Models of Production Rates in American Black Duck Populations

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Abstract
Understanding the relationship between the annual reproductive success and changes in environment is important for appropriate waterfowl management. We developed predictive models of American black duck (Anas rubripes) production rates as a function of biotic (black duck and mallard [A. platyrhynchos] abundance) and abiotic factors (spring precipitation and temperature) across predefined breeding areas, from 1990 to 2001. We used male age ratios in the fall population, estimated from wing samples of harvested black ducks corrected for differential vulnerability via band-recoveries, as the index to annual reproduction. Information criteria suggested that a model containing predictors for density-dependence, competition with mallards, spring precipitation, and temperature and stratum-specific coefficients was the best model of black duck production rates. However, coefficients of this model were highly imprecise, leading to relatively poor predictive ability, possibly due to multicollinearity among predictors and the relatively short time span of analysis. We fit several models that included only black duck and mallard abundance as predictors; of these, models with constant slopes and stratum-specific intercepts performed best. Model-averaged parameter estimates supported inverse relationships between black duck and mallard abundance and age ratios, with stronger relative effects for black duck density-dependence. Both effects have implications for adaptive harvest management, in that harvest potential for black ducks may differ greatly depending on combinations of number of each species and the relative belief in alternative hypotheses about the impacts of mallards. Much variability in age ratios remained unexplained by our models, some possibly due to the lack of habitat explanatory variables but also apparently due to random factors. Model improvement could be achieved by incorporating recent developments in the modeling of random effects, especially via Markov Chain Monte Carlo methods. More research is also needed to incorporate recently acquired habitat predictors into predictive modeling for black ducks and other ducks breeding in eastern North America. These results provide critical input for models of adaptive harvest management, currently under consideration as an approach for developing an international (Canada–U.S.) harvest strategy for black ducks. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):947–954; 2006)

Key words
age ratios, American black ducks, Anas platyrhynchos, Anas rubripes, likelihood, mallards, models, population dynamics, production.

The productivity of waterfowl populations is largely determined by various biotic and abiotic factors, such as population density, climatic conditions, and habitat availability. Understanding how waterfowl production is influenced by spatial and temporal variation in these factors is important to further understanding of dynamics and for developing effective management programs (Sheaffer 1998). A productivity model for American black ducks (Anas rubripes) is needed to help managers forecast the effects of alternative management, as under adaptive harvest management (AHM; Johnson et al. 1993, Conroy et al. 2002).

Previous studies have proposed mechanisms for, and estimated the effects of, biotic and abiotic factors on the productivity of breeding ducks. For example, in midcontinental mallards (Anas platyrhynchos), a strong relationship exists between the number of ponds in the spring and recruitment (Anderson 1975, Martin et al. 1979, Heitmeyer and Fredrickson 1981). Modeling efforts for midcontinental mallards have been particularly successful given long-term population data and limited factors that may affect production. For eastern breeding mallards, sympatric with black ducks, Sheaffer (1998) concluded that spring and winter precipitation, and breeding population size were good indicators of recruitment. Predictive relationships between recruitment and biotic factors, such as those found in midcontinental and eastern mallards, have yet to be identified for black ducks. Identification of these relationships may be further hampered by the difficulty in surveying black duck populations.

American black ducks are likewise thought to be influenced by abiotic (weather, habitat) factors and density-dependence (Conroy et al. 2002). Black ducks breed and nest in a variety of habitats across their range, and it is hypothesized that production is influenced by various wetland characteristics, such as the dominant vegetation type, wetland availability, or wetland fertility (Kirby 1988, Merendino and Ankney 1994). Weather conditions, especially spring precipitation and temperature, are also thought to influence black duck production rates. Precipitation, although less variable in the eastern portions of North America than in the prairie core of mallard habitat, is also thought to influence productivity for eastern mallards (Sheaffer 1998) and, therefore, presumably black ducks. Similarly, unusually cold periods during spring may negatively influence black duck brood survival (Ringelman and Longcore 1982). In addition to the above, black ducks may be influenced by mallards, through competition for habitats, mates, or both. Exact mechanisms for these hypothesized impacts remain in dispute, but they are mainly focused during the breeding period and are thought to be more intense in portions of the historical black duck range that have recently undergone increases in mallard abundance (Ankney et al. 1987, 1989, D’Eon et al. 1995, Conroy et al. 2002; but see Conroy et al. 1989).

Previous studies of factors influencing black duck production have been limited in spatial scale to individual wetlands, or...
wetland complexes, such that the data are not appropriate for application to the entire range of the black duck. Conroy et al. (2002) developed predictive models for black duck production at the population level. However, the nature of their data limited inference to a single, continental-level scale. In addition, their analysis utilized a midwinter index to black duck breeding abundance, due to the absence of breeding ground surveys until the 1990s.

Since 1990, the Canadian Wildlife Service (CWS) has conducted annual helicopter plot surveys of black ducks, mallards, and other waterfowl species over a broad expanse of the black duck range for which systematic surveys have not been historically conducted (Kaczyński and Chamberlain 1968, Black Duck Joint Venture [BDJV] 1992). These additional years of data on black duck and mallard abundances, together with meteorological data available over the same period and harvest-based estimates of fall age ratios, allow development of predictive models of black duck production that account for important sources of geographic and temporal variation in causative factors. Our objective was to develop and evaluate predictive models of annual reproduction in black ducks for use in AHM, based on current breeding surveys, which account for temporal and spatial variation in biotic and abiotic factors across the Canadian black duck range.

**Study Area**

The BDJV helicopter plot survey (BDJV 1992) consisted of 250 25-km² plots surveyed by helicopter, divided into 4 strata: the Atlantic highlands, and the eastern, central, and western boreal regions (Fig. 1). The survey used a rotating sample methodology, in which a group of plots was retained from one year to the next while others were discarded and replaced with other plots. The rotation was such that all plots were surveyed once every four years (B. T. Collins, CWS, unpublished report). Our analysis incorporates survey data from 1990 to 2001.

Breeding strata were defined by consensus of the Black Duck Adaptive Management Working Group (Conroy et al. 2004a,b)
and are based on existing BDJV survey strata (Fig. 1) and
distribution and derivation of black duck harvest (Smith 1997,
Zimpfer 2004). The eastern breeding area (area E) included all of
the Atlantic provinces (New Brunswick, Prince Edward Island,
Nova Scotia, Newfoundland) and the portion of Quebec located
east of 70° longitude. The central (C) area was that portion of
Quebec located between 70° and 76° longitude and a small portion
east of eastern Ontario, with the western (W) area the remainder of
Ontario (Fig. 2). For modeling our purposes, delineations of
breeding areas also served as Canadian harvest areas.

**Methods**

We defined age ratios as the number of young males per adult
duck in the fall population. We used males as the basis for age
ratios because female black ducks exhibit higher and more variable
mortality rates, inducing annual variation in the number of adults
surviving to fall (and thus the denominator of age ratio
calculations). Males, by contrast, exhibit lower annual variation
in mortality, and thus male-based age ratios may better reflect true
annual variation in reproduction rates (F. A. Johnson, United
States Fish and Wildlife Service [USFWS], personal commu-
nication).

We used wing frequencies by age and breeding area to estimate
the age ratio in the harvest for each area. We obtained wing data
from the Canadian Parts Collection Survey (PCS) maintained by
the CWS (J. F. Gobeil and B. T. Collins, CWS, unpublished
data). We used band-recovery data to provide corrections for
unequal harvest vulnerability between adults and juveniles, and
thereby adjust harvest age ratios to fall population age ratios.
We obtained banding and recovery data from the United States
Geological Survey (USGS) Bird Banding Laboratory (BBL), in
Laurel, Maryland, USA. We included only bandings of normal
wild male black ducks banded preseason (1 Jul–30 Sep) in Canada
from 1990 to 2001, corresponding to the years of our population
survey data (above) and weather covariates (described below).
Recoveries included only black ducks shot or found dead during
the hunting season. We used direct recoveries of young and adult
males banded in Canada and recovered in each of the respective
harvest areas to adjust harvest age ratios for differential
vulnerability to estimate age ratio in the fall population. We
restricted recovery data to direct recoveries of preseason-banded
birds to assure close correspondence between the breeding
population of inference and the harvest/recovery samples used
for age ratio estimation. Most direct recoveries of black ducks in
Canada occurred within the respective breeding regions, with
<5% estimated movement between regions between the banding
and harvest periods (Zimpfer 2004), suggesting that recoveries
and wings in the defined harvest areas mostly represent birds
breeding in the respective areas.

We derived model expectations for a single breeding population,
but our methodology can be readily extended to multiple breeding
populations. A full description of the likelihood stratified by years
and areas is provided in Appendix 1. The fall (preharvest but
postreproduction) population of $N$ black ducks contains unknown
numbers of young and adults ($N = N_a + N_j$), resulting in a true
ratio of young-to-adults ($A = N_j/N_a$). Young ($N_j$) and adults ($N_a$)
in the fall population are harvested at age-specific harvest rates ($h_p$
and $h_y$, $j = a, y$). The expected proportion of young in the harvest ($P$) is thus

$$E(P) = \frac{N_j}{N_j + N_a}.$$  

The relationship between this observable fraction and population
age ratio ($A$) is given by

$$E(P) = \frac{N_j/N_a}{(N_j/N_a) + h_p/h_y} = \frac{A}{A + \tau}$$

where $\tau = h_p/h_y$, is a correction for the relative vulnerability of
adults to young, and $P$ is the proportion of young in the harvest,
estimated by samples of wings ($W$) obtained from the PCS
(Martin and Carney 1977). The wing sample was apportioned
into respective age classes, $W_p$ and $W_a$ for young wings and adult
wings, where $W_j \sim Bin(P,W)$ and $W = W_p + W_a$

The relative vulnerability correction $\tau$ was estimated from age-
stratified bandings ($R_{ja}, j = a, y$) and recoveries ($m_{ja}, j = a, y$). The
expected numbers of juvenile ($m_j$) and adult ($m_a$) direct recoveries are

$$E(m_j|R_{ja}) = f_j R_j$$

$$E(m_a|R_{ja}) = f_a R_a$$

where $m_j \sim Bin(f_j R_j), m_a \sim Bin(f_a R_a)$, and $f_j$ and $f_a$ are the
direct recovery rates of young and adults, respectively. We
reparameterized this model as

$$E(m_j|R_{ja}) = f_j R_j$$

$$E(m_a|R_{ja}) = f_a R_a$$

to allow for estimation of $\tau$ under the assumption that band-
reporting rates do not differ for recovery of adults and juveniles,
but where $\tau$ potentially may be constrained to be constant over
areas, years, or both.

We were not primarily interested in point estimates of fall age
ratios ($A$), rather in modeling biotic or abiotic factors that
influenced age ratios spatially and temporally. Therefore, we
modeled $A$ as a log-linear function of predictors thought to
influence production rates

\[ \log_e(A_{it}) = \beta_{0i} + \sum_{k=1}^{p} \beta_{ki} X_{it}, \]

where \( X \) are candidate predictors black duck and mallard abundance, precipitation and temperature (Appendix 1). Prediction coefficients (\( \beta \)), harvest (\( h \)) and vulnerability (\( \tau \)) rates were simultaneously estimated via joint maximum likelihood in program SURVIV (White 1983).

A priori we thought that several predictors would likely influence production rates in black ducks, chiefly black duck density (\( N_{bi} \)), mallard density (\( M_{bi} \)), spring temperature (\( TEMP_{bi} \)), and precipitation (\( PPT_{bi} \)), and we included these in the log-linear model. We obtained environmental data from the Historical Canadian Climate Database (HCCD; http://www.cccma.ec.gc.ca/hccd/), maintained by the Canadian Meteorological Service. The HCCD summarizes temperature (°C) and precipitation (mm) data from 130 stations across Canada. We assigned each weather station to a breeding area based on georeferenced coordinates contained in the HCCD. The data contained in the database were homogenized to account for known sources of heterogeneity, such as changes in site location over time, changes in collection procedures, and differences among equipment (Mekis and Hogg 1999). We averaged annual spring temperatures (Mar, Apr, May) across all stations in a given breeding area from 1990 to 2001. We then standardized temperatures and precipitation to the 12-year average by

\[ \frac{X_{it} - \bar{X}_i}{SD_i} \]

where \( i \) = breeding area, (west, central, east) and \( t \) = year. We obtained black duck and mallard abundance estimates from the BDJV plot surveys, and we summarized them according to our population breeding areas (Fig. 2). We standardized black duck and mallard abundance as above but based on means and 3/2 deviations computed across both years and areas; thus, the standardized values represent both geographic and temporal variation in abundance. We chose to standardize weather covariates within region because we were principally interested in annual variations in weather conditions (e.g., unusually cold or wet springs) versus regional climatic factors (e.g., western precipitation levels tending to be lower than eastern).

Initially, we considered including habitat variables, similar to those proposed by Conroy et al. (2002) for incorporation in our predictive models. However, like these authors, we concluded that the available data were inappropriate descriptors of spatial and temporal habitat quality, and therefore we abandoned attempts to include habitat variables as predictors. As discussed later, we remain convinced that habitat variables ultimately need to be incorporated in predictive models for black ducks.

We modeled area-specific effects in 2 ways. First, we removed area-specific intercepts from the general model (\( \log_e(A_i) = \beta_{0i} + \beta_1 N_i + \beta_2 M_i + \beta_3 TEMP_i + \beta_4 PPT_i \)), while allowing the intercept to vary among areas. Under this model, covariates have equal influence across all areas, yet some breeding populations may have inherently different natural production rates.

Although \( \tau \) is a nuisance parameter, estimation of this parameter is required to obtain estimates of our model coefficients. A priori we expected that \( \tau \) (relative vulnerability of adults and juveniles to harvest) would be similar among years but potentially could differ among years due to regional differences in migration chronology and harvest timing. Admittedly, such differences could be expected across years, but this leads to models in which parameters cannot be identified if other parameters (e.g., age ratios) are also allowed to vary over year and regions. Therefore, we considered our most general model one in which \( \tau \) was constrained to be constant over years and regions, while \( A \) varied over both years and regions (Table 1). Alternative models in which \( \tau \) was allowed to vary over areas, time, or both provided little additional predictive value (\( \Delta QAIC_c < 2 \)), frequently failed to converge, and were eliminated from further consideration.

We calculated model-averaged parameter estimates and unconditional standard errors and confidence intervals following Burnham and Anderson (2002), from models that cumulatively provided 99% of \( \Delta QAIC_c \) weight. We calculated \( \Delta QAIC_c \) for all models (including the global model) and model weights for specific classes of models, namely 1) models containing 1 or more covariate (\( N, M, PPT, TEMP \)) predictors, including null (intercept-only model); and 2) models as above but excluding weather covariates. In each case, we re-normalized model weights to reflect changes in the model set and calculated as

\[ w_i = \frac{e^{(-0.5A_i)}}{\sum_{r=1}^{R} e^{(-0.5A_r)}} \]

where \( A_i = QAIC_{ci} - QAIC_{cmin} \) and \( QAIC_{ci} \) is the score if the \( i \)-th model and \( QAIC_{cmin} \) is the lowest scoring model of the set under consideration (Burnham and Anderson 2002). We considered these 2 sets of models separately because whereas we were interested in explaining variation in reproduction rates due to annual variation in weather (set 1), current black duck AHM models treat weather factors as random variables, and they predict reproduction as a function of black duck and mallard abundance alone. In addition to considering the \( QAIC_c \) model weights as evidence of support for covariate models, we also performed analysis of deviance (White and Burnham 1999) by computing \( F \) statistics as

\[ F = \frac{D'_c - D'_e}{df_c - df_e} \]

where \( D'_c, D'_e \) are corrected deviations computed as \( D'_e = D_0 - D'_i; D'_c = \sum_{k=1}^{K} d_k - D'_i; d_k = K_k - K_0 - 1, \) and \( D_i = -2 \ln L_i \) for the global (\( k = \ell \)), covariate (\( i = c \)), and intercept-only models under comparison, where \( K_i \) and \( K_0 \) are the number of parameters in the global and intercept-only models, respectively, and \( K_i \) is the number of coefficients (excluding intercept) in the covariate model under consideration.
Table 1. Information-theoretic ranking for models predicting fall age ratios for American black ducks using program SURVIV.

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model name</th>
<th>No. parameters</th>
<th>ΔQAIC_c^a</th>
<th>ΔQAIC_c^b</th>
<th>Model wt.</th>
<th>ΔQAIC_c^c</th>
<th>Model wt.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>τ(A) h*(A^t)(t*h)^t</td>
<td>73</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>25</td>
<td>B0(A)^a+N(A)^b</td>
<td>M(A)^c+PPT(A)^d*TEMP(A)</td>
<td>57</td>
<td>47.614</td>
<td>0</td>
<td>0.978</td>
<td>—</td>
</tr>
<tr>
<td>24</td>
<td>B0(A)+N(A)+M(A)+PPT(A)+TEMP(A)</td>
<td>51</td>
<td>55.654</td>
<td>8</td>
<td>0.018</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>22</td>
<td>B0(A)-N(A)+M(A)+PPT(A)+TEMP(A)</td>
<td>45</td>
<td>58.68</td>
<td>11</td>
<td>0.004</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>23</td>
<td>B0(A)+N(A)^2+M(A)+PPT(A)^2*TEMP(A)</td>
<td>44</td>
<td>63.234</td>
<td>15</td>
<td>0.000</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>20</td>
<td>B0(A)+N(A)+M(A)+PPT(A)+TEMP(A)</td>
<td>43</td>
<td>79.705</td>
<td>32</td>
<td>0.000</td>
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<tr>
<td>21</td>
<td>B0(A)+N(A)+M(A)+PPT(A)+TEMP(A)</td>
<td>42</td>
<td>82.905</td>
<td>35</td>
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<tr>
<td>15</td>
<td>B0(A)+PPT(A)*TEMP(A)</td>
<td>42</td>
<td>90.453</td>
<td>42</td>
<td>0.000</td>
<td>—</td>
<td>—</td>
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<tr>
<td>19</td>
<td>B0(A)+PPT(A)*TEMP(A)</td>
<td>41</td>
<td>90.478</td>
<td>42</td>
<td>0.000</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>B0(A)+N(A)+M(A)</td>
<td>41</td>
<td>115.301</td>
<td>67</td>
<td>0.000</td>
<td>0</td>
<td>0.471</td>
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<tr>
<td>9</td>
<td>B0(A)+N(A)</td>
<td>40</td>
<td>116.502</td>
<td>68</td>
<td>0.000</td>
<td>1.201</td>
<td>0.258</td>
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<td>B0(A)+N(A)+M(A)</td>
<td>42</td>
<td>117.35</td>
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<td>2.049</td>
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<tr>
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<td>118.36</td>
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<td>3.073</td>
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<td>120.462</td>
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<tr>
<td>5</td>
<td>B0(A)+N(A)</td>
<td>39</td>
<td>128.793</td>
<td>81</td>
<td>0.000</td>
<td>13.492</td>
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<tr>
<td>7</td>
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<td>129.413</td>
<td>81</td>
<td>0.000</td>
<td>14.112</td>
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<td>B0(A)+PPT(A)</td>
<td>39</td>
<td>139.545</td>
<td>91</td>
<td>0.000</td>
<td>—</td>
<td>—</td>
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<tr>
<td>10</td>
<td>B0(A)+M(A)</td>
<td>40</td>
<td>161.571</td>
<td>113</td>
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<td>46.27</td>
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<td>18</td>
<td>B0(A)+TEMP(A)</td>
<td>39</td>
<td>164.88</td>
<td>117</td>
<td>0.000</td>
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<td>—</td>
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<tr>
<td>6</td>
<td>B0(A)+M(A)</td>
<td>39</td>
<td>174.926</td>
<td>128</td>
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<td>59.625</td>
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<td>B0(A)</td>
<td>39</td>
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<td>176.206</td>
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<td>3</td>
<td>B0(A)</td>
<td>38</td>
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<td>131</td>
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<td>13</td>
<td>B0(A)+PPT(A)</td>
<td>37</td>
<td>231.026</td>
<td>183</td>
<td>0.000</td>
<td>—</td>
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</table>

^a Adjusted for small sample size and quasi-likelihood (variance inflation factor \( \hat{\epsilon} = 1.14 \)).

^b Considering only covariate models (excluding global model).

^c Global model incorporating area-(a) and year-(t) specific effects on juvenile harvest rates (h) and fall age ratios (A); vulnerability (t) specified as constant over areas and years. Fit of global model \( \chi^2 = 39.23, df = 35, P = 0.29 \).

^d Intercepts equal among western and central areas vs. eastern area.

Results

The CWS wing surveys resulted in 12,680 wings over our study period with \( \pi = 352 \) (range 80–902) wings per breeding region per year. The BBL data for our study period were comprised of 170 direct recoveries (\( \pi = 5 \), range 0–12 per region per year) of 9,043 adult banded birds (\( \pi = 252 \), range 45–711 per region per year) and 1,557 direct recoveries (\( \pi = 43 \), range 9–21 per region per year) of 26,818 juvenile banded birds (\( \pi = 745 \), range 113–1,949 per region per year). Black duck survey estimates averaged 176,268 breeding ducks per region per year, ranging from 60,592 (area C, 1994) to 403,908 (area E, 2000). Mallard estimates averaged 40,857 per area per year, ranging from 852 (area E, 1994) to 225,170 (area W, 2000). Spring precipitation and temperatures varied among regions and over years, with precipitation lowest in area W (\( \bar{W} = 207 \text{ mm}, SD = 18 \)), intermediate in area C (\( \bar{C} = 243 \text{ mm}, SD = 44 \)), and highest in area E (\( \bar{E} = 327 \text{ mm}, SD = 52 \)). Temperatures were highest in area C (\( \bar{C} = 4.4 \text{ C}, SD = 1.7 \)), intermediate in area W (\( \bar{W} = 2.9 \text{ C}, SD = 2.0 \)), and lowest in area E (\( \bar{E} = 2.1 \text{ C}, SD = 1.3 \)). We standardized these predictors as described above and used them in conjunction with the wing and recovery data and the likelihood (Appendix) to fit the series of specified models using SURVIV.

We found little evidence of temporal or spatial variation in vulnerability (\( \tau \)) and the model in which \( \tau \) was constrained to be constant over areas, but age ratios (\( A \)) were allowed to vary among areas and years (unconstrained by covariate relationships) fit the data (\( \chi^2 = 39.23, df = 35, P = 0.29 \), Table 1). We therefore took this model as the global model for comparison to models for which \( A \) was constrained, either by hypotheses of equality over areas or years or by the specified covariate relationships. For all of these constrained models, we retained the assumption of constant \( \tau \), and we focused on modeling sources of variation in \( A \) (Table 1). Initial analyses suggested that intercepts (\( \beta_h \)) differed little between areas W and C; thus, for all subsequent analyses (except for the global model or models in which all intercepts were constrained to be equal) we constrained these to a common value (i.e., 2 intercepts, 1 in common with W and C, and 1 for E).

The global model, specifying unconstrained time- and area-dependence in age ratios, was by far the best-performing model compared to all covariate models (DQAIC_c = 47.6 for the best-performing covariate model, incorporating \( N, M, PPT, TEMP, \) and interactions). Nevertheless, analysis of deviance suggested that this covariate model explained a substantial portion of the temporal and spatial variation in age ratios (\( P = 22.72, df = 6, 66, P < 0.001 \)). After normalizing over covariate models (i.e., excluding the global model), 2 models provided 
>99% of cumulative model weight, and we used those to compute model-averaged estimates of coefficients for age ratios as a function of black duck abundance, mallard abundance, and weather covariates (Table 2). Stratum-specific coefficients for black duck abundance were <0 as expected a priori, but estimates for mallard abundance and weather effects were both positive and negative across strata. Effects were generally weak, with most unconditional confidence intervals encompassing zero.

Upon further examination, we noted multicollinearity among
numbers of predicted age ratios of 2.28 at standardized black duck and mallard density effects on age ratios (e.g., mallard effects) and which provide sensible predictions regarding estimates with signs expected a priori (i.e., negative density and averaged estimates over these 4 models (Table 3) provided point models.

wide, suggesting limitations in the predictive ability of these models. However, unconditional SEs were large and confidence intervals not only exceeded 100% CI, but were also relatively wide, suggesting limitations in the predictive ability of these models.

Discussion

Our analyses have the benefit of examining factors that may affect recruitment on a subpopulation basis and are based on direct estimates of breeding populations in specific portions of the breeding range. Nevertheless, our analyses were limited by the short time span of data (12 yr) available, which consequently limited the range of variation observed in important factors such as black duck and mallard abundance. Given these limitations, we were unable to find a consistent relationship between weather predictors and age ratios, and analyses that included these factors seemed to us to be overparameterized, model-selection criteria notwithstanding.

Models in which weather effects were removed continued to explain a substantial portion of the variation in age ratios and add to the body of evidence of density-dependence and the influence of mallards on black duck population dynamics. Models in which the density-dependent coefficient was homogeneous across breeding areas seemed to perform better—despite lower information weights—than models with stratum-dependent coefficients, apparently due to multicollinearity in more complex models. While our models do not identify the mechanism by which density dependence occurs, we suggest that for black ducks it is likely to be mediated by habitat, for instance the abundance of suitable wetlands (Diefenbach and Owen 1989). Mallard effects were relatively weak compared to black duck density effects; however, both factors have implications for long-term harvest management.

Inclusion of weather covariates in models intended for AHM prediction may be of limited value, because these variables usually are modeled as random terms in the AHM process. Rather than attempting to explain intrinsically random variation by covariates, it may be more fruitful to instead estimate the parameters of random-effect distributions, a type of modeling easier to implement using Markov Chain Monte Carlo methods than via maximum likelihood methods (Barry et al. 2003, Fonnesbeck and Conroy 2004, Conroy et al. 2005).

As black duck surveys continue and additional years of data become available for age ratio estimation, we anticipate improvements in the precision of parameter estimates, and thus the predictive capability of these models. We anticipate that our models, in some form, will be incorporated into AHM for black ducks; it should also be possible to make predictions under alternative assumptions (e.g., about mallard impacts) and to test these assumptions against monitoring data and provide future weight to models supported by the data.

Management Implications

Our results have important management implications for both black ducks and mallards, and must be considered in developing

### Table 2. Model-averaged estimates of coefficients for predicting fall age ratios for American black ducks from models that considered black duck abundance (N), mallard abundance (M), spring precipitation (PPT), and spring temperature (TEMP) as predictors.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Area</th>
<th>Estimate</th>
<th>SE</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>W</td>
<td>0.444</td>
<td>0.230</td>
<td>−0.007, 0.896</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.444</td>
<td>0.230</td>
<td>−0.007, 0.896</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.553</td>
<td>1.287</td>
<td>−1.971, 3.076</td>
</tr>
<tr>
<td>N</td>
<td>W</td>
<td>−0.539</td>
<td>0.295</td>
<td>−1.117, 0.039</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>−1.799</td>
<td>0.284</td>
<td>−2.355, −1.242</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>−0.440</td>
<td>0.955</td>
<td>−2.312, 1.432</td>
</tr>
<tr>
<td>M</td>
<td>W</td>
<td>−0.258</td>
<td>0.145</td>
<td>−0.542, 0.026</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>1.842</td>
<td>0.558</td>
<td>0.748, 2.938</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.276</td>
<td>1.776</td>
<td>−3.206, 3.757</td>
</tr>
<tr>
<td>PPT</td>
<td>W</td>
<td>−0.146</td>
<td>0.144</td>
<td>−0.429, 0.137</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.093</td>
<td>0.053</td>
<td>−0.011, 0.198</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.018</td>
<td>0.072</td>
<td>−0.123, 0.159</td>
</tr>
<tr>
<td>TEMP</td>
<td>W</td>
<td>0.102</td>
<td>0.081</td>
<td>−0.058, 0.262</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.204</td>
<td>0.065</td>
<td>0.077, 0.332</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>−0.033</td>
<td>0.052</td>
<td>−0.133, 0.068</td>
</tr>
<tr>
<td>N*M</td>
<td>W</td>
<td>0.461</td>
<td>0.417</td>
<td>−0.356, 1.27</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>−0.779</td>
<td>1.187</td>
<td>−3.106, 1.548</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>−0.543</td>
<td>0.990</td>
<td>−2.484, 1.397</td>
</tr>
<tr>
<td>PPT*TEMP</td>
<td>W</td>
<td>0.159</td>
<td>0.143</td>
<td>−0.121, 0.438</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>−0.086</td>
<td>0.077</td>
<td>−0.237, 0.065</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>−0.286</td>
<td>0.088</td>
<td>−0.459, −0.113</td>
</tr>
</tbody>
</table>

* Western (W), central (C), and eastern (E) breeding areas (Fig. 2).

# Table 3. Model-averaged estimates of coefficients for predicting fall age ratios for American black ducks from models that considered only black duck abundance (N) and mallard abundance (M) as predictors.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Area</th>
<th>Estimate</th>
<th>SE</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>W, C</td>
<td>0.187</td>
<td>0.094</td>
<td>0.003, 0.370</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.344</td>
<td>0.103</td>
<td>0.143, 0.546</td>
</tr>
<tr>
<td>N</td>
<td>—</td>
<td>−0.217</td>
<td>0.040</td>
<td>−0.296, −0.139</td>
</tr>
<tr>
<td>M</td>
<td>—</td>
<td>−0.074</td>
<td>0.040</td>
<td>−0.153, 0.004</td>
</tr>
<tr>
<td>N*M</td>
<td>—</td>
<td>−0.004</td>
<td>0.088</td>
<td>−0.176, 0.167</td>
</tr>
</tbody>
</table>

* Western (W), central (C), and eastern (E) breeding areas (Fig. 2).

* Weighted averaged over models 4, 8, 9, and 11 (Table 1).

* Unconditional SE incorporating model uncertainty (Burnham and Anderson 2002).
strategies for harvest and habitat management for both species. Evidence of density-dependence in black duck reproduction suggests that black ducks currently may not be at levels greatly below carrying capacity. Therefore, optimal harvest may occur at population levels at the range observed in recent years. However, this relationship is complicated by the influence of mallards, which effectively reduce black duck carrying capacity, thereby diminishing harvest opportunity for black ducks. Under this hypothesis, harvest opportunity for black ducks could be increased by reducing numbers of mallards, thus potentially creating a conflict between harvest goals based on single-species management.

Despite our inability to develop habitat predictors of black duck production, habitat is nonetheless undoubtedly a critical element of management for black ducks, ultimately setting the limits within which black duck populations may operate. Future research should include efforts to incorporate remotely sensed habitat predictors (e.g., Grenier et al. 1993) into continental-scale population modeling for black ducks and other species for which habitat predictors are otherwise lacking.

Finally, the influence of black duck density dependence, mallard impacts, and habitat factors on black duck production rates is subject to great uncertainty. We therefore recommend that harvest and habitat management be incremental and subject to information feedback under adaptive management (Lancia et al. 1996).

Acknowledgments

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Literature Cited


The data are comprised of the following for each area ($i = 1, 2, 3$) and year ($t = 1, 2, \ldots, 12$).

1. $W_{it}$, wings reported in the harvest survey ($W_{it}^a$ adults and $W_{it}^j$ juveniles).
2. $R_{it}^a$ banded $m_{it}^a$, direct recoveries of adults,
3. $R_{it}^j$ banded $m_{it}^j$, direct recoveries of juveniles.

The likelihood for each year and area combination is formed as the product of a conditional (on total wings reported) binomial for the wing data, and 2 unconditional binomials for the band-recovery data:

$$L_{it} = \left( \frac{W_{it}^a}{W_{it}} \right)^{W_{it}^a} \left( \frac{W_{it} - W_{it}^a}{W_{it}} \right)^{W_{it} - W_{it}^a} \times \left( \frac{R_{it}^a}{m_{it}^a} \right)^{m_{it}^a} \left(1 - \frac{R_{it}^a}{m_{it}^a}\right)^{m_{it}^a - m_{it}^a} \times \left( \frac{R_{it}^j}{m_{it}^j} \right)^{m_{it}^j} \left(1 - \frac{R_{it}^j}{m_{it}^j}\right)^{m_{it}^j - m_{it}^j}.$$ 

By assumption of independence among areas and years we obtain the overall likelihood as

$$L = \prod_{t=1}^{12} \prod_{i=1}^3 L_{it}.$$ 

Age ratios are specified via a log-linear model as

$$\log_e (A_{it}) = \beta_{0i} + \sum_{k=1}^{p} \beta_{ki} X_{it},$$

where $X$ are candidate predictors (standardized black duck and mallard abundance, precipitation, and temperature). Specific models are formed via constraints on the above parameter space. For instance, the model specifying constant vulnerability but unconstrained variation in age ratios is formed by

$$\tau_{it} = \tau, \quad \beta_{ki} = 0, \quad i = 1, 2, 3; \quad t = 1, \ldots, 12; \quad k = 1, \ldots, p.$$ 

The model as above but specifying area-specific intercepts is obtained by

$$\tau_{it} = \tau, \quad \beta_{0it} = \beta_{0i}; \quad \beta_{hi} = 0, \quad i = 1, 2, 3; \quad t = 1, \ldots, 12; \quad k = 1, \ldots, p.$$ 

Models specifying covariate effects (including interactions) are formed by allowing selected coefficients ($\beta_{ki}$) to take on nonzero values. Intercepts or slopes are made homogeneous over areas by constraints.

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