Research Article

Modeling Movement and Fidelity of American Black Ducks

NATHAN L. ZIMPFER,1 D. B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30607, USA
MICHAEL J. CONROY,2 United States Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, D. B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30607, USA

Abstract

Spatial relationships among stocks of breeding waterfowl can be an important component of harvest management. Prediction and optimal harvest management under adaptive harvest management (AHM) requires information on the spatial relationships among breeding populations (fidelity and inter-year exchange), as well as rates of movements from breeding to harvest regions. We used band-recovery data to develop a model to estimate probabilities of movement for American black ducks (Anas rubripes) among 3 Canadian breeding strata and 6 harvest regions (3 in Canada, and 3 in the United States) over the period 1965–1998. Model selection criteria suggested that models containing area-, year-, and age-specific recovery rates with area- and sex-specific movement rates were the best for modeling movement. Movement by males to southern harvest areas was variable depending on the originating area. Males from the western breeding area predominantly moved to the Mississippi Flyway or southern Atlantic Flyway ($W_{ij} = 0.353$, SE = 0.0187 and $W_{ij} = 0.473$, SE = 0.037, respectively), whereas males that originated in the eastern and central breeding strata moved to the northern Atlantic flyway ($W_{ij} = 0.842$, SE = 0.010 and $W_{ij} = 0.578$, SE = 0.0222, respectively). We used combined recoveries and recaptures in Program MARK to estimate fidelity to the 3 Canadian breeding strata. Information criteria identified a model containing sex- and age-specific fidelity for black ducks. Estimates of fidelity were 0.9695 (SE = 0.0249) and 0.9554 (SE = 0.0434) for adult males and females, respectively. Estimates of fidelity for juveniles were slightly lower at 0.9210 (SE = 0.0931) and 0.8870 (SE = 0.0475) for males and females, respectively. These models have application to the development of spatially stratified black duck harvest management models for use in AHM. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1770–1777; 2006)

Key words

adaptive harvest management, American black duck, Anas rubripes, fidelity, harvest, model, movement probability, population dynamics.

Waterfowl biologists historically have recognized the importance of migratory corridors to the appropriate setting of harvest regulations (Geis et al. 1971, Bellrose 1980). Researchers are developing adaptive harvest management (AHM; Williams and Johnson 1996) as a means to guide an international harvest strategy for American black ducks (Anas rubripes; Conroy et al. 2003, 2004). However, researchers currently base dynamic models of black duck populations (Conroy et al. 2002) on a single, continental population, with abundance indexed by midwinter waterfowl surveys. Previous banding and recovery analyses (Blandin 1982, Krementz et al. 1987, 1988) suggest regional differences in survival and harvest rates. More recent surveys and research indicate that the abundance and productivity of American black duck populations, as well as the strength of biotic relationships such as density dependence and competition from mallards (Anas platyrhynchos), varies from eastern to western portions of the range (Conroy et al. 2002, Zimpfer and Conroy 2006). However, population status and growth rates are likely not uniform over the black duck range. For instance, by the 1970s evidence existed that black duck abundance had declined in regions of Ontario that provide black ducks to the Mississippi Flyway (Collins 1974). More recent population surveys suggest that black duck numbers in Ontario have declined, while black duck numbers in the Maritimes are stable or increasing (Conroy et al. 2002). Black duck management would benefit from the use of models that incorporate multiple breeding stocks of black ducks.

Within an AHM framework, spatial stratification offers advantages over traditional single-population models. Spatial stratification would aid in reducing uncertainty surrounding east–west differences in population size and vital rates that would not be captured if modeled as a single population. Spatially stratified AHM requires stratum-specific estimates of reproduction rates and survival probabilities, probabilities of movement from breeding strata to harvest regions, and probabilities of inter-year fidelity to breeding strata.

Previous studies have proposed multiple breeding populations of black ducks based on similarities in survival, recovery rates, and recovery distributions in groups of banding stations (e.g., Lemieux and Moisan 1959, Geis et al. 1971). For example, Lemieux and Moisan (1959) determined that black ducks banded in 4 stations in Quebec followed 2 migratory paths, one via Maritime Canada and the northeastern United States, the other more directly south via the St. Lawrence River. Using preseason banding and recovery data from 1946 to 1960, Geis et al. (1971) proposed 25 major banding reference areas for black ducks. Blandin (1982) derived an additional 2 reference areas based

---

1 Present address: United States Fish and Wildlife Service, Office of Migratory Bird Management, 11500 American Holly Drive, Laurel, MD 20708, USA
2 E-mail: mconroy@uga.edu
on additional banding data. Pendleton and Sauer (1992) proposed 6 distinct populations using additional banding and recovery data, and clustering techniques to group adjacent degree blocks. Although these analyses are beneficial for identifying populations, they do not provide estimates of the probability of movement between major breeding and harvest strata, which are required for modeling the impacts of harvest on a stock-specific basis (Munro and Kimball 1982, Conroy et al. 2005). There is very little quantitative information about fidelity of black ducks to specific breeding areas. It is suspected that black ducks exhibit a high degree of fidelity (Blandin 1982), but this has not been extensively studied. In a study of black ducks breeding in Maine and Vermont, Coulter and Miller (1968) found that 25% of black duck hens nested in the same general area in later years. They suggested that the return rates of hens were likely to be greater because they were unable to locate all nests and capture all banded hens on the study area. Studies of fidelity in other waterfowl species also suggest that fidelity in black ducks is likely to be high, but may vary among ages and sexes (see Anderson et al. 1992).

Our objective was to use band-recovery models to estimate movement and fidelity for multiple breeding strata of black ducks. Our estimates provide a necessary component of spatially stratified AHM for black duck (Conroy et al. 2003, 2004) in conjunction with models predicting area-specific reproduction rates (young/adult in the autumn population; Zimpfer and Conroy 2006).

Study Area

As an initial step in developing AHM for black ducks, the Black Duck Adaptive Management Working Group (BDAMWG; Conroy et al. 2004) provisionally agreed to boundaries for 3 breeding strata and 6 harvest regions. Although not the subject of this paper, it is important to understand our movement and fidelity parameters in the context of these defined areas (Fig. 1). We defined breeding and harvest strata to depict the greatest amount of biological realism surrounding the migration of black ducks. However, we constrained these delineations by major political boundaries, which serve as units of management.

We derived breeding strata from the Black Duck Joint Venture (BDJV) breeding ground survey (BDJV 1992). We reduced the original 4 strata (Dickson and Serie 1993) to 3 breeding strata by combining the 2 easternmost strata into 1 (Fig. 1), based on previous analysis of harvest distribution and derivation (Smith 1997, Conroy et al. 2003, 2004). Although black ducks breed in both Canada and the United States, the principal part of the breeding range is in Canada. Harvest regions developed by BDJV in Canada were determined as coterminous with the breeding strata, under the assumption that most Canadian harvest is of birds produced in the same geographic region. By contrast, most black ducks surviving the harvest period in Canada, or originating in United States breeding areas, migrate to wintering areas in the United States. We based harvest regions in the United States on previous analysis of harvest distribution (Smith 1997) constrained by bio-political units (i.e. flyways; Fig. 1). Between 1999 and 2004, the Mississippi Flyway had accounted for an average of 16% of the continental black duck harvest (Office of Migratory Bird Management, Laurel, Md., data on file), and thus was designated as a single harvest unit. Band-recovery data suggested that the Atlantic Flyway receives migrating and wintering birds from >1 breeding population, with the northerly portion of the flyway having greatest affinity to the eastern and southern breeding populations (Zimpfer 2004; Fig. 1). By consensus, therefore, the BDAMWG agreed to consider harvest management at a sub-flyway scale, with northern and southern harvest regions (Fig. 1).

Methods

Movement Probabilities

We used band-recovery data and multinomial models to estimate movement probabilities from breeding strata to harvest regions. The general structure of our model was the same as that described by Conroy et al. (2005); our emphasis here is on modeling of movement rather than factors affecting recovery probabilities. We obtained banding and recovery data from the United States Geological Survey (USGS) Bird Banding Laboratory (BBL), in Laurel, Maryland. We included only normal wild black ducks banded preseason (1 Jul–30 Sep) in Canada from 1965–1998, and recoveries of black ducks shot or found dead during the hunting season. We recognize that these criteria may miss some individuals that undergo a northerly migration for dispersal or molting (e.g., birds banded in the United States and recovered in Canada), but we believe these components to be small relative to overall migration and that our analysis approximates movement at the continental scale. We poststratified banding and recovery data by age, sex, time, banding, and recovery area.

We estimated movement using a multinomial likelihood
model coded in Program SURVIV (White 1983). The model estimates direct recovery probabilities \( (f_j) \) and movement \((\Psi_{ij})\) from breeding areas to harvest areas (Fig. 2). We modeled these parameters as area-, age-, sex-, and time-specific under the most general (global) model. We defined movement as the probability that a bird banded in stratum \( i \) is recovered in region \( j \) during the first hunting season after banding where movement occurs as a single step from banding to harvest area (Fig. 2). This approximation is necessary because we had no data (i.e., recaptures) of banded individuals between the initial banding and time of recovery (in most cases, recaptures are inter-year and occur during summer trapping; we use these for the fidelity analyses described later).

We illustrate the model development with a single age-sex class, but the methodology is readily extendable to multiple age and sex cohorts (Appendix 1). Bandings, \( R_{jt} \), potentially occur in 3 banding strata \( i = 1, 2, 3 \), in year \( t = 1, \ldots, 34 \). The probability that a bird banded in stratum \( i \) and recovered in Canadian harvest region \( j \) in year \( t \) is

\[
\pi_{ijt} = \Psi_{ijt} f_{jt} \quad i = 1, 2, 3; \quad j = 1, 2, 3
\]

where \( \Psi_{ijt} \) is the probability of moving from banding stratum \( i \) to harvest region \( j \) by the hunting season, with recovery rate \( f_{jt} = b_{jt} \lambda_{jt} \) where, \( b_{jt} \) and \( \lambda_{jt} \) are time- and area-specific harvest and band-reporting probabilities. Harvest and reporting probabilities are not separately identifiable under our model, but under the assumption that reporting is constant over time and among areas, recovery probabilities are an index to harvest probabilities. Our interest focused on estimating movement, not harvest probabilities, and therefore required no assumptions about the constancy of band-reporting probabilities. The expected number of observed recoveries, \( m_{ijt} \) in Canadian harvest region \( j = 1, 2, 3 \), from banding stratum \( I = 1, 2, 3 \) in year \( t = 1, \ldots, 34 \) is then

\[
E(m_{ijt}) = R_{jt} \pi_{ijt} = R_{jt} \Psi_{ijt} f_{jt} \quad i = 1, 2, 3; \quad j = 1, 2, 3.
\]

We based recoveries in United States harvest areas on a conditional argument that birds survived harvest in Canadian harvest areas and then moved to 1 of the 3 United States harvest areas and did not survive harvest. We obtained banded birds not recovered (either not harvested or harvested but not reported) from subtraction of the total bands recovered in each of the 5 harvest areas from the total bandings.

We explored hypotheses about variation in movement or recovery probabilities over time or space, or by age and sex, by constraining the general model (allowing for variation in all these dimensions). For example, under the hypothesis that movement did not vary over years, but harvest rates did vary, the former are constrained to be equal over time and the latter are allowed to vary. Some cases also required constraints to allow parameter identifiability; such constraints should be biologically plausible. For example, constraining recovery probabilities to be equal in the northern and southern Atlantic Flyway may be justified, given that regulations are set at the flyway level.

![Figure 2: Schematic of movement pathways that we used to develop the likelihood for estimating movement rates of American black ducks banded in Canada and recovered in Canada and the United States, 1965–1998 (Appendix 1), where \( W_{ij} \) is the probability that a black duck banded in area \( i \) moves to harvest area \( j \), and \( f_j \) is probability of recovery (a banded bird is harvested and reported) for harvest area \( j \).](Image 290x593 to 533x744)

In the United States and Canada, season lengths and bag limits became progressively more restrictive between 1965 and 1998 (Francis et al. 1998). In 1983, a legal challenge regarding the management of black ducks resulted in regulations with further restrictions of harvest (Grandy 1983). To account for this temporal effect (but with fewer parameters than a purely year-specific model), we defined 2 periods based on major changes in black duck regulations, following Francis et al. (1998). In our dataset, 1983 represented an identifiable change in black duck regulations where regulations shifted from moderate to restrictive. In addition, some evidence exists for shifts in the distribution of breeding black ducks during this period, with apparent declines in the relative number of black ducks in the western region (Conroy et al. 2002). Therefore, we constructed period-specific models for recovery and movement based on the periods 1965–1982 and 1983–1998.

There exists strong a priori evidence of regional differences in recovery caused by differing harvest regulations, particularly between the United States and Canada (Conroy et al. 2005). Because recovery is the product of harvest and reporting probabilities, regional differences in band reporting may also induce regional differences in recovery (Conroy and Blandin 1984, Williams et al. 2002). Additionally, we expected movement to harvest areas to differ among breeding areas, because these were partially defined based on previous analysis of harvest distribution (Geis et al. 1971, Smith 1997). Therefore, we considered only models that included area-specific effects for movement and recovery probabilities.

We used information theory to evaluate alternative models (Burnham and Anderson 2002). In this approach, the likelihood is used to calculate the weight of evidence for each of several plausible alternatives, as opposed to null-hypothesis testing (Anderson et al. 2000, 2001, Burnham and Anderson 2001, Guthery et al. 2001, 2005). To evaluate alternative models, we used model ranking based on Akaike’s Information Criterion (AIC), adjusted for small
sample sizes, and extra-binomial variation to obtain QAICₖ (Burnham and Anderson 2002). We calculated model weights as

\[ w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{m=1}^{k} e^{(-0.5\Delta_m)}} \]

where \( \Delta_i = QAIC_{i} - QAIC_{min} \), QAICₖ is the score of the ith model, and QAICₖ,ₘᵢₙ is the lowest-scoring model (Burnham and Anderson 2002).

**Fidelity**

We define fidelity as the probability that a black duck banded and released in year \( t \) in breeding stratum \( i \) returns to stratum \( i \) in year \( t + 1 \), conditional on having survived the interval \([t, t + 1] \). We used joint band-recovery and recapture data to allow separate estimation of survival for each breeding stratum \( i = 1, 2, 3 \) (Fig. 1). For estimation of fidelity, we included only normal wild black ducks banded preseason (1 Jul–30 Sep) in each of the breeding areas in Canada between 1966 and 2000 for analysis. Recoveries included only black ducks shot or found dead during the hunting season but included all recovery locations during the hunting season. We obtained recaptures from the BBL encounters file; we limited recaptures to birds recaptured in 1 of the 3 breeding areas and to instances in which the year of recapture was later than initial capture (thus eliminating recaptures during the original banding period).

We estimated fidelity in Program MARK (White and Burnham 1999) using the joint recapture–recovery model developed by Burnham (1993). This model takes advantage of the overlap between recoveries from all areas and recaptures in the breeding areas to allow separate estimation of apparent survival (\( \Phi \)), recapture (\( p \)), recovery (\( r \)), and fidelity (\( F \)). Apparent survival is the probability of surviving and not permanently emigrating over the interval \([t, t + 1] \). Capture probability is the probability of capture, conditional on the individual being alive and in the sample (Cooch and White 2005). Recovery is the probability that banded birds are shot or found dead and reported between \( t \) and \( t + 1 \). Estimation of \( \Phi \) and \( F \) allows derivation of true, demographic survival \( S \) by the relationship \( \Phi = F S \). The dataset included 34 encounter occasions, and we identified 12 attribute groups (3 breeding strata, and 4 age–sex classes) in which it was conceivable that fidelity may have varied. We used a logit link function to maintain the parameter space between 0.0 and 1.0.

We examined models that included both interactive and additive effects. Over-dispersion of mark-recapture data is common because of a lack of independence among the individuals being studied or heterogeneity in the parameters, resulting in underestimated variances (Anderson et al. 1994). The standard estimation of the variance inflation factor, \( \hat{c} \), led to unrealistic estimates, which we suspected to be a result of sparse recovery and recapture data because there were a number of cells that contained no recoveries or recaptures. We corrected variances by estimating \( \hat{c} \) using a bootstrap goodness-of-fit procedure contained in program MARK, which evaluates goodness-of-fit from simulated data from a given model, thus, not violating assumptions of over-dispersion and independence among individuals. We ran 100 bootstrap simulations, calculating the model deviance for each run. Based on these simulations, we calculated \( \hat{c} \) as the ratio of the deviance estimated from actual data to the average deviance from simulated data. We corrected AIC values, and we reranked models using QAICc.

**Results**

**Movement**

Data for the movement analysis included 176,142 bandings and 16,598 recoveries over 34 years (1965–1998). Under the full model parameterization, which resulted in unreliable (e.g., unusually large standard errors) parameter estimates because of problems with numerical convergence. We improved estimation by constraining annual recovery rates to be equal each year between the northern and southern portions of the Atlantic Flyway. This was a reasonable a priori decision because regulatory frameworks are set at flyway level and not by regions. Additionally, we constrained movement \( \Psi_{ij} \) to zero for movement to nonadjacent Canadian harvest regions because there were negligible numbers of recoveries (zero in most years) from breeding stratum \( W \) in stratum \( E \) and vice versa.

The best approximating model, \( f_{j0} \Psi_{ia} \), as identified by QAICc, suggested that recovery rates \( (f) \) were area- \((a)\), year- \((y)\), and age-specific \((g)\), and movement \( (\Psi) \) was area- and sex-specific \((s)\); Table 1. In addition, we considered models not including area effects. These models were uniformly poorer in performance than models including area effects, and we therefore excluded them from further analysis. Lower-ranked models with similar constraints on movement probabilities contained a negligible portion of total QAIC, weight \((<0.01)\), suggesting only a small degree of uncertainty associated with model selection (Table 1). Therefore, we based subsequent inference on movement on the model \( f_{j0} \Psi_{ia} \). Under this model, the harvest of most black ducks in Canada occurs in the same geographic area as banding \((\Psi_{ij} > 0.9)\), Table 2). Movement from breeding areas to northern harvest areas ranged from a low of \( \Psi_{ij} = 0.015 \) (SE = 0.002) by females moving from the eastern to the central harvest area, to a high of \( \Psi_{ij} = 0.046 \) (SE = 0.006) by males moving from the central breeding area to the western harvest area. Movement from northern harvest areas to southern harvest areas varied depending on the originating area. Males from the western area not harvested in Canada moved predominately to the Mississippi Flyway or the southern Atlantic Flyway \( (\Psi_{ij} = 0.353, SE = 0.033 \) and \( \Psi_{ij} = 0.473, SE = 0.037, \) respectively). The remaining males moved to the northern Atlantic Flyway \( (\Psi_{ij} = 0.174, SE = 0.017) \). Estimates of movement by male black ducks from the eastern and central areas indicate strong tendencies to move to the northern Atlantic Flyway, with estimated probabilities of 0.842 (SE = 0.010) and 0.578 (SE =
parameters.

We corrected models for over-dispersion using model deviance also suggested over-dispersion in the data. Small differences in general and more constrained models. Small differences in the deviance between models often failed to converge or were severely over-fitted, in all parameters during model development. Very general [S(\(gsa\)), age (\(g\)), sex (\(s\)), or period (1965–1982 vs. 1983–1998; \(p\)) variation in recovery (\(f\)) or movement (\(\Psi\)) parameters.

Fidelity
The data set contained 189,663 bandings, 2,545 unique recapture records (first recapture only), and 27,935 recoveries over the 1996–2000 period. We allowed for interactive and additive effects of area (\(a\)), age (\(g\)), sex (\(s\)), and time (\(t\)) in all parameters during model development. Very general models often failed to converge or were severely over-fitted, as noted by small differences in the deviance between general and more constrained models. Small differences in model deviance also suggested over-dispersion in the data. We corrected models for over-dispersion using \(\hat{c} = 2.8900\), where we estimated \(\hat{c}\) from the most general model fit \([S(\(ags\)), \rho(\(ag\)), \rho(\(ags\)), F(\(ags\))]\) containing 42 parameters. After correction of AIC, for over-dispersion, the top-ranked model was \(S(\(ags\)), \rho(\(g\)), \rho(\(ags\)), F(\(g+i\)), \) which contained 97.48% of the total model weight (Table 3). All other models contained <1% of the total model weight, and we did not retain them in the model set. Estimated fidelity was highest for the adult age class, at 0.9695 (SE = 0.0249) and 0.9554 (SE = 0.0434) for males and females, respectively (Table 4). The fidelity of young females (0.8870 ± 0.0475) was similar to that of young males (0.9210 ± 0.0931), and males and females had nearly identical fidelity. Juvenile fidelity was lower, but the differences were small relative to standard errors.

Discussion
Our results provide estimates of movement and fidelity rates that can be used for further modeling of multiple breeding strata of black ducks. However, our results must be interpreted in the context of the broad-scale regions defined in our analyses, and do not provide inference, for example, about fidelity to specific sites.

<table>
<thead>
<tr>
<th>Model</th>
<th>No. of parameters</th>
<th>QAICc (^b)</th>
<th>ΔQAICc</th>
<th>Wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Psi((ga)))</td>
<td>360</td>
<td>7,623.89</td>
<td>0.00</td>
<td>0.991</td>
</tr>
<tr>
<td>(\Psi((ga)))</td>
<td>360</td>
<td>7,633.85</td>
<td>9.96</td>
<td>0.007</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>350</td>
<td>7,636.46</td>
<td>12.57</td>
<td>0.002</td>
</tr>
<tr>
<td>(\Psi((pga)))</td>
<td>380</td>
<td>7,645.85</td>
<td>21.96</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>40</td>
<td>7,967.38</td>
<td>343.49</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((pgsa)))</td>
<td>120</td>
<td>7,969.54</td>
<td>345.65</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>40</td>
<td>7,982.56</td>
<td>358.67</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((pgsa)))</td>
<td>2,040</td>
<td>8,093.02</td>
<td>469.13</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>720</td>
<td>8,207.98</td>
<td>584.09</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>60</td>
<td>8,672.75</td>
<td>1,048.86</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>30</td>
<td>8,699.82</td>
<td>1,075.93</td>
<td>0.000</td>
</tr>
<tr>
<td>(\Psi((gsa)))</td>
<td>380</td>
<td>9,015.97</td>
<td>1,392.08</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\(^{a}\) Models specify year (\(y\)), age (\(g\)), sex (\(s\)), area (\(a\)), or period (1965–1982 vs. 1983–1998; \(p\)) variation in recovery (\(f\)) or movement (\(\Psi\)) parameters.

\(^{b}\) QAICc indicates quasi-Akaike’s Information Criterion adjusted for small sample sizes.

<table>
<thead>
<tr>
<th>Harvest area</th>
<th>(\Psi)</th>
<th>SE</th>
<th>(\Psi)</th>
<th>SE</th>
<th>(\Psi)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>(W)</td>
<td>0.975</td>
<td>0.005</td>
<td>0.029</td>
<td>0.006</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>(C)</td>
<td>0.025</td>
<td>0.005</td>
<td>0.954</td>
<td>0.007</td>
<td>0.015</td>
<td>0.002</td>
</tr>
<tr>
<td>(E)</td>
<td>0.000</td>
<td>0.000</td>
<td>0.017</td>
<td>0.004</td>
<td>0.985</td>
<td>0.002</td>
</tr>
<tr>
<td>(AFN)</td>
<td>0.306</td>
<td>0.031</td>
<td>0.317</td>
<td>0.036</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>(AFS)</td>
<td>0.504</td>
<td>0.038</td>
<td>0.569</td>
<td>0.026</td>
<td>0.294</td>
<td>0.082</td>
</tr>
<tr>
<td>(W)</td>
<td>0.979</td>
<td>0.003</td>
<td>0.048</td>
<td>0.006</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>(C)</td>
<td>0.021</td>
<td>0.003</td>
<td>0.938</td>
<td>0.007</td>
<td>0.028</td>
<td>0.003</td>
</tr>
<tr>
<td>(E)</td>
<td>0.000</td>
<td>0.000</td>
<td>0.016</td>
<td>0.003</td>
<td>0.972</td>
<td>0.003</td>
</tr>
<tr>
<td>(AFN)</td>
<td>0.353</td>
<td>0.033</td>
<td>0.016</td>
<td>0.006</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>(AFS)</td>
<td>0.174</td>
<td>0.017</td>
<td>0.578</td>
<td>0.022</td>
<td>0.842</td>
<td>0.010</td>
</tr>
</tbody>
</table>

\(^{a}\) \(W\), \(C\), and \(E\) represent the western, central, and eastern Canadian breeding and harvest areas, respectively. \(MF\), \(AFN\), and \(AFS\) correspond with the United States harvest areas in the Mississippi Flyway, northern Atlantic Flyway, and southern Atlantic Flyway, respectively.
Table 3. Selected models from Program MARK for estimating fidelity of Canadian-banded (1966–2000) American black ducks to breeding population regions and their associated quasi-Akaike’s Information Criterion adjusted for small sample sizes (\(\text{QAIC}_c\)) model weights.

<table>
<thead>
<tr>
<th>Model</th>
<th>No. of parameters</th>
<th>(\Delta\text{QAIC}_c)</th>
<th>Wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(ags),p(gs),(ags),F(gs),F(g+s)</td>
<td>31</td>
<td>0.00</td>
<td>0.97483</td>
</tr>
<tr>
<td>S(ags),p(gs),(ags),F(gs),F(gs)</td>
<td>40</td>
<td>9.37</td>
<td>0.00901</td>
</tr>
<tr>
<td>S(ags),p(ags),r(ags),F(gs)</td>
<td>40</td>
<td>9.42</td>
<td>0.00879</td>
</tr>
<tr>
<td>S(ags),p(ags),r(ags),F(g+s)</td>
<td>39</td>
<td>10.03</td>
<td>0.00648</td>
</tr>
<tr>
<td>S(ags),p(g),r(ags),F(gs)</td>
<td>38</td>
<td>14.16</td>
<td>0.00082</td>
</tr>
<tr>
<td>S(ags),p(ags),r(ags),F(gs)</td>
<td>42</td>
<td>19.16</td>
<td>0.00007</td>
</tr>
</tbody>
</table>

a Models specify age- (g), sex- (s), or area-specific (a) variation in survival (S), recapture (p), recovery (r), or fidelity (F) parameters.

b All main effects were interactive, unless otherwise indicated with a “+” indicating additive main effects.

**Movement**

For the geographic breeding strata we defined, most black duck harvest occurs in the same area as breeding, with relatively little migration among breeding strata prior to the hunting season. By contrast, ducks from a particular breeding strata that survive harvest in Canada migrate in significant numbers to all 3 harvest regions in the United States. We found little, if any, differences in these movement rates in relation to age or between earlier (1965–1982) versus later (1983–1998) time periods, and we found small but statistical differences between males and females.

The number of movement pathways utilized in this analysis may not reflect all of the true pathways individuals utilized. We estimated a direct movement rate from breeding area to harvest area. In reality, black ducks may pass through one or more northern harvest regions while migrating to southern harvest regions. It is plausible that movement rates estimated in northern harvest regions could be biased high if a large portion of the black ducks harvested in these regions were transients in the process of migrating to the more southerly harvest regions (e.g., southern Atlantic Flyway). Repeated observations or capture of banded birds (or using other techniques such as radio-marking) as movement occurs from breeding strata to the point of being harvested would have allowed the estimation of movement rates on an incremental basis. In addition, some black ducks (e.g., in coastal Atlantic Canada or the Canadian portion of the Great Lakes region) may not migrate to the United States (Geis et al. 1971). This portion of the population is not eligible for harvest in United States harvest regions, potentially biasing estimates of recovery and movement rates to United States harvest regions.

Table 4. Estimates of fidelity rate for each age–sex class of American black ducks banded in Canada from 1966–2000, for the quasi-Akaike’s Information Criterion adjusted for small sample sizes selected model in Program MARK.

<table>
<thead>
<tr>
<th>Age</th>
<th>Sex</th>
<th>(\hat{F})</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ad</td>
<td>F</td>
<td>0.9554</td>
<td>0.0434</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>0.9695</td>
<td>0.0249</td>
</tr>
<tr>
<td>Juv</td>
<td>F</td>
<td>0.8870</td>
<td>0.0475</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>0.9210</td>
<td>0.0931</td>
</tr>
</tbody>
</table>

Our approach allows the estimation of movement and recovery rates in a common framework and is complementary to other approaches allowing combined inference on movement rates and factors affecting regional harvest (recovery) rates (Conroy et al. 2005). The estimates also allow exploration of spatially based harvest management models, such as those researchers are currently exploring for black ducks under an AHM framework.

**Fidelity**

To date, the study conducted by Coulter and Miller (1968) is the only one to examine breeding fidelity in black ducks. Their return rates of hens were approximately 25%, based on a sample of 89 banded black ducks over the 7-year study. However, Coulter and Miller (1968) did not adjust the estimates for annual survival, precluding comparison to our estimated fidelity rates. Failure to account for annual survival of individuals is likely to reduce estimates of return rates, because the estimator assumes that all individuals have equal opportunity to return; however, individuals harvested during the hunting season are not eligible to return to breed the next year (Anderson et al. 1992). In addition, Coulter and Miller (1968) also recognized that they were unable to find all the black duck nests or catch all previously banded hens, which further reduced their estimate of return rates. Arnold et al. (2002) used this methodology to estimate breeding-site fidelity of female redheads (Aythya americana) and concluded that age-specific differences existed in fidelity rates, with adult females having a greater propensity to return to the same breeding stratum than young females, 0.923% versus 0.744%, respectively. Similar estimates by Arnold et al. (2002) suggest that our estimates of fidelity rates are realistic.

We found that black ducks have a high probability of returning to the same breeding stratum; however, we can only apply our results to breeding strata previously defined at a specific resolution. Our breeding strata were relatively coarsely defined, and thus our analysis was incapable of detecting interchange at finer scales of resolution. In particular, it is inappropriate to interpret our estimates of fidelity in terms of return to specific nesting sites. In addition, the distribution of banding stations within breeding strata is nonrandom, potentially making lack of site fidelity harder to detect. Thus, we urge researchers to interpret our results with caution and to consider the limitations of our study design and data.

Previous studies suggest that western stocks of black ducks may have experienced greater declines than eastern stocks, although the evidence for stock-specific differences in population growth is equivocal (Conroy et al. 2002). Our estimates of fidelity rates suggest that we cannot attribute changes in the distribution of black ducks to changes in migratory patterns and fidelity to breeding strata. Furthermore, our fidelity estimates indicate that western-, central-, and eastern-breeding black ducks are equally likely to return to their respective breeding strata. Thus, explanations for changes in relative numbers of black ducks range-wide, if they have occurred, must be sought in other factors, such as
area-specific differences in production rates and survival rates.

Management Implications

At the level of geographic resolution considered, our estimates of movement between breeding and harvest regions indicate that harvest management potentially could be directed in a stock-specific manner (e.g., so as to avoid overexploitation of low-density or declining stocks [primarily in western portions of the range], or to take advantage of more robust [eastern] populations). However, the degree of stock-specificity of this management would be lower in the United States than in Canada, particularly with respect to management in the Atlantic Flyway, the southern portion of which receives substantial contribution from the central and western breeding populations. Furthermore, stock-specific differences in population growth, if confirmed, would limit the efficacy of stock-specific management, even on a sub-flyway basis. Finally, previous work provides evidence that range-wide age ratios of black duck populations have decreased over time (Conroy et al. 2002). If this apparent trend continues, it may overwhelm fine-scale efforts such as region-specific harvest management.

Literature Cited


Notation is similar to that in Conroy et al. (2005). The data comprised the following for each breeding stratum, harvest region, and year:

- \( R_{ijt}^a \) = banded black ducks of age–sex class \( a \) (ad F, ad M, juv F, juv M) released in breeding stratum \( i \) and year \( t \), \( m_{ijt}^a \) = number of ducks of age–sex class \( a \) released in breeding stratum \( i \) in year \( t \) (direct recoveries) in harvest region \( j \) in Canada (\( j = 1, 2, 3 \)).

- The parameters of the general (unconstrained) model are \( \Psi_{ijt}^a \) = probability that a duck banded in breeding stratum \( i \) moves to harvest region \( j \) in Canada in year \( t \), \( j = 1, 2, 3 \).

- We based recoveries in United States harvest regions on a conditional argument of surviving harvest in Canadian harvest regions.

- \( \Psi_{ij}^a \) = probability that duck banded in breeding stratum \( i \) moves to harvest region \( j \) in the United States, \( j = 4, 5, 6 \), conditional on not having been recovered in Canada during year \( t \).

- \( f_{ijt}^a \) = direct recovery rates in harvest region \( j \) and year \( t \), \( j = 1, \ldots, 6 \).

The likelihood for each age–sex, year and area combination is formed as

\[
L_{ijt}^a = \left( R_{ijt}^a \right) \prod_{j=1}^{3} \left( \Psi_{ij}^a f_{ijt}^a \right) m_{ijt}^a \prod_{j=4}^{6} \left( \beta_{ijt}^a \Psi_{ij}^a f_{ijt}^a \right)^{m_{ijt}^a} \left( 1 - \sum_{j=1}^{3} \Psi_{ijt}^a f_{ijt}^a - \sum_{j=4}^{6} \beta_{ijt}^a \Psi_{ij}^a f_{ijt}^a \right)^{m_{ijt}^a},
\]

where

\[
\beta_{ijt}^a = 1 - \sum_{j=1}^{3} \Psi_{ijt}^a f_{ijt}^a.
\]

By assumption of independence among ages, areas, and years with respect to movement and harvest rates, we obtain the overall likelihood as

\[
L = \prod_{a=1}^{4} \prod_{i=1}^{3} \prod_{t=1}^{12} L_{ijt}^a.
\]

Specific models are formed via constraints on the above parameter space.

Associate Editor: Hall.