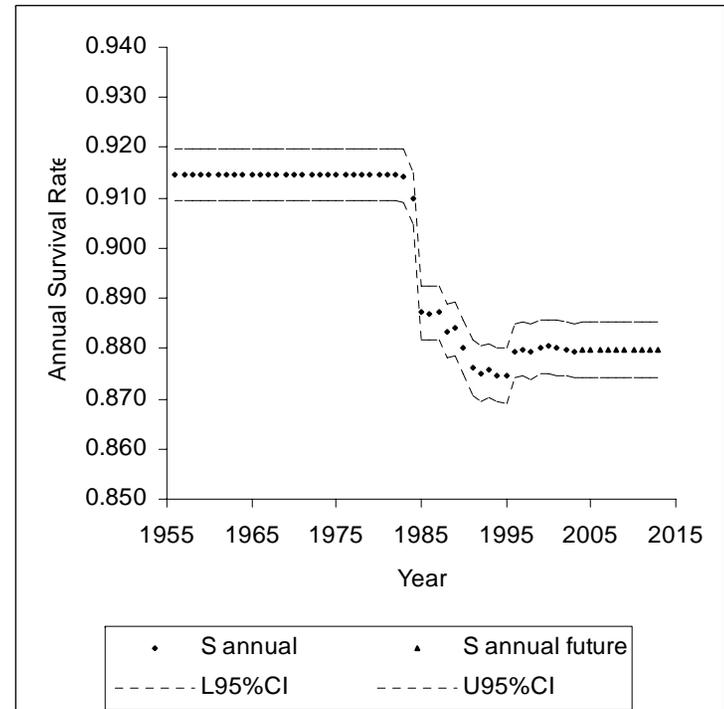
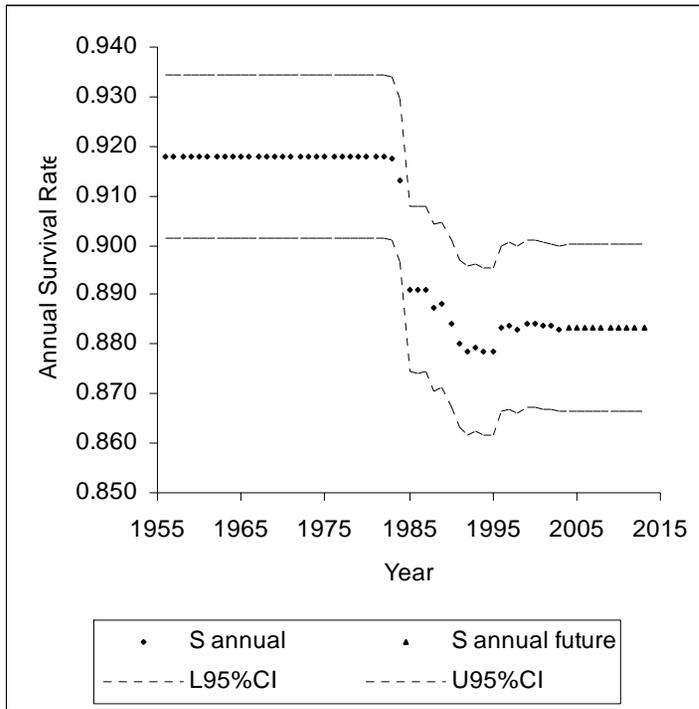


Figure 3.1 (Continued).

Linear recruitment, equal weighting

Linear recruitment, unequal weighting

S(t)



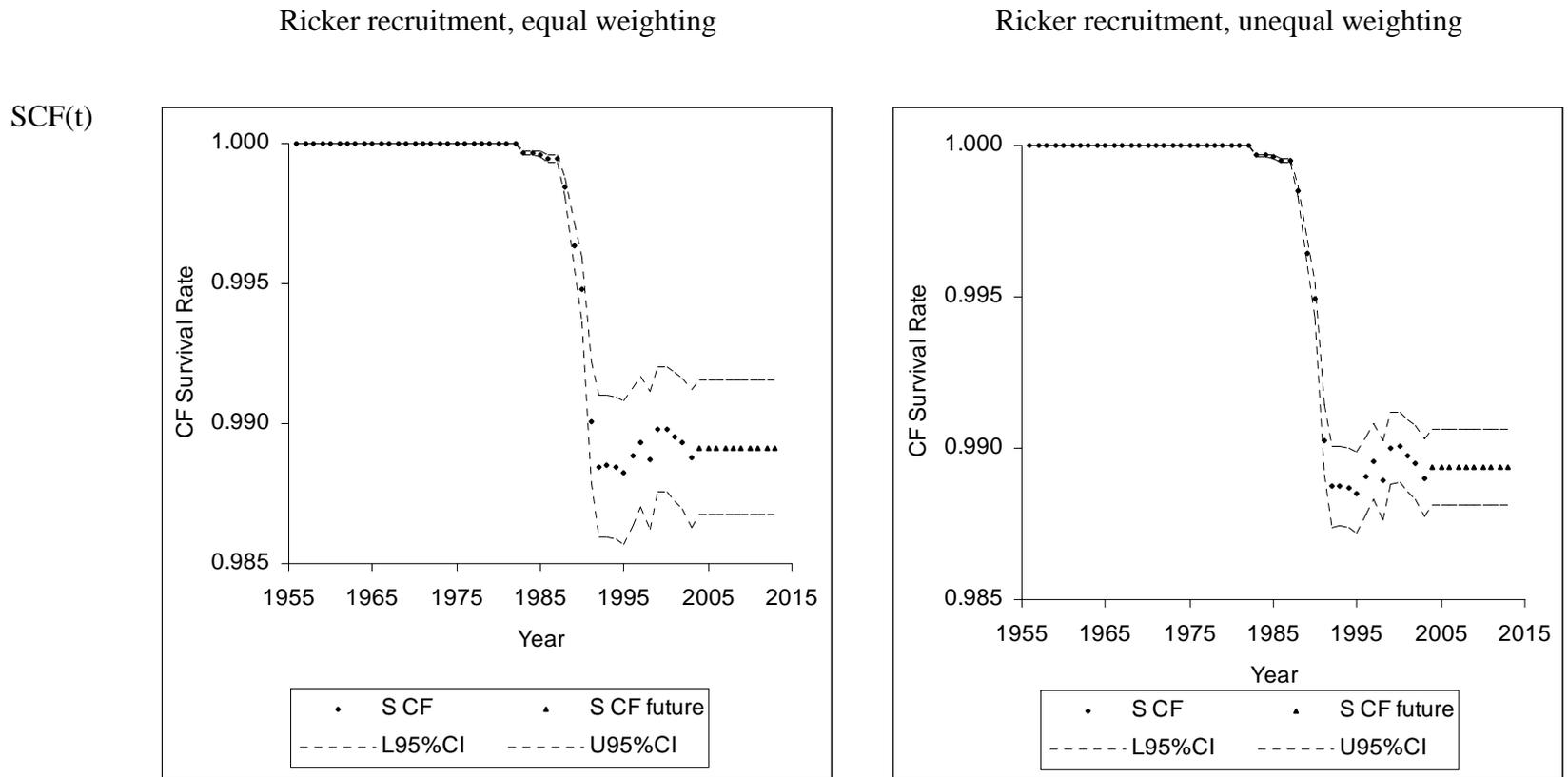


Figure 3.2. Survival harvest estimates for the Ricker recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013. Predictions assumed that harvest continued at its current level.

Figure 3.2 (Continued).

Ricker recruitment, equal weighting

Ricker recruitment, unequal weighting

SAF(t)

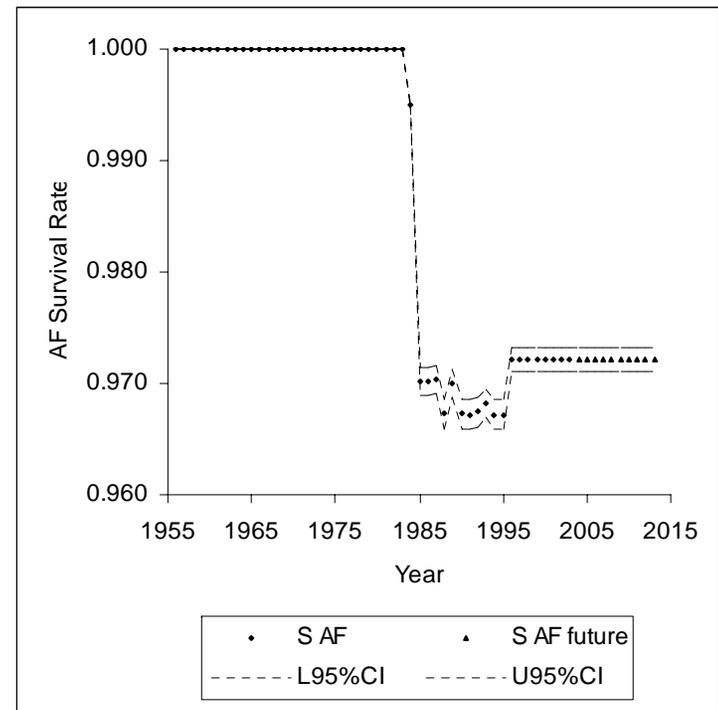
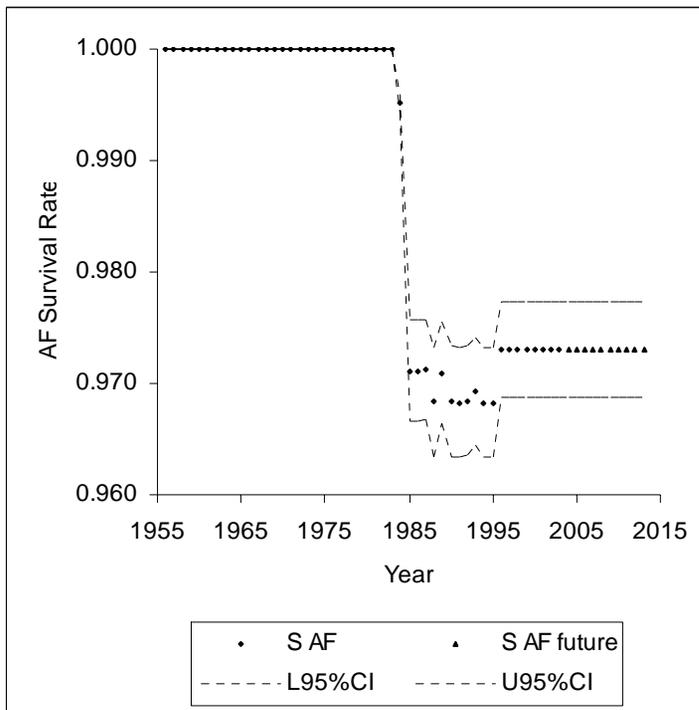
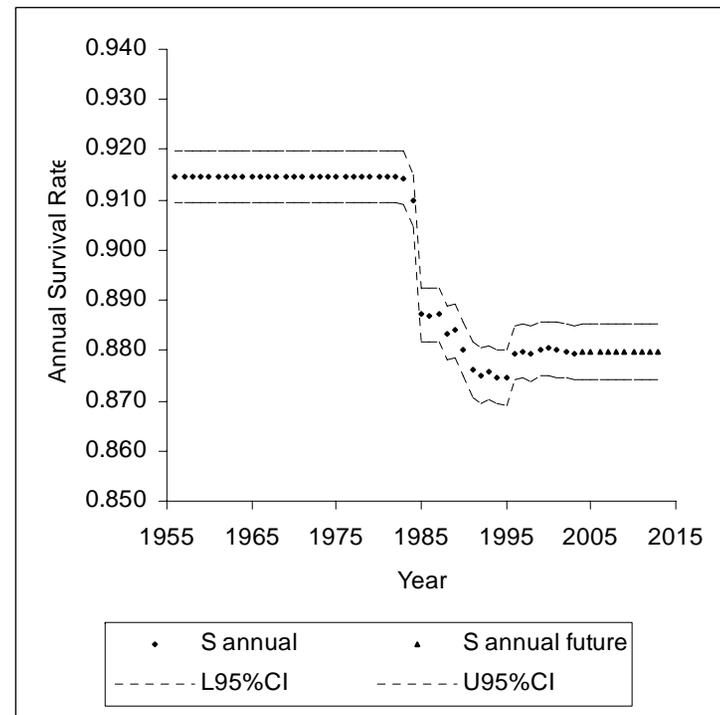
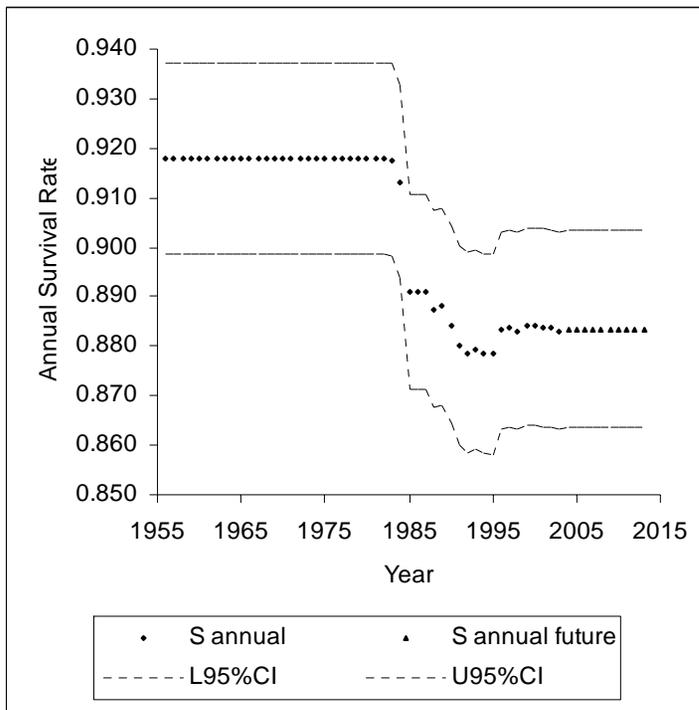


Figure 3.2 (Continued).

Ricker recruitment, equal weighting

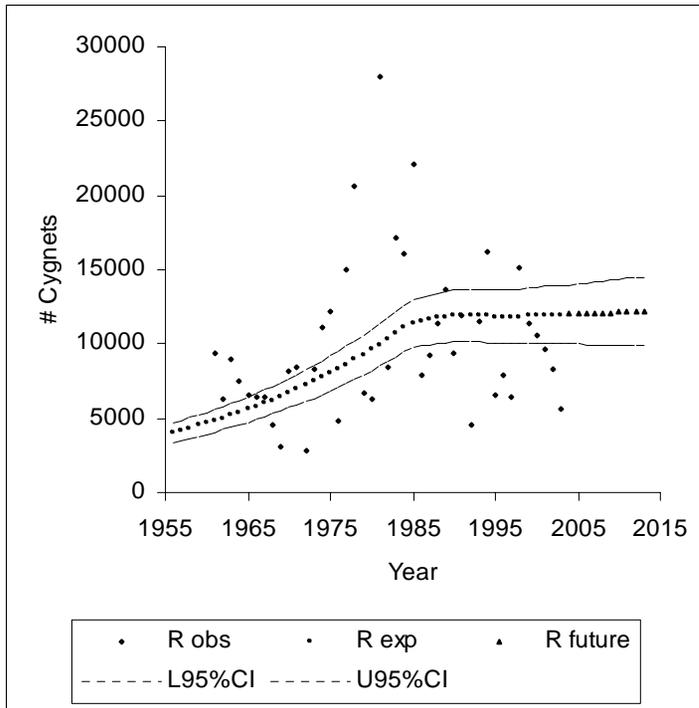
Ricker recruitment, unequal weighting

S(t)



R(t)

Linear recruitment, equal weighting



Linear recruitment, unequal weighting

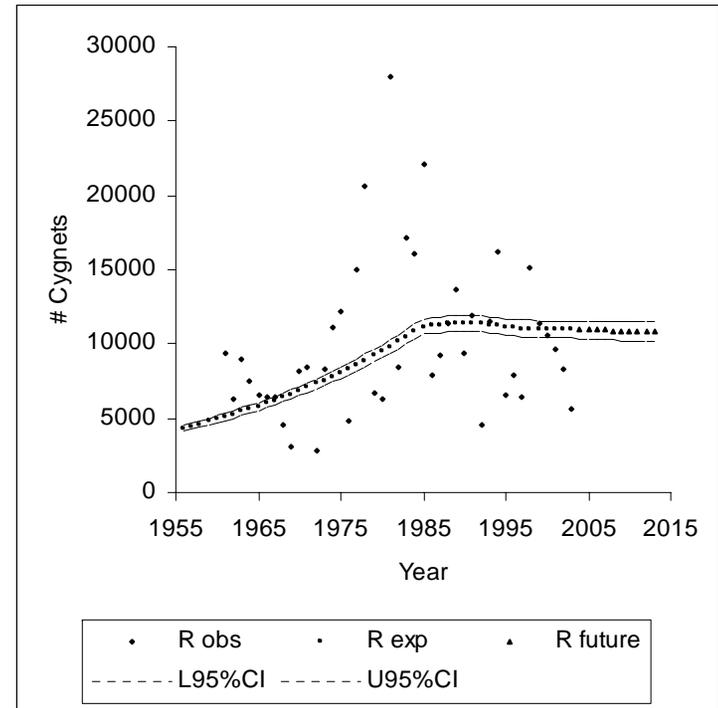


Figure 3.3. Recruitment estimates for the linear recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013. Predictions assumed that harvest continued at its current level.

Figure 3.3 (Continued).

Linear recruitment, equal weighting

Linear recruitment, unequal weighting

Recruitment Model

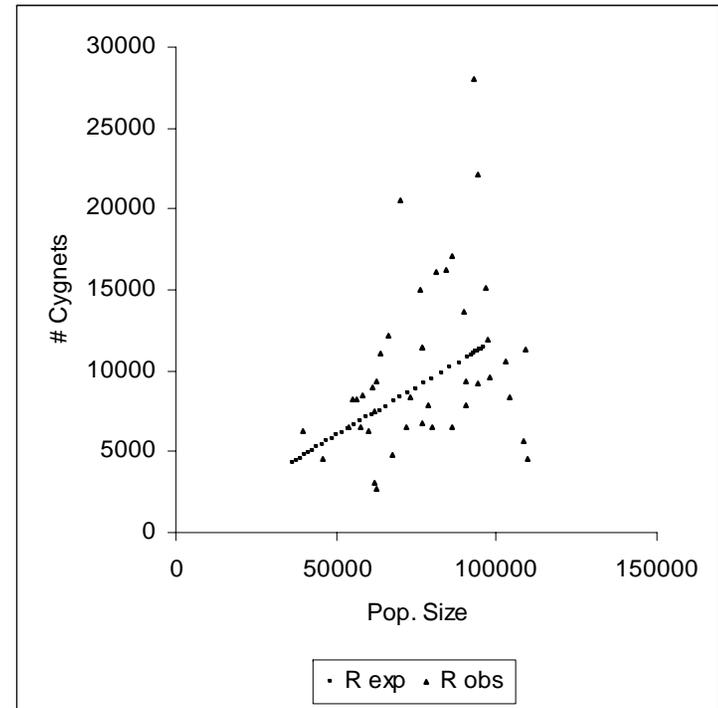
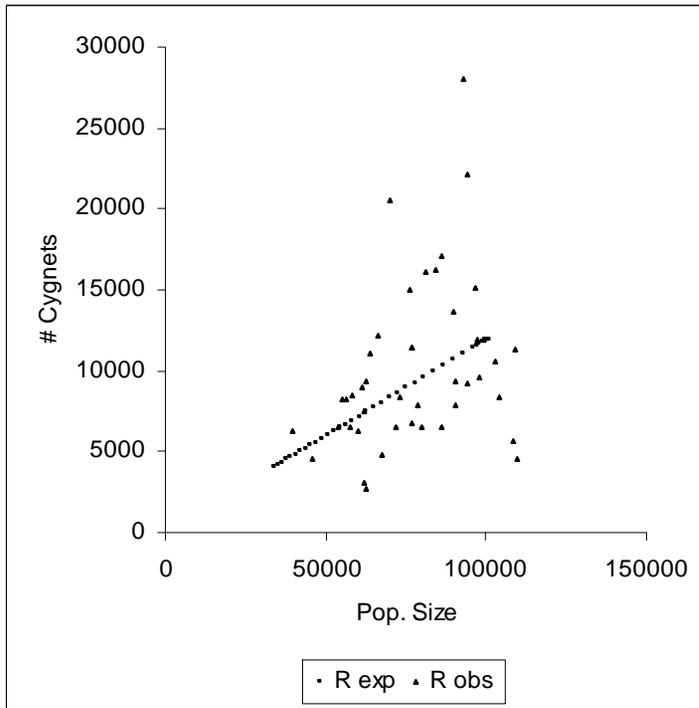
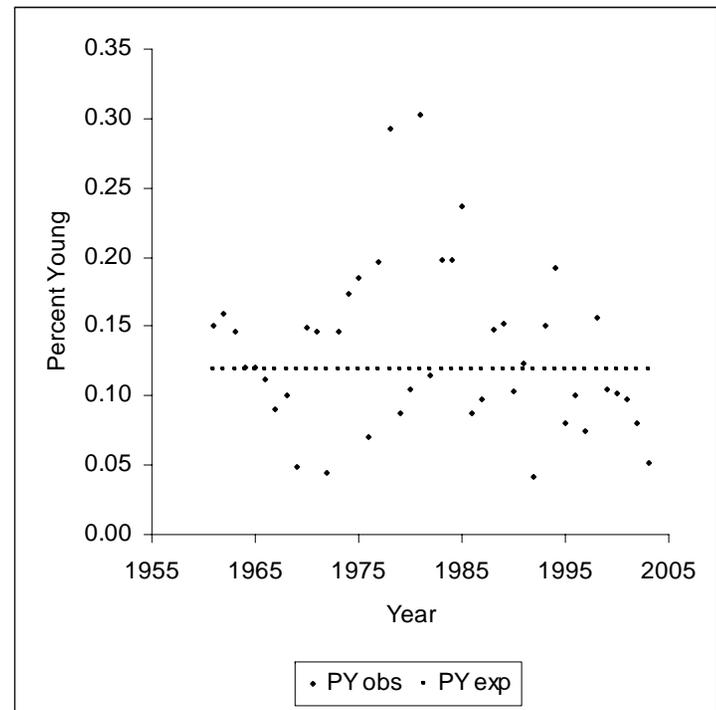
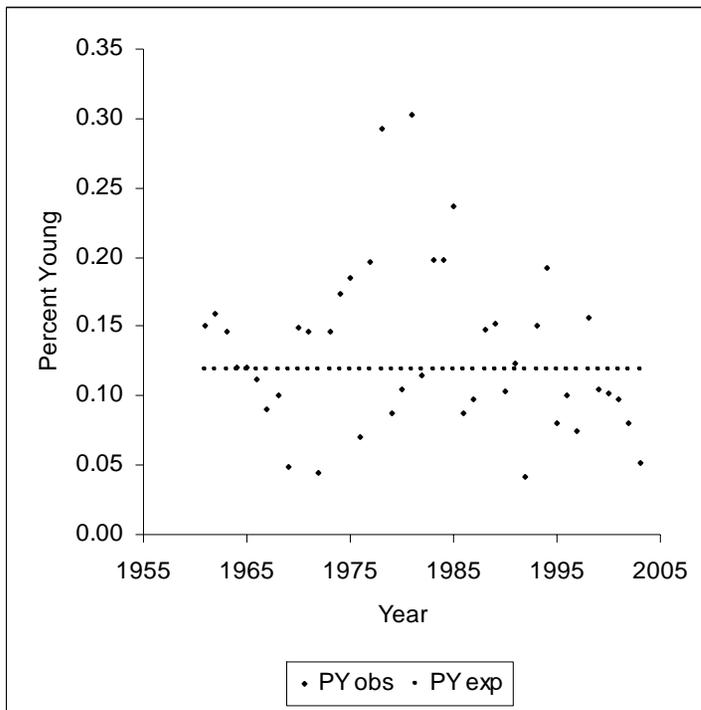


Figure 3.3 (Continued).

Linear recruitment, equal weighting

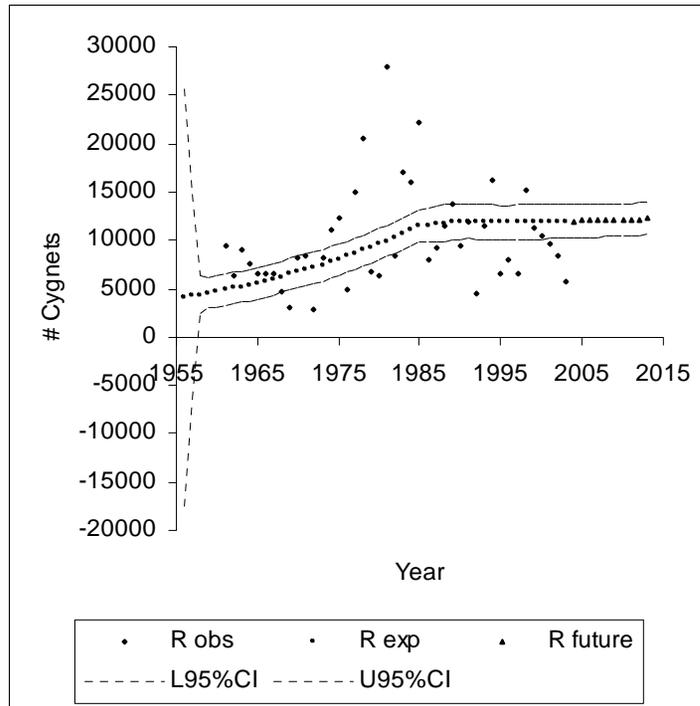
Linear recruitment, unequal weighting

PY



R(t)

Ricker recruitment, equal weighting



Ricker recruitment, unequal weighting

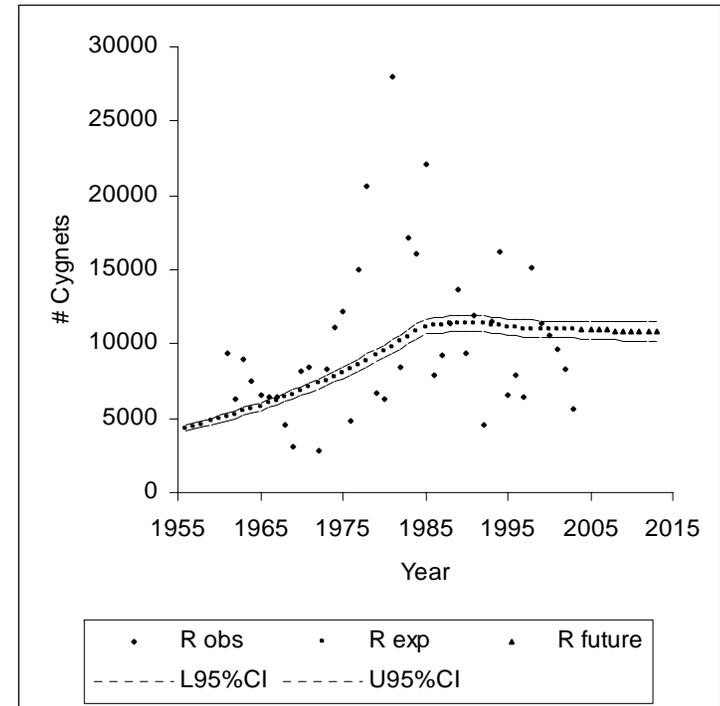


Figure 3.4. Recruitment estimates for the Ricker recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013. Predictions assumed that harvest continued at its current level.

Figure 3.4 (Continued).

Ricker recruitment, equal weighting

Ricker recruitment, unequal weighting

Recruitment Model

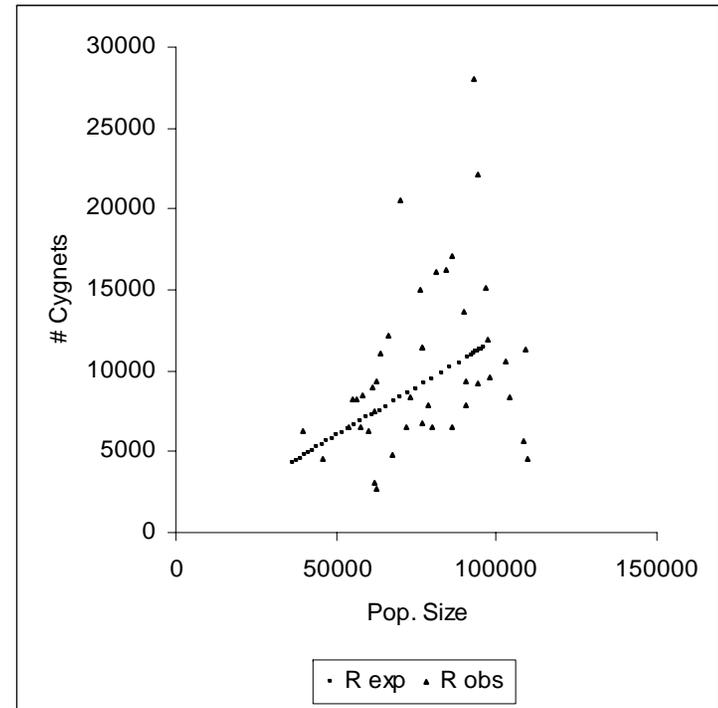
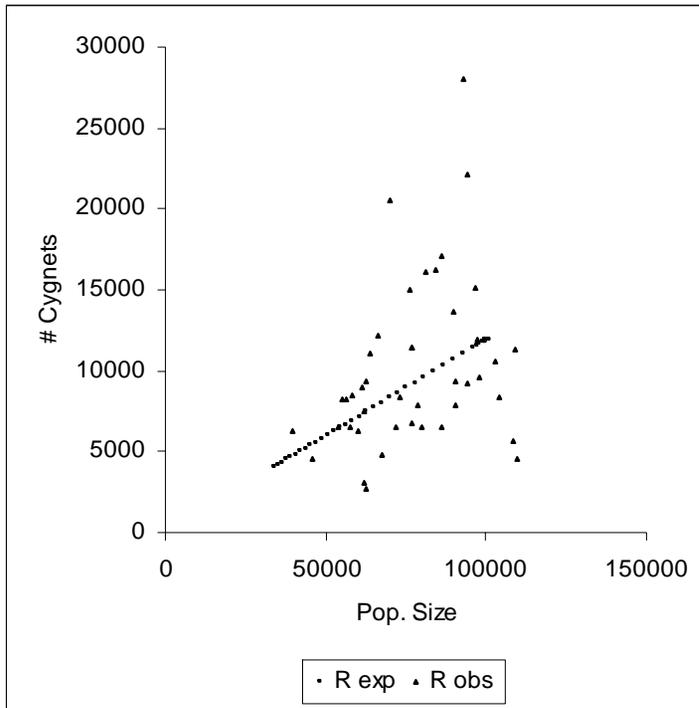
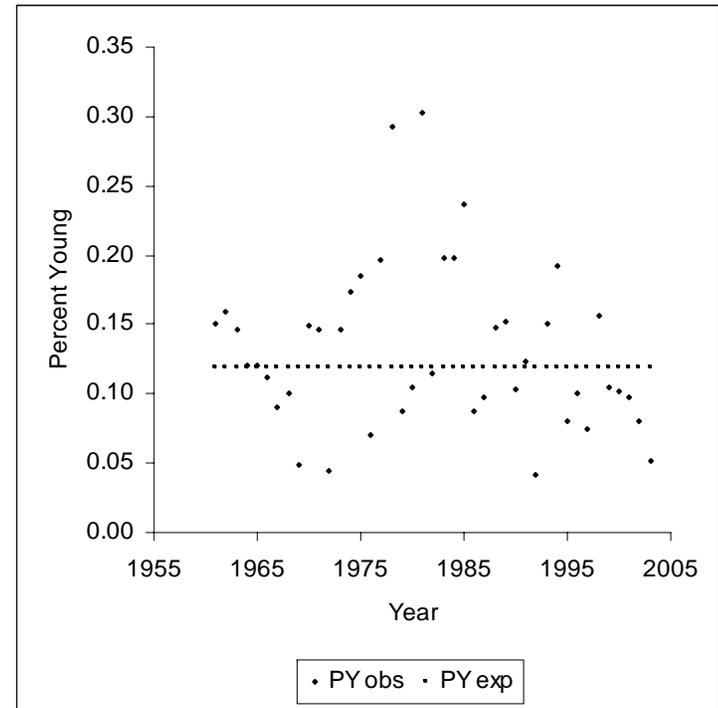
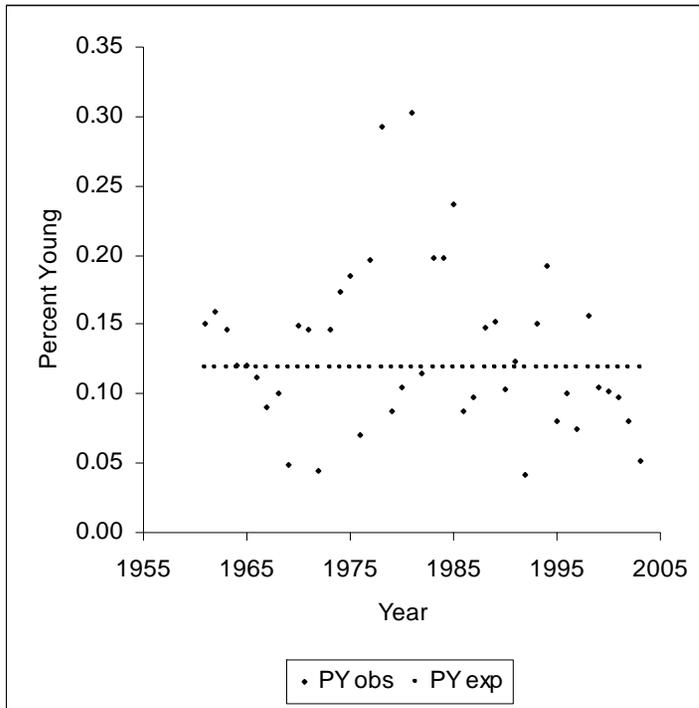


Figure 3.4 (Continued).

Ricker recruitment, equal weighting

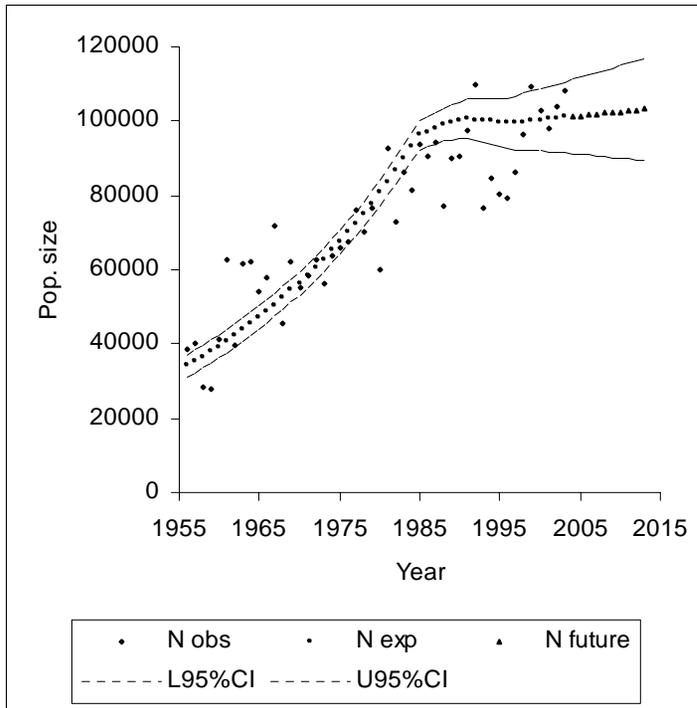
Ricker recruitment, unequal weighting

PY



N(t)

Linear recruitment, equal weighting



Linear recruitment, unequal weighting

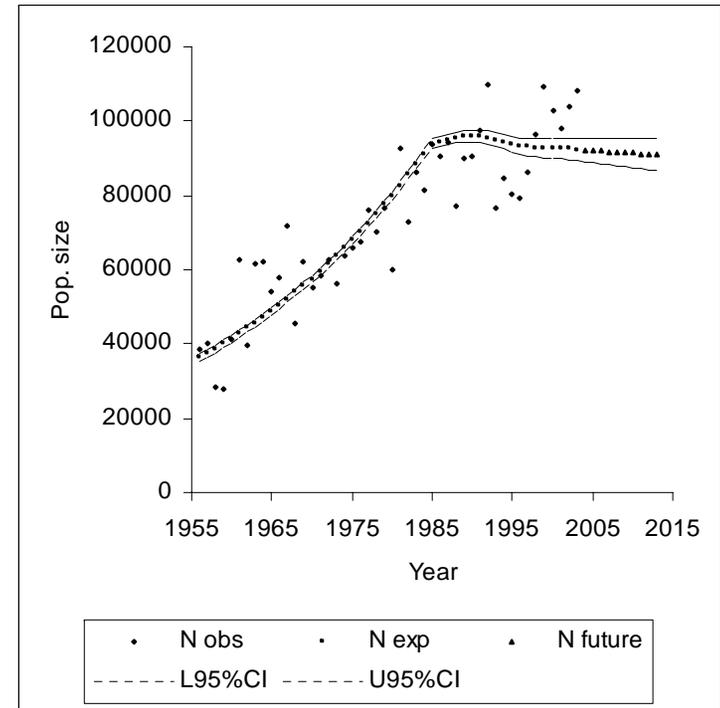


Figure 3.5. Population and harvest estimates for the linear recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013. Predictions assumed that harvest continued at its current level.

Figure 3.5 (Continued).

Linear recruitment, equal weighting

Linear recruitment, unequal weighting

HCF(t)

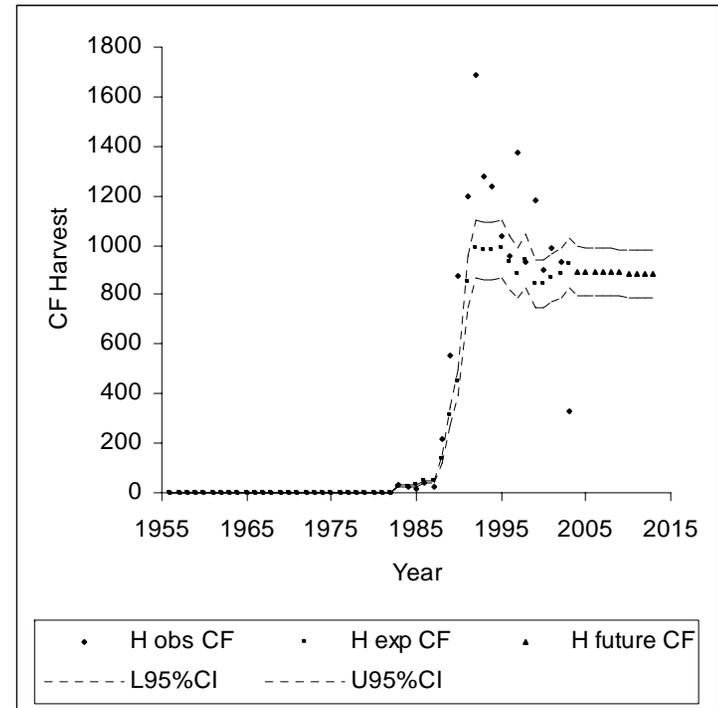
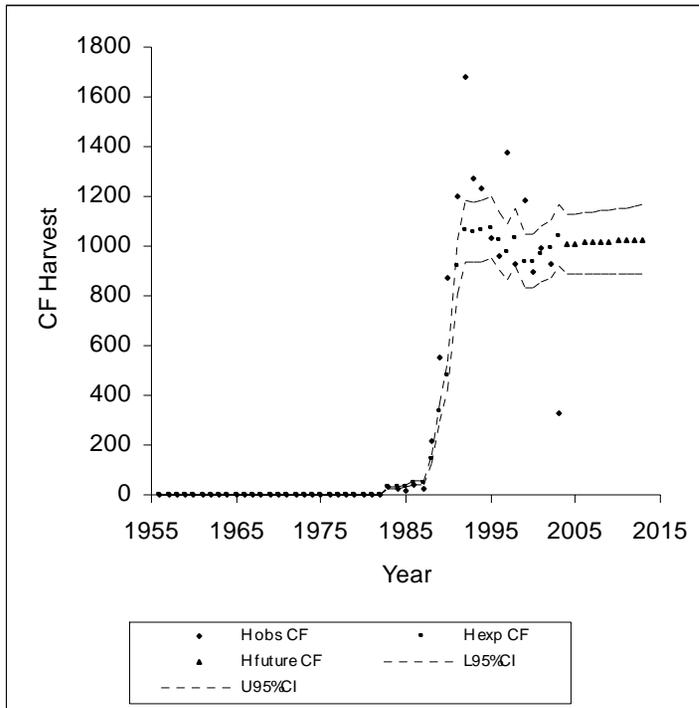
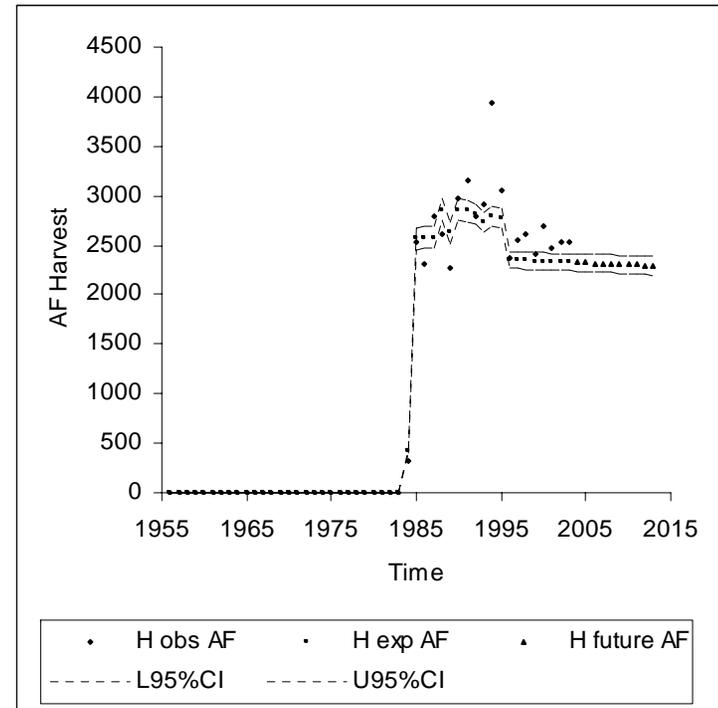
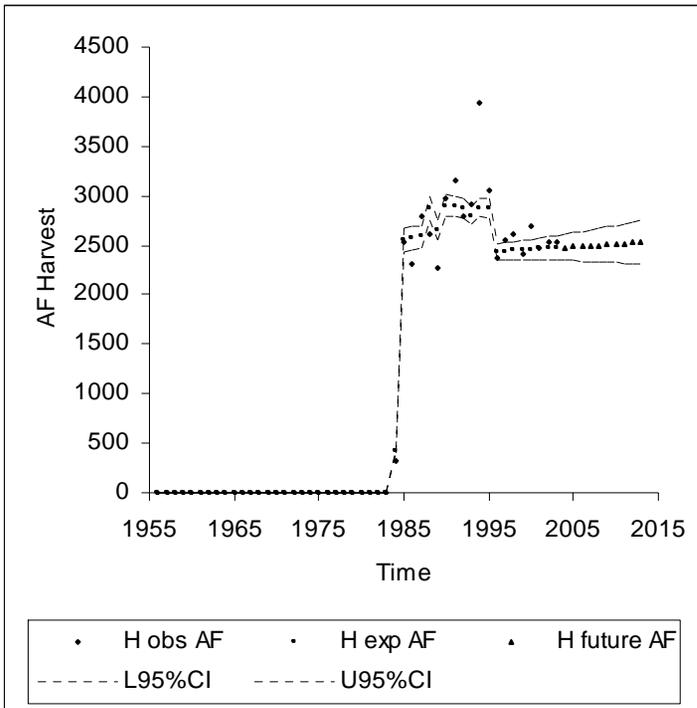


Figure 3.5 (Continued).

Linear recruitment, equal weighting

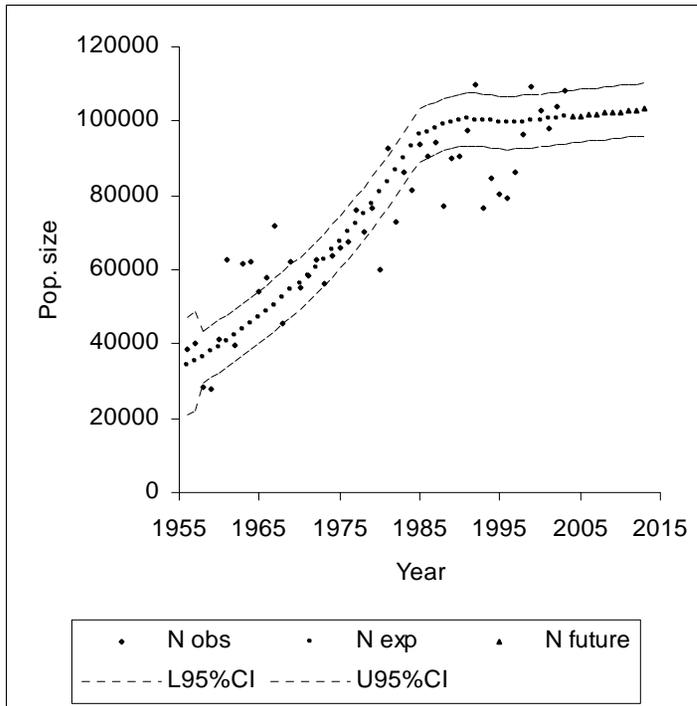
Linear recruitment, unequal weighting

HAF(t)



N(t)

Ricker recruitment, equal weighting



Ricker recruitment, unequal weighting

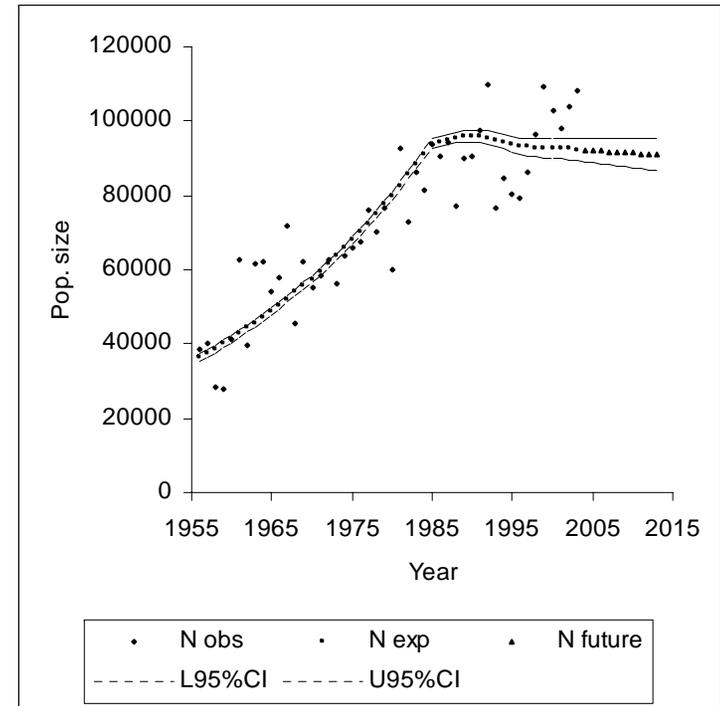


Figure 3.6. Population and harvest estimates for the Ricker recruitment function for North American Eastern Population tundra swans at 2 data set weights, with 10-year predictions and 95% confidence intervals, 1956–2013. Predictions assumed that harvest continued at its current level.

Figure 3.6 (Continued).

Ricker recruitment, equal weighting

Ricker recruitment, unequal weighting

HCF(t)

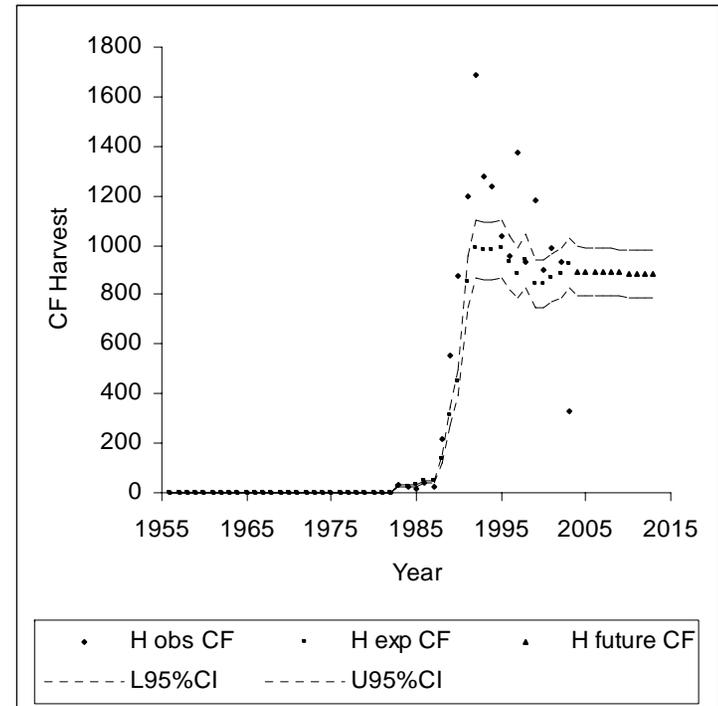
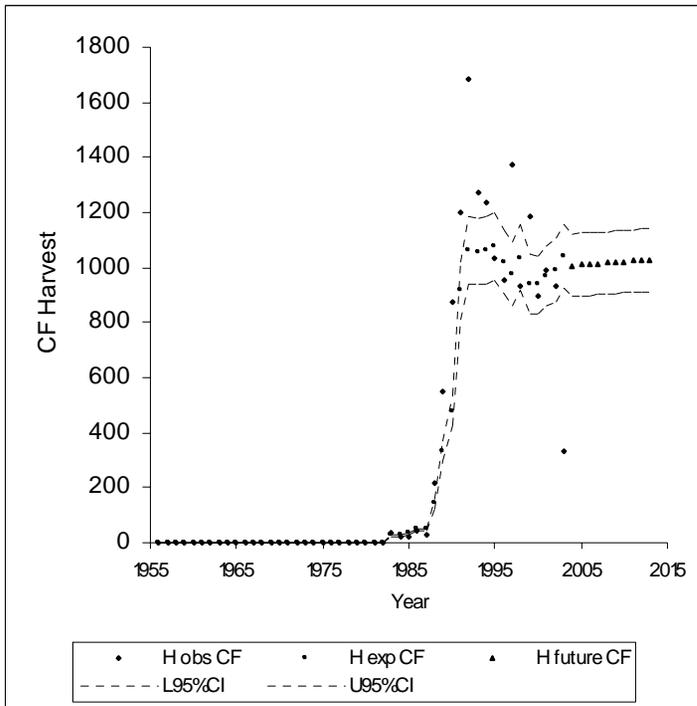
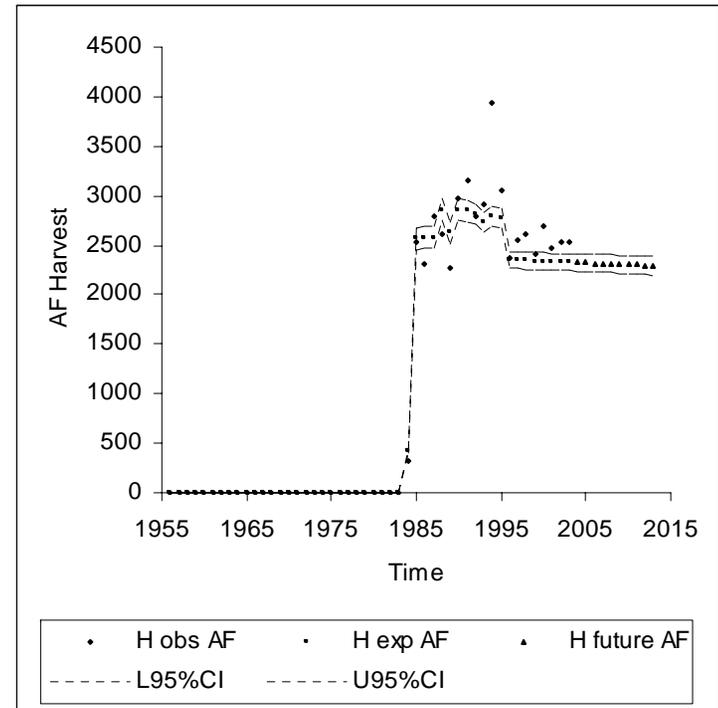
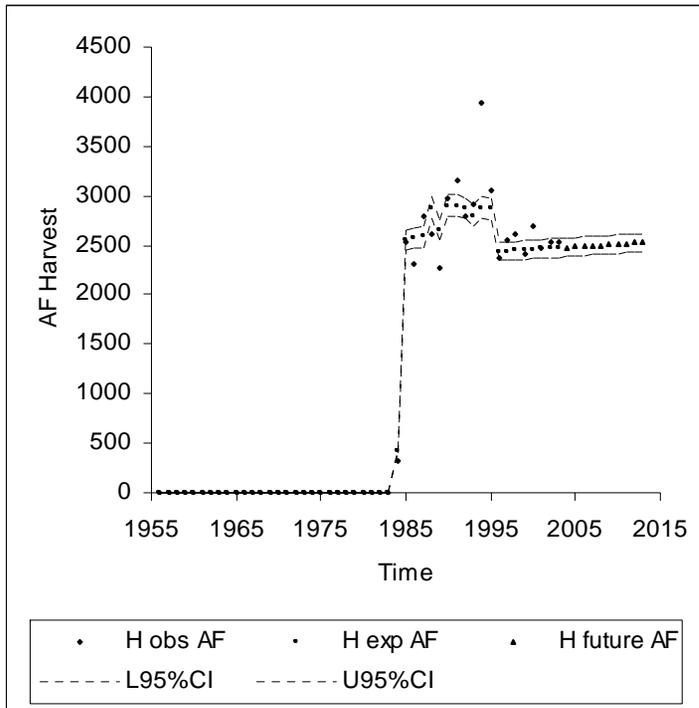


Figure 3.6 (Continued).

Ricker recruitment, equal weighting

Ricker recruitment, unequal weighting

HAF(t)



Model Selection

All models fit the data well. AIC values from models with higher weight on MWI and PY data were about 10 times lower than AIC values from models with equal weights on all data sets. This indicated a significantly better fit for models with higher weight on MWI and PY. Differences in AIC values between recruitment models with the same weighting schemes were 2 units, due to the extra parameter necessary for the Ricker recruitment model. This indicated that the extra parameter did not measurably improve fit. Density dependence was not evident in recruitment data, models with linear recruitment had (slightly) lower AIC values, and the model of linear recruitment was more parsimonious. Therefore, the linear model was more appropriate for estimation. Unequal weights resulted in slightly better fit of expected values to observed data and also increased precision of estimates. Therefore, the linear model with unequal weighting was the most appropriate model of EP tundra swan population dynamics.

Sensitivity Analyses

Starting conditions

Parameter estimates were insensitive to changes in starting conditions for all parameters (Table 3.3). Point estimates of initial population size, α , q_1 , q_2 , and non-hunting mortality did not change when the calculated “reasonable” starting value was decreased or increased up to 10 times.

Table 3.3. Sensitivity of North American Eastern Population tundra swan model parameter estimates to starting conditions, using linear recruitment and unequal data set weighting, 1956–2003. Results compared when starting values were multiplied by 0.1, 0.5, 2, and 10.

Parameter	Starting value [†]	Estimate	Estimate when starting value multiplied by:			
			0.1	0.5	2	10
$N(1956)$	32,860	36,316	36,316	36,316	36,316	36,316
α	0.13000	0.11880	0.11880	0.11880	0.11880	²
$q1$	0.00670	0.00317	0.00317	0.00317	0.00317	0.00317
$q2$	0.00670	0.01218	0.01218	0.01218	0.01218	0.01218
$S_{nh}(\cdot)$	0.81718	0.91471	0.91471	0.91471	0.91471 ³	²

[†] Calculated from data.

² Not applicable.

³ Starting value 0.95, because true α and $S_{nh}(\cdot)$ should never exceed 1.0.

Weighting

Results were slightly sensitive to data set weights (Table 3.4). As weight was increased on a data set, expected values were forced to lie closer to the observed values of that data set. Therefore, expected values were closer to observed values of the data set with higher weight. Higher weights on MWI and PY produced more logical and consistent results, whereas higher weights on Atlantic Flyway and Central Flyway harvest estimates produced unlikely population size estimates. Weighting factors of 100 were unreasonable for all data sets because aberrant population growth rates and harvests were predicted at this weighting factor. However, with reasonable weight values on MWI and/or PY (weight=5,10), results were very consistent, with population growth after 10 years differing by no more than 0.03 and change in harvest varying by no more than 2%.

Table 3.4. Comparison of predicted population growth rates (λ ¹) and average harvest (\bar{H} ²) of North American Eastern Population tundra swans from a population model with linear recruitment. Model predictions made for 13 sets of data set weighting factors. Relative weight for each data set in the objective function ranged from 1–100.

Mid-Winter Index	Relative weight on data set			λ	\bar{H}
	Central Flyway harvest	Atlantic Flyway harvest	% Young in Production Survey		
1	1	1	1	1.02	3,521
5	1	1	5	0.99	3,272
10	1	1	10	0.99	3,199
100	1	1	100	1.05	2,450
1	5	5	1	1.08	3,847
1	10	10	1	1.09	3,909
1	100	100	1	1.11	4,016
5	1	1	1	0.99	3,271
10	1	1	1	0.99	3,199
100	1	1	1	1.06	2,394
1	1	1	5	1.02	3,524
1	1	1	10	1.02	3,528
1	1	1	100	1.04	3,607

¹ $\lambda = N(2013)/N(2003)$

² \bar{H} = average Central and Atlantic Flyway harvest for 2004–2013.

Model Validation

Although I selected the linear model with unequal weights for EP tundra swans, I am presenting both linear and Ricker recruitment models with unequal weights in this model validation because density-dependent control on WP tundra swans has been suggested in recent years (Aldrich et al. 2004).

Survival

Survival rate estimates were similar between both sets of recruitment models (Figure 3.7). Survival during the Alaska subsistence hunting period was estimated at about 0.86 for all years. The rate was estimated as constant over time of lack of data on the amount of subsistence harvest prior to the surveys. Therefore, this survival rate estimate was not informative. Survival during the Pacific Flyway hunting period was estimated as 1.0 in the years prior to implementation of the hunting season and

declined as the number of permits increased, to the current rate of about 0.975. Non-hunting survival rate was estimated at about 0.85, and overall annual survival rate, the product of the 2 hunting season survival rates and the non-hunting survival rate, ranged from about 0.75 in 1949 to 0.73 in recent years.

Recruitment

As with EP data, no density-dependent pattern or structure was apparent in the recruitment data (Figure 3.8). Predicted recruitment amount and PY were somewhat sensitive to recruitment function.

Estimation

When comparing the linear recruitment model with the Ricker model, the linear model predicted: larger population sizes, larger harvests, greater rate of increase of population size, greater rates of increase in subsistence harvest, and greater rate of increase in sport harvest (Figure 3.9). Parameter estimates were precise, with cv's ranging from 0.008 to 0.082. Precision of population size and harvest estimates decreased as predictions were made farther out into the future, as shown by the flared confidence band around predictions beyond 2003.

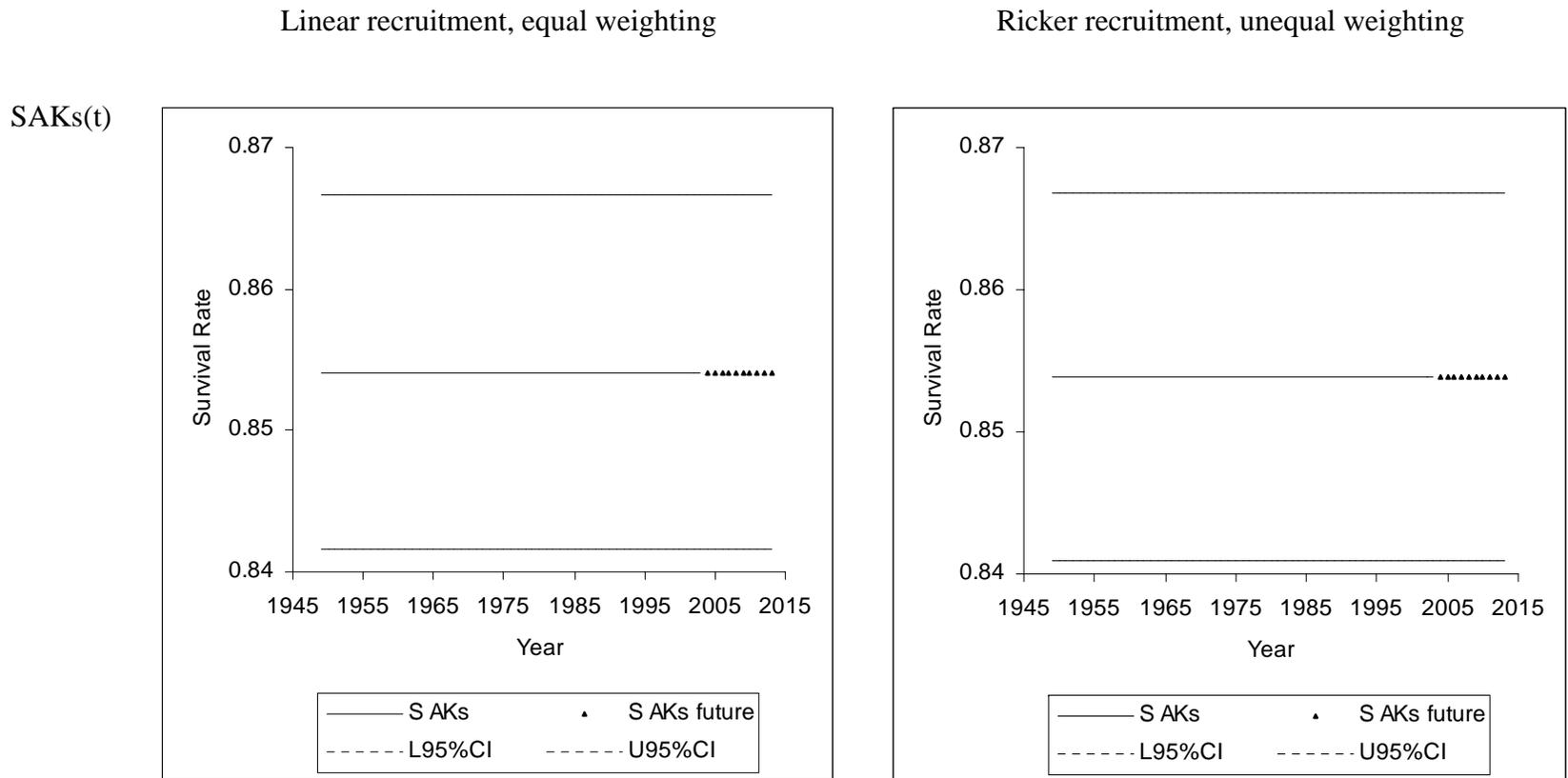


Figure 3.7. Survival estimates for North American Western Population tundra swans for 2 recruitment functions with 10-year predictions and 95% confidence intervals, 1949–2013. Predictions assumed that harvest continued at its current level.

Figure 3.7 (Continued).

Linear recruitment, equal weighting

Ricker recruitment, unequal weighting

SPF(t)

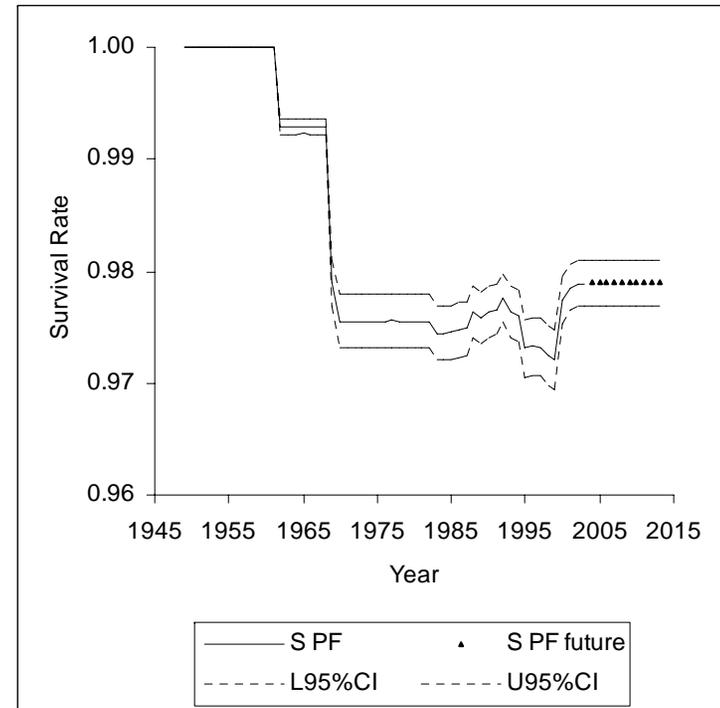
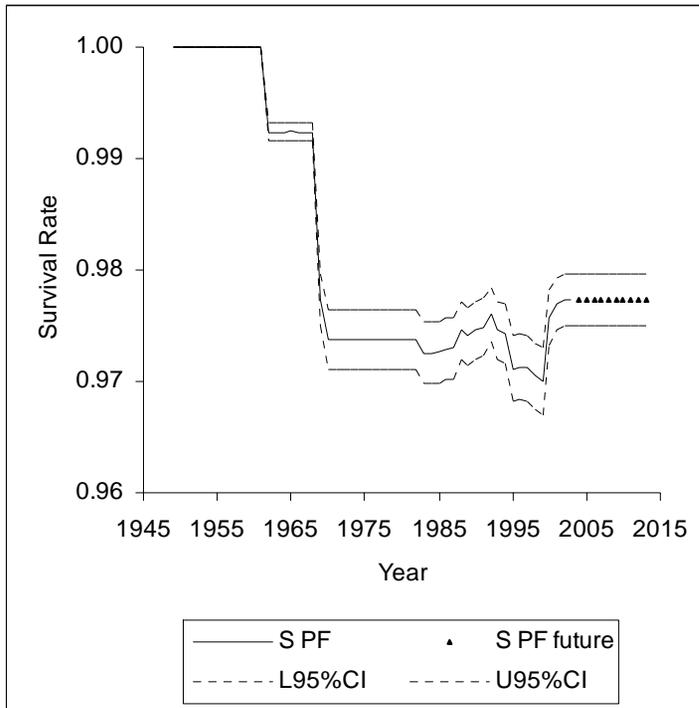


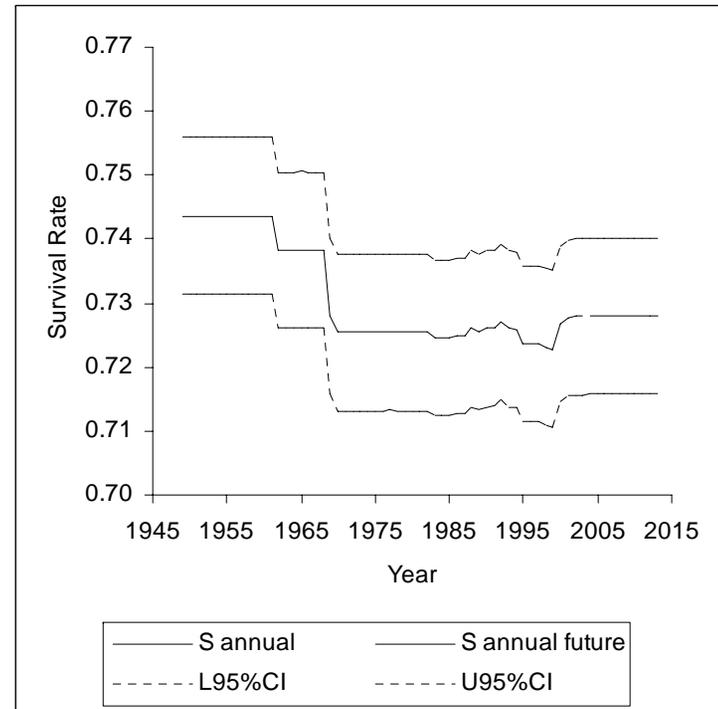
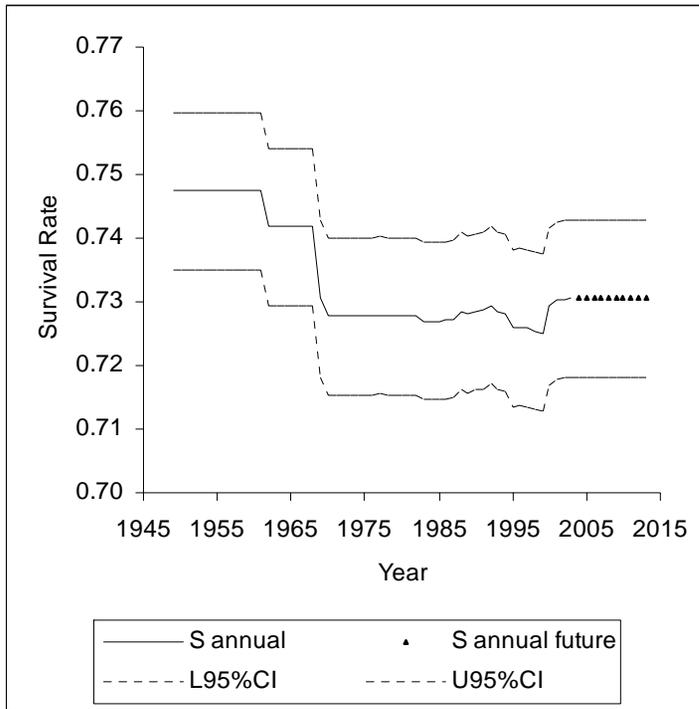
Figure 3.7 (Continued).

Linear recruitment, equal weighting

Ricker recruitment, unequal weighting

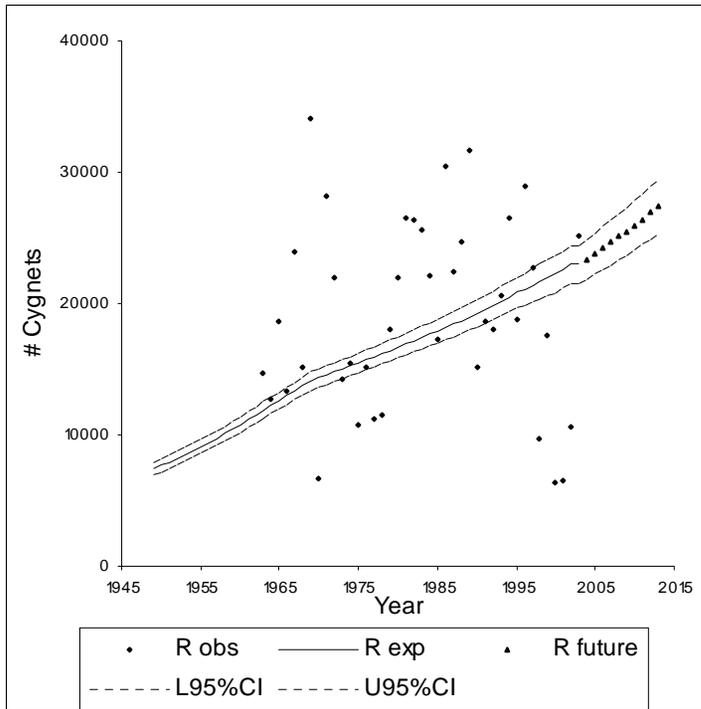
S(t)

140



R(t)

Linear recruitment, equal weighting



Ricker recruitment, unequal weighting

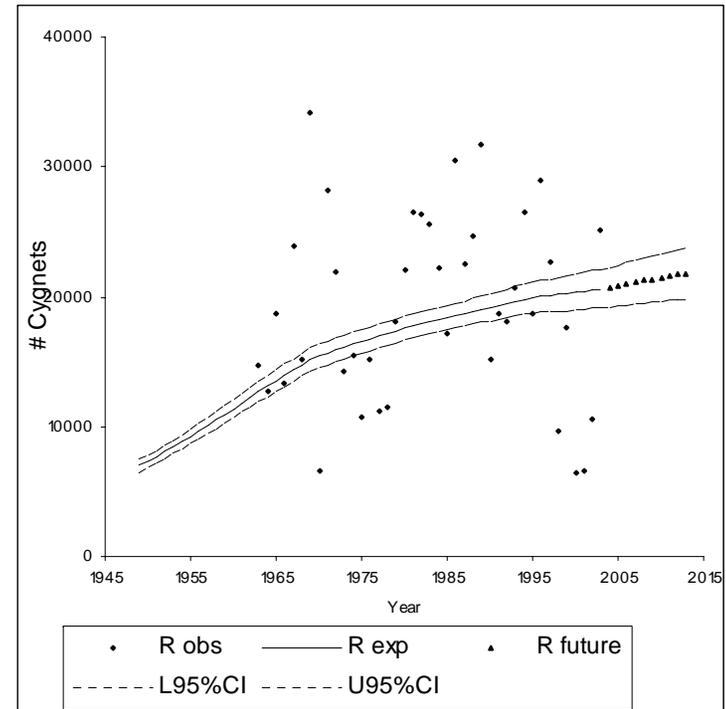


Figure 3.8. Recruitment estimates for North American Western Population tundra swans for 2 recruitment functions with 10-year predictions and 95% confidence intervals, 1949–2013. Predictions assumed that harvest continued at its current level.

Figure 3.8 (Continued).

Linear recruitment, equal weighting

Ricker recruitment, unequal weighting

Recruitment
Model

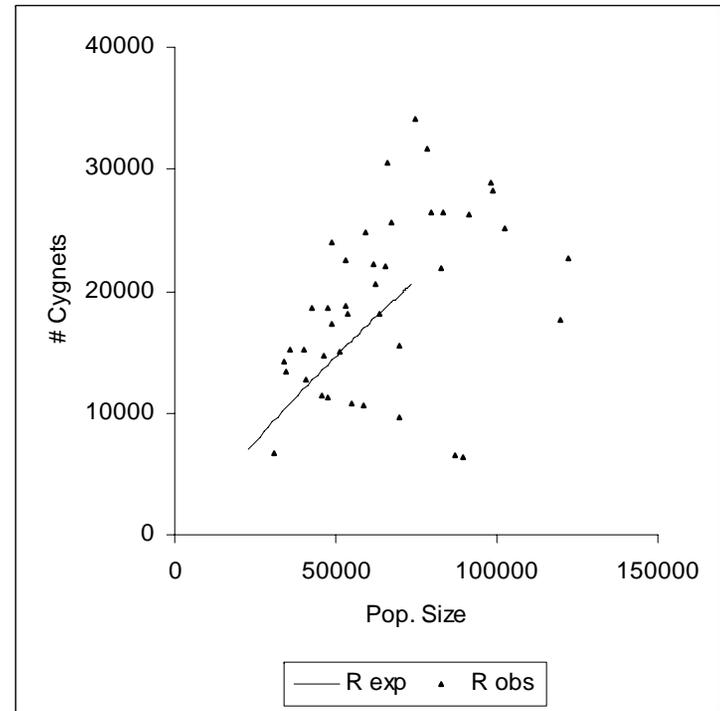
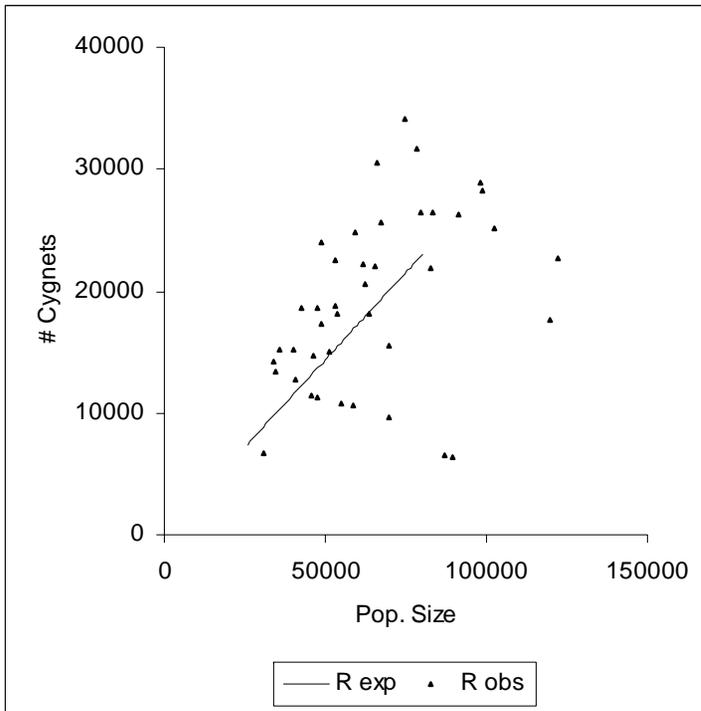
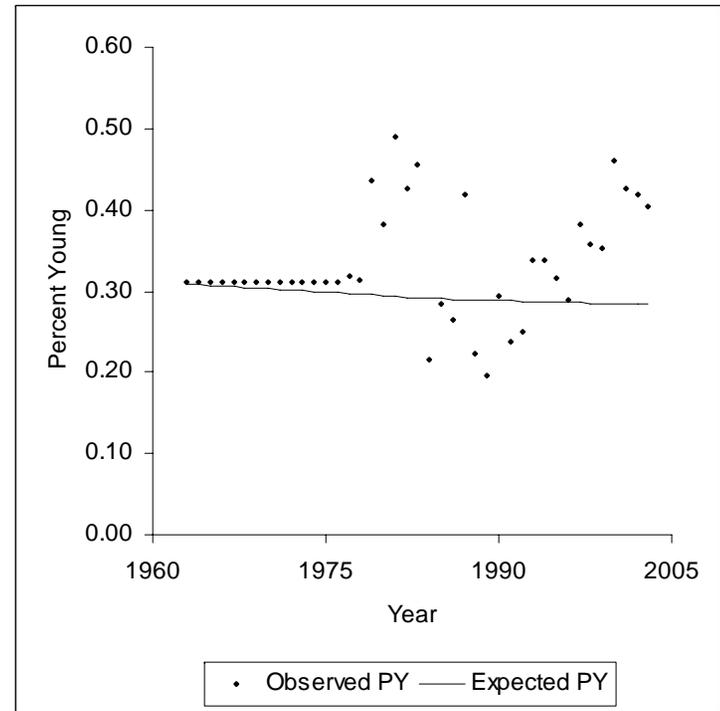
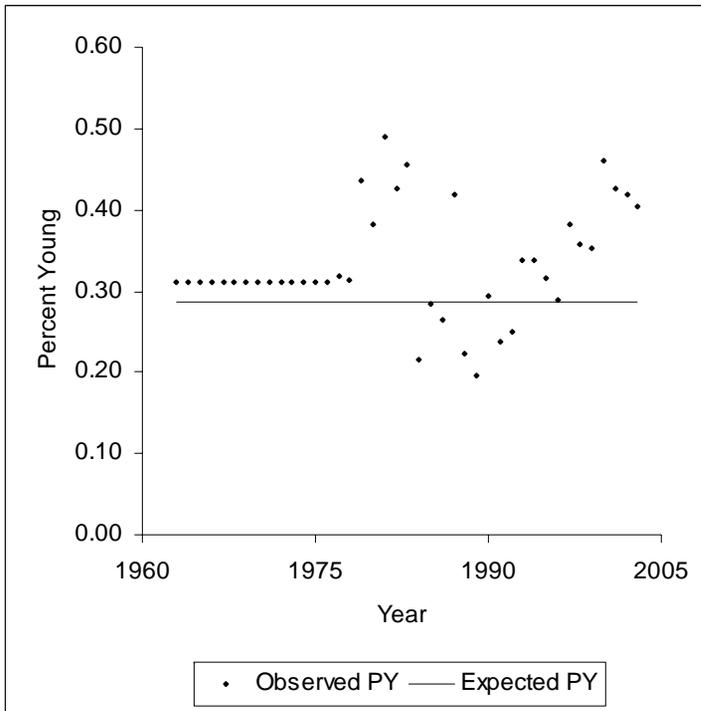


Figure 3.8 (Continued).

Linear recruitment, equal weighting

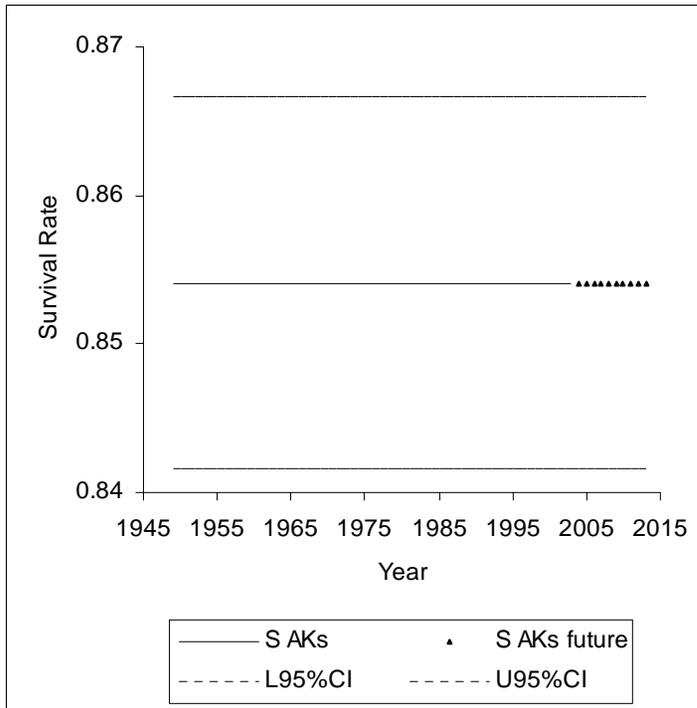
Ricker recruitment, unequal weighting

PY



N(t)

Linear recruitment, equal weighting



Ricker recruitment, unequal weighting

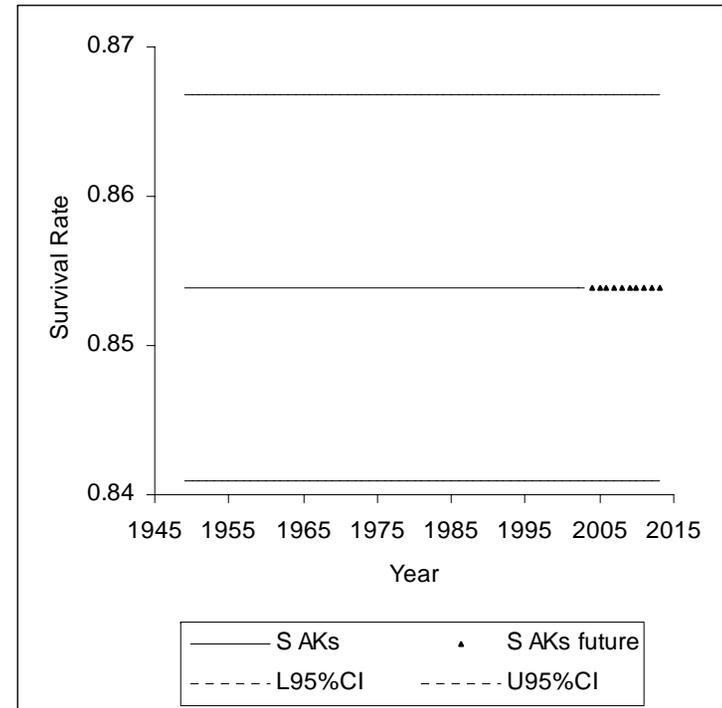


Figure 3.9. Population and harvest estimates for WP tundra swans for 2 recruitment functions with 10-year predictions and 95% confidence intervals. Predictions assumed that harvest continued at its current level.

Figure 3.9 (Continued).

Linear recruitment, equal weighting

Ricker recruitment, unequal weighting

HAKs(t)

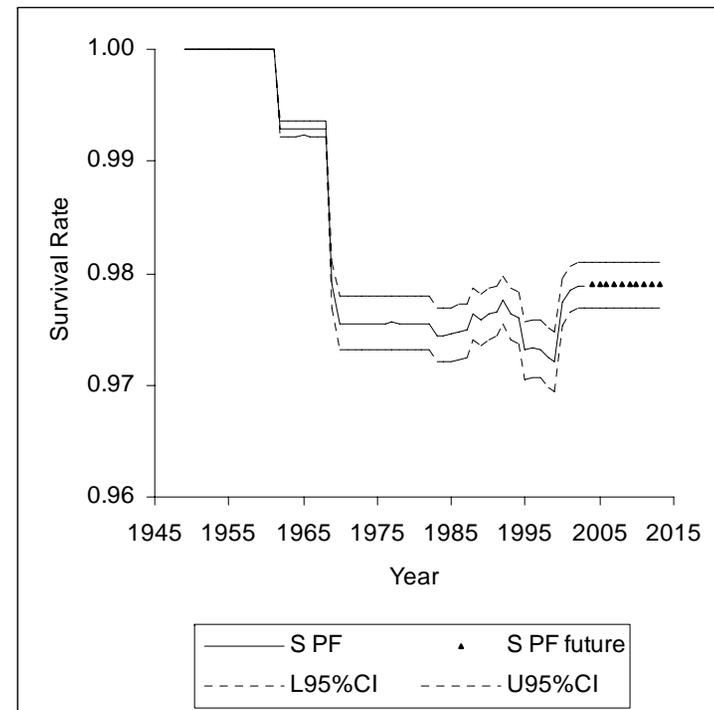
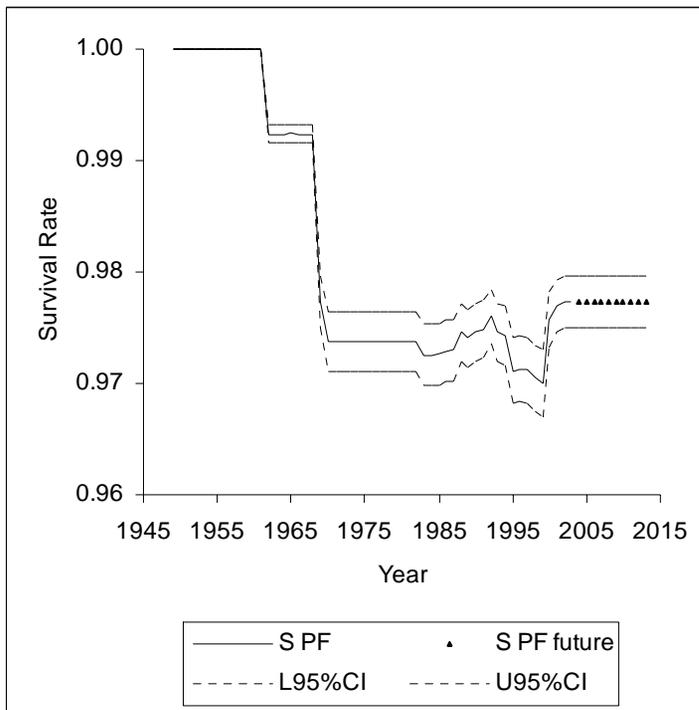
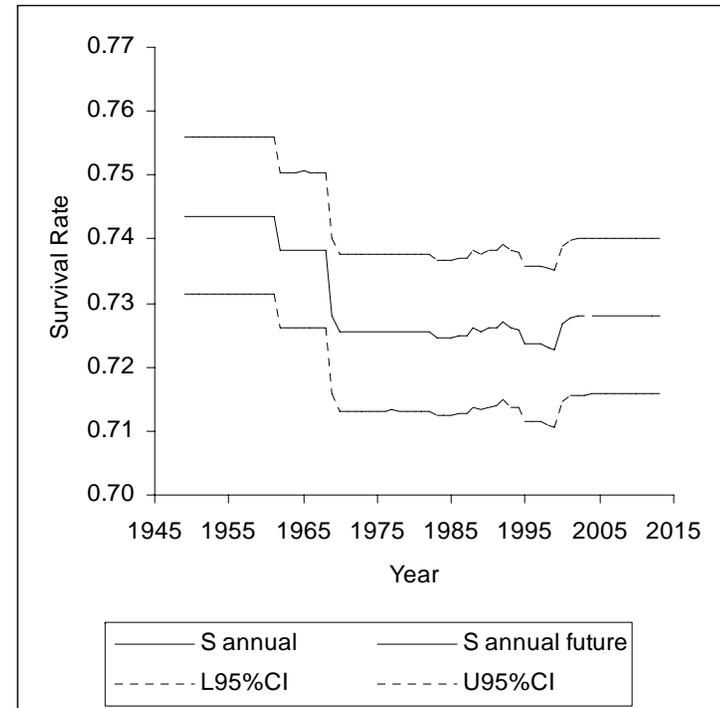
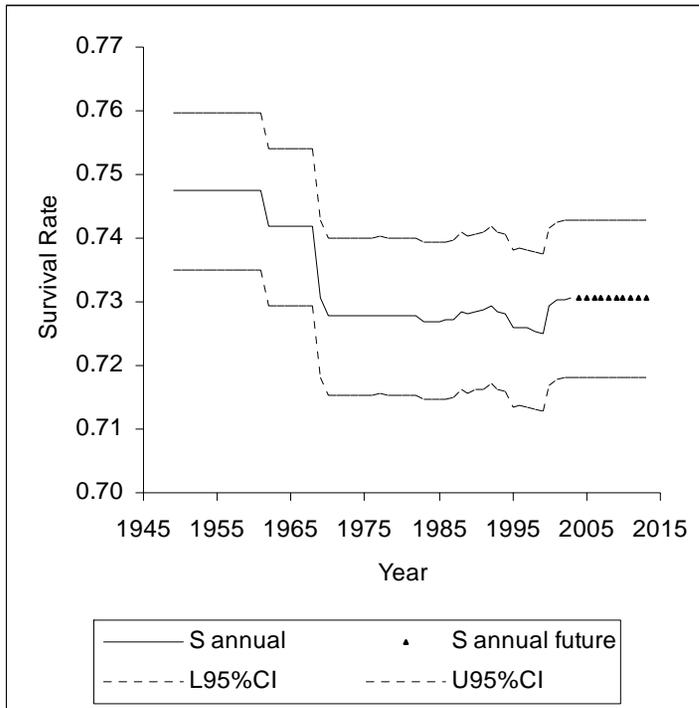


Figure 3.9 (Continued).

Linear recruitment, equal weighting

Ricker recruitment, unequal weighting

HPF(t)



Model predictions

All of the harvest regimes resulted in population sizes above the population goal of a 3-year average of 80,000 swans (Table 3.5). The same number of permits added to either Central Flyway or Atlantic Flyway harvest did not predict the same reported harvest, because hunters are slightly more successful in the Atlantic Flyway. Average population size and 10-year growth rate decreased as the number of hunting permits increased. Population size was predicted to increase by 34% per year if hunting ceased. This seems high but actually follows the trajectory of the population prior to commencement of a sport harvest season. These trends together suggest that sport harvest has and will likely continue to impact on EP tundra swan population dynamics.

Table 3.5. Predictions of North American Eastern Population tundra swan population size and harvest in the Atlantic and Central Flyways, using the linear recruitment model with unequal weights, 2004–2013.

Number of annual permits for next 10 years			\bar{N} ¹	λ ²	\bar{H} ³	ΔH (%) ⁴
Atlantic Flyway	Central Flyway	Total				
0	0	0	119,983	1.34	0	-100
2,800	1,750	4,550	104,518	1.15	1,746	-46
5,600 ⁵	3,500 ⁵	9,100	91,092	0.99	3,199	-2
5,900	3,500	9,400	90,506	0.98	3,260	0
5,600	3,800	9,400	90,125	0.97	3,301	+1
5,900	3,800	9,700	89,546	0.97	3,662	+3

¹ λ = 3-year average of predicted population size 8, 9, and 10-year predictions (i.e., $(N(2011)+N(2012)+N(2013))/3$).

² 10-year population growth rate (i.e., $N(2013)/N(2003)$).

³ Average annual predicted harvest for 2004–2013.

⁴ Percent change in average annual predicted harvest from predicted 2003 harvest.

⁵ Current year permit levels.

DISCUSSION

Using MWI, PY, and harvest data, this model of EP tundra swan population dynamics provided reasonable, precise predictions of population size, harvest, and survival. Population size predictions were sensitive to the number of hunting permits issued each year. Model results were fairly insensitive to starting values and to the form of the recruitment function (either linear density independence or Ricker density dependence). This result was not surprising, given the lack of evidence of density dependence in the recruitment data. Based on parsimony, AIC, and model fit, the model with linear recruitment was selected as the most appropriate for population predictions. However, the data and model should be re-examined periodically for evidence of density dependence. If EP tundra swans are regulated by population density dependence, this might be more apparent at larger population sizes. The lack of pattern in productivity data also suggested that a review of protocol or re-design of productivity surveys might generate more informative data.

Models in which population survey and productivity data were weighted 10 times more heavily than harvest data provided more precise and biologically sensible results than those in which population and productivity data were weighted equally with harvest data. Models with greater weight on harvest data did not perform well. This result was expected, because harvest regulations were not updated annually in response to population survey data, so harvest amounts were not expected to mirror population dynamics. Within these limits, predictions of population size and harvest amount did not change more than 3%. Low sensitivity of model predictions to reasonable data set weights and starting values suggested that the model should be useful for predicting effects of changes in harvest regulations and determining whether the management goal has been met (3-year average population size of $\geq 80,000$ swans).

Model validation with WP tundra swan data illustrated a system that was more sensitive to recruitment function. Predictions from this model were not as good as those from the EP model, probably because of less consistent population surveys. For example, predicted WP harvest for 2004–2013 averaged 12,977 swans per year when linear recruitment was assumed, but only 10,995 swans per year when Ricker recruitment was assumed. Smaller population growth was predicted under Ricker recruitment as well. Harvest predictions would also likely change if other estimates of subsistence harvest were used prior to commencement of subsistence harvest surveys. Therefore, before the utility of this method for WP swan management can be determined, the following is recommended: (1) explore data from the May Aerial Survey data, instead of MWI data, because this survey area covers most of the breeding ground and seems to provide more consistent information on population size (Pacific Flyway Waterfowl Council 2001); (2) combine productivity data from Utah, Washington, and other sources to estimate PY from a larger portion of the winter range; (3) develop more statistically rigorous estimates for subsistence harvest prior to 1985; and (4) perform sensitivity analyses with these new data sets.

Although increases of 300–600 permits were explored here, effects of any change in number of permits can easily be assessed. If managers were interested in estimating effects of adding EP tundra swan hunting permits to the Mississippi Flyway (R. Malecki, New York Cooperative Fish and Wildlife Research Unit, personal communication), a reasonable approach for prediction would be to add the effect of those permits to the Central Flyway harvest parameters. Because EP tundra swans migrate through both the Central and Mississippi Flyways, one might expect hunter success should be more similar in those 2 flyways than between the Atlantic and Mississippi Flyways (however, see Chapter 1, Table 1.2). If an EP swan-hunting season were implemented in the Mississippi Flyway, the appropriateness of this

assumption should be assessed after a few years with harvest data. Therefore, the Mississippi Flyway would need to monitor harvest as rigorously as the other 2 flyways.

This assessment was similar to that advocated by White and Lubow (2003), who developed a set of population models using multiple sources of observed data to objectively manage Colorado mule deer (*Odocoileus hemionus*). As with this model of EP tundra swan dynamics, their model-fitting procedure adjusted parameter estimates to achieve the best overall fit of the model to the observed data. However, there were several differences between the two assessments. The White and Lubow (2003) assessment included (1) more complicated model structures, including some with age and sex classes; (2) parameter estimation using weighted least squares, with standard error of the point estimate as the weighting factor; (3) weighting of data points by inverse of variance; and (4) less robust, but more user-friendly, spreadsheet software. EP tundra swan data were not of sufficient quality to consider more complicated models than the simple balance equation used here, and all data sets lacked variance estimates; therefore, observation weighting was not an option.

This assessment differed from a previous EP tundra swan stochastic simulation model, EPSWAN (Sheaffer 1996), in several important ways. This model was not intended as an exploratory model and thus was not useful for exploring the influence of vital rates, such as non-hunting mortality or crippling loss, on population dynamics. This model also does not contain the degree of biological detail or age and sex structure included in the EPSWAN model, but instead relies upon integrated measures of population dynamics that are available each year. The EPSWAN stochastic simulation model and this assessment model complement each other and can be used together to provide the basis for sound management of EP tundra swans.

This assessment differs from the adaptive harvest management (AHM) procedures used for several waterfowl species, including black ducks (*Anas rubripes*) and mallards (*A. platyrhynchos*; USFWS 2004), because it does not include competing models, nor was it harvest optimized. A typical AHM approach includes several competing models of population dynamics and seeks to best predict responses to management actions. System response to management action helps clarify the biological processes at work (USFWS 2004). This format would not be appropriate for recruitment-model selection here because predictions from both recruitment models were too similar. At this time, there are no competing hypotheses to explore for improved management that can be reasonably captured in a model set. However, this does not preclude using formal adaptive management methods in the future, should managers find alternative hypotheses they wish to compare.

MANAGEMENT IMPLICATIONS

At current levels of harvest, the population size is predicted to decline 1%/year. Harvest regimes including 300 more permits in the Central and/or Atlantic Flyways suggested that this increased harvest will increase the annual rate of population decline to 2–3%/year. Consistent-yet-slight negative growth rates over time can result in long-term population declines, and should be reviewed carefully for species such as tundra swans, with relatively low production rates and delayed onset of breeding. These analyses suggest that the number of harvest permits is near or has slightly exceeded the maximum level that can be sustained by this population at the current population size goal.

This model provided reasonable and precise estimates of population size, harvest amount, and survival rates for EP tundra swans as assessed by comparing results with observed values and data from the literature. Therefore, I believe this

model is a useful tool that will allow EP swan managers to evaluate harvest strategies and assess population status relative to management objectives. Although model performance would be improved by estimates of annual survival rate, variances for survey data, and information on age and sex structure of the population, results of this assessment suggested that the existing operational databases were sufficient to monitor the population. This assessment would benefit from objective methods for selecting relative weights for data sets, but results were fairly insensitive to changes in reasonable model weights.

Of particular interest to EP tundra swan managers, results suggested that precise annual survival rates are not necessary for EP management. This suggests that biologists can consider eliminating banding EP tundra swans for the purpose of monitoring annual survival rate. This recommendation assumes that the monitoring databases used in the model continue to provide quality data. If distributions of wintering EP swans change such that MWI surveys do not provide adequate coverage (e.g., WP tundra swans), it would be important to re-design survey coverage or to implement a separate tundra swan survey.

The technique may also be useful for management of populations with fairly limited data, especially those waterfowl species with the same databases as EP tundra swans, for example WP tundra swans and Atlantic brant (*Branta bernicla hrota*; Atlantic Flyway Waterfowl Council Technical Section 2002). However, utility of the method for other populations depends on the quality of the data, which is more than sufficient for EP tundra swans. The population model was flexible and general, so that one could tailor the model for the needs of other species, including incorporating subsistence harvest, varying allocations of hunting permits, or evaluating different population goals.

APPENDIX C. Data used in Eastern population tundra swan model.

Table C.1. Data used in population model.

Year	Eastern Population tundra swans						Western Population tundra swans				
	MWI ¹	PY ²	# of permits allowed in AF ³	Harvest in AF	# of permits allowed in CF ⁴	Harvest in CF	MWI	PY	# of permits allowed in PF ⁵	Harvest in PF	Subsistence harvest in AK ⁶
1949							16,066				6,616
1950							16,829				6,616
1951							31,687				6,616
1952							19,220				6,616
1953							27,674				6,616
1954							26,206				6,616
1955							34,725				6,616
1956	38,699		0	0	0	0	46,282				6,616
1957	40,224		0	0	0	0	42,970				6,616
1958	28,181		0	0	0	0	49,946				6,616
1959	27,717		0	0	0	0	39,600				6,616
1960	41,100		0	0	0	0	35,508				6,616
1961	62,500	0.15	0	0	0	0	40,828				6,616
1962	39,400	0.16	0	0	0	0	32,356		1,000	320	6,616
1963	61,400	0.15	0	0	0	0	46,350	0.31	1,000	392	6,616
1964	62,100	0.12	0	0	0	0	40,545	0.31	1,000	335	6,616
1965	54,000	0.12	0	0	0	0	42,649	0.31	995	336	6,616

¹ Mid-Winter Index.

² Percent Young on the wintering ground.

³ Atlantic Flyway.

⁴ Central Flyway.

⁵ Pacific Flyway

⁶ Estimated from Georgette 2000, Walker 2003, Priest and Usher 2004.

Table C.1 (Continued).

Year	Eastern Population tundra swans						Western Population tundra swans				
	MWI ¹	PY ²	# of permits allowed in AF ³	Harvest in AF	# of permits allowed in CF ⁴	Harvest in CF	MWI	PY	# of permits allowed in PF ⁵	Harvest in PF	Subsistence harvest in AK ⁶
1966	57,800	0.11	0	0	0	0	34,804	0.31	1,000	491	6,616
1967	72,000	0.09	0	0	0	0	48,946	0.31	1,000	246	6,616
1968	45,600	0.10	0	0	0	0	35,630	0.31	1,000	520	6,616
1969	62,200	0.05	0	0	0	0	74,879	0.31	3,000	1,377	6,616
1970	55,000	0.15	0	0	0	0	31,000	0.31	3,500	1,199	6,616
1971	58,200	0.15	0	0	0	0	98,856	0.31	3,495	1,109	6,616
1972	62,800	0.04	0	0	0	0	82,847	0.31	3,500	1,028	6,616
1973	56,517	0.15	0	0	0	0	33,917	0.31	3,500	1,191	6,616
1974	63,827	0.17	0	0	0	0	69,768	0.31	3,500	1,377	6,616
1975	66,083	0.19	0	0	0	0	54,872	0.31	3,500	1,383	6,616
1976	67,728	0.07	0	0	0	0	51,350	0.31	3,500	1,109	6,616
1977	76,238	0.20	0	0	0	0	47,269	0.32	3,488	1,575	6,616
1978	70,244	0.29	0	0	0	0	45,597	0.31	3,500	1,152	6,616
1979	76,826	0.09	0	0	0	0	53,523	0.44	3,500	1,293	6,616
1980	59,857	0.11	0	0	0	0	65,209	0.38	3,500	1,156	6,616
1981	92,765	0.30	0	0	0	0	83,553	0.49	3,500	1,619	6,616
1982	72,907	0.12	0	0	0	0	91,314	0.43	3,500	1,244	6,616
1983	86,464	0.20	0	0	109	34	67,302	0.46	3,650	1,168	6,616
1984	81,235	0.20	1,000	313	108	22	61,873	0.22	3,650	1,194	6,616
1985	93,909	0.24	6,000	2,523	120	19	48,798	0.29	3,645	673	4,183
1986	90,766	0.09	6,000	2,302	170	41	66,157	0.27	3,608	947	6,015
1987	94,504	0.10	5,968	2,801	171	27	52,798	0.42	3,593	600	7,373
1988	77,110	0.15	6,595	2,605	499	216	59,193	0.22	3,372	855	6,616
1989	90,150	0.15	6,044	2,261	1,167	552	78,658	0.20	3,454	1,094	6,686

Table C.1 (Continued).

Year	Eastern Population tundra swans						Western Population tundra swans				
	MWI ¹	PY ²	# of permits allowed in AF ³	Harvest in AF	# of permits allowed in CF ⁴	Harvest in CF	MWI	PY	# of permits allowed in PF ⁵	Harvest in PF	Subsistence harvest in AK ⁶
1990	90,593	0.10	6,589	2,983	1,673	872	40,052	0.29	3,378	1,232	6,051
1991	97,424	0.12	6,600	3,145	3,204	1,200	47,618	0.24	3,342	923	5,737
1992	109,788	0.04	6,561	2,796	3,719	1,684	63,737	0.25	3,189	717	7,878
1993	76,593	0.15	6,400	2,903	3,712	1,275	62,202	0.34	3,375	699	6,419
1994	84,527	0.19	6,600	3,944	3,732	1,235	79,406	0.34	3,422	1,222	8,682
1995	80,222	0.08	6,600	3,050	3,791	1,033	52,942	0.32	3,843	659	10,184
1996	79,021	0.10	5,600	2,372	3,607	957	98,064	0.29	3,818	1,368	9,465
1997	86,120	0.08	5,600	2,542	3,441	1,374	122,521	0.38	3,832	1,193	5,995
1998	96,544	0.16	5,600	2,611	3,645	932	70,048	0.36	3,934	1,654	6,878
1999	109,041	0.10	5,600	2,418	3,295	1,183	119,777	0.35	3,995	1,388	5,929
2000	103,082	0.10	5,600	2,694	3,284	899	89,622	0.46	3,221	957	4,151
2001	98,167	0.10	5,600	2,466	3,381	991	87,327	0.43	3,063	713	4,228
2002	103,834	0.08	5,600	2,540	3,453	932	58,675	0.42	3,014	743	6,616
2003	108,187	0.05	5,600	2,529	3,625	332	102,736	0.40	3,013	1,034	6,616

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