The Auk 115(4):988–997, 1998

RECRUITMENT MODELS FOR MALLARDS IN EASTERN NORTH AMERICA

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ABSTRACT.—Recruitment models developed for Mallards (*Anas platyrhynchos*) have demonstrated a correlation between wetland habitat conditions on the prairie-parkland region of North America and annual reproductive success. Waterfowl habitat in eastern North America is composed of a variety of forested, inland, and coastal habitats that are subject to different environmental conditions than those in the prairies and parklands. My objective was to develop models relating environmental conditions in eastern North America to the annual reproductive success of eastern Mallards. I used estimated age ratios in the harvest to estimate the proportion of young in the fall population and developed multiple linear regression models to identify combinations of environmental and demographic variables that were correlated with annual recruitment. Annual recruitment was negatively correlated with population size and positively correlated with precipitation. Models with the best predictive ability contained either the Midwinter Inventory or the Breeding Bird Survey index, cumulative precipitation in winter (January and February) or May, and the ratio of precipitation during April in Pennsylvania to that in New Jersey. These models explained 61 to 72% ($P < 0.001$) of the annual variation in recruitment. Future attempts to model the population dynamics of Mallards in eastern North America should consider the effects of population size and precipitation on annual reproductive success. *Received 18 April 1997, accepted 23 March 1998.*

THE DEMOGRAPHY OF MANY BIRD SPECIES is influenced by weather (e.g. Rotenberry and Wiens 1991, Sherry and Homes 1995) and population density (e.g. Kaminski and Gluesing 1987, Larsson and Forslund 1994). Improved knowledge of these relationships is central to understanding the population dynamics of a species and to developing effective monitoring and conservation strategies. Factors that influence the annual production of Mallards (*Anas platyrhynchos*) include age and breeding experience, body condition, wetland conditions, nesting habitat, weather, predation, and population density (Johnson et al 1992). Wetland habitat conditions on breeding areas are thought to influence several aspects of the reproductive biology of the Mallard, and considerable research has been conducted to understand the relationship between reproductive success and habitat conditions on major breeding areas. Previous studies have shown a strong correlation between spring pond numbers on the prairie-parkland regions of North America and subsequent age ratios of Mallards in the fall (Anderson 1975a, Martin et al. 1979, Heitmeyer and Fredrickson 1981). Significant correlations also occur between cumulative winter and spring precipitation and reproductive success (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987). Recruitment models developed for Mallards nesting in the prairie-parkland region have demonstrated good predictive ability and have been used in the process of setting harvest regulations (Anderson 1975a, Williams et al. 1996, Johnson et al. 1997).

Nationwide harvest regulations for Mallards are based primarily on population and habitat surveys conducted annually in the prairie-parkland regions where densities of wetlands and breeding Mallards are highest (Caithamer and Smith 1995). Prior to 1990, no annual surveys were conducted to monitor numbers of Mallards breeding in eastern North America. Midwinter estimates for eastern Mallards totaled less than 10% of the continental population (Pospahala et al. 1974), and harvest of Mallards in the Atlantic Flyway (1961 to 1975) comprised less than 10% of the continental Mallard harvest (Munro and Kimball 1982). Relatively few Mallards (<2%) banded in the prairie-parkland regions are reported from the Atlan-

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tic Flyway (Anderson and Henny 1972), and about 75% of the Mallards banded in the Atlantic Flyway remain in the east (Munro and Kimball 1982). Therefore, efforts to manage what seems to be a regional Mallard population using data collected from the prairie-parklands may be unrealistic, and a better understanding of the population dynamics of the Mallard in eastern North America is needed.

Waterfowl habitats in the Atlantic Flyway are subject to environmental conditions that differ markedly from the prairie-parkland region (Strange et al. 1989). Although geographic factors and habitat conditions can affect survival and recruitment, comprehensive analyses of band recoveries have suggested only small differences in survival rates of Mallard that breed and winter in different regions of North America (Anderson 1975b, Nichols and Hines 1987). Recently established surveys in the Atlantic Flyway states and eastern Canada have shown that numbers of breeding Mallards in these regions have increased steadily since 1990 (H. W. Heusmann unpubl. data). If management strategies are to address specific questions relating to eastern Mallards, then the development of models incorporating factors important to the biology of eastern populations is required. My objective was to develop models relating environmental conditions in eastern North America to the annual reproductive success of eastern Mallards.

METHODS

Breeding populations of Mallards in the Atlantic Flyway are affiliated with the banding "reference areas" (Fig. 1) as defined by Anderson and Henny (1972): (1) the mid-Atlantic region (no. 15), the northeastern United States (no. 16), and eastern Canada (no. 8). Development of recruitment models required a quantitative measure of annual breeding success for birds breeding in eastern reference areas. The only long-term information on annual productivity of eastern Mallards was the age ratio in the United States harvest estimated from the U.S. Fish and Wildlife Service (USFWS) Parts Collection Survey (Martin and Carney 1977). Because eastern and prairie-parkland Mallards cannot be distinguished in the harvest, use of harvest age ratios as an index of annual recruitment requires identification of areas where the harvest is derived primarily from eastern stocks. Band recovery data, when weighted to reflect population size, can provide this information (Martin et al. 1979).

Band recoveries from 1961 to 1975 (Munro and Kimball 1982) indicated that more than 80% of the harvest of Mallards banded in eastern breeding areas occurred in the Atlantic Flyway. Band recoveries from 1990 to 1994 indicated that more than 70% of the harvest of birds banded in the northeastern United States occurred in the Atlantic Flyway states, with an additional 8 to 15% occurring in eastern Canada (Sheaffer and Malecki 1998). In contrast, most of the 1990 to 1994 harvest from birds banded in eastern Canada occurred in eastern Canada (54 to 73%), with an additional 10 to 35% occurring in the Atlantic Flyway states (Sheaffer and Malecki 1998).

Within the Atlantic Flyway states, more than 90% of the harvest of female Mallards in the New England (Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, and Vermont), mid-Atlantic (New Jersey, New York, Pennsylvania, and West Virginia) and Chesapeake (Delaware, Maryland, and Virginia) states from 1990 to 1994 was derived from eastern reference areas (Sheaffer and Malecki 1998). In contrast, more than 20% of the harvest of female Mallards in the southeastern states was derived from prairie-parkland regions. Prairie-parkland Mallards also made up more than 20% of the harvest of male Mallards in the Atlantic Flyway states. To minimize bias in age ratios from Mallards breeding outside eastern reference areas, I estimated age ratios using females only. In addition, I omitted harvest data from the Chesapeake states because of bias due to state and private programs in Maryland that annually release substantial numbers of captive-reared Mallards (L. J. Hindman pers. comm.). Data on age ratios in the Canadian harvest were not available for all years. Therefore, I restricted my analysis to age ratios of female Mallards in New England and mid-Atlantic harvests.

I calculated age ratios in the harvest using numbers of young and adult female Mallards in the USFWS Parts Collection Survey (Martin and Carney 1977) from New England and mid-Atlantic states. Numbers of wings from each state were weighted by the size of the state Mallard harvest, and the age ratio in year i ($A_{harv,i}$) was calculated as:

$$A_{harv,i} = \left(\sum y_i\right) \Big/ \left(\sum a_i\right), \qquad (1)$$

where y_i and a_i were the weighted number of wings from young and adult females in state i, respectively. I estimated the female age ratio in the fall population ($A_{pop,i}$) as:

$$A_{pop,i} = A_{harv,i} / V_i, \qquad (2)$$

where V_i was the estimated relative vulnerability of young and adult females to harvest (Martin et al. 1979). The harvest vulnerability of young relative to adults was estimated as the ratio of direct recovery

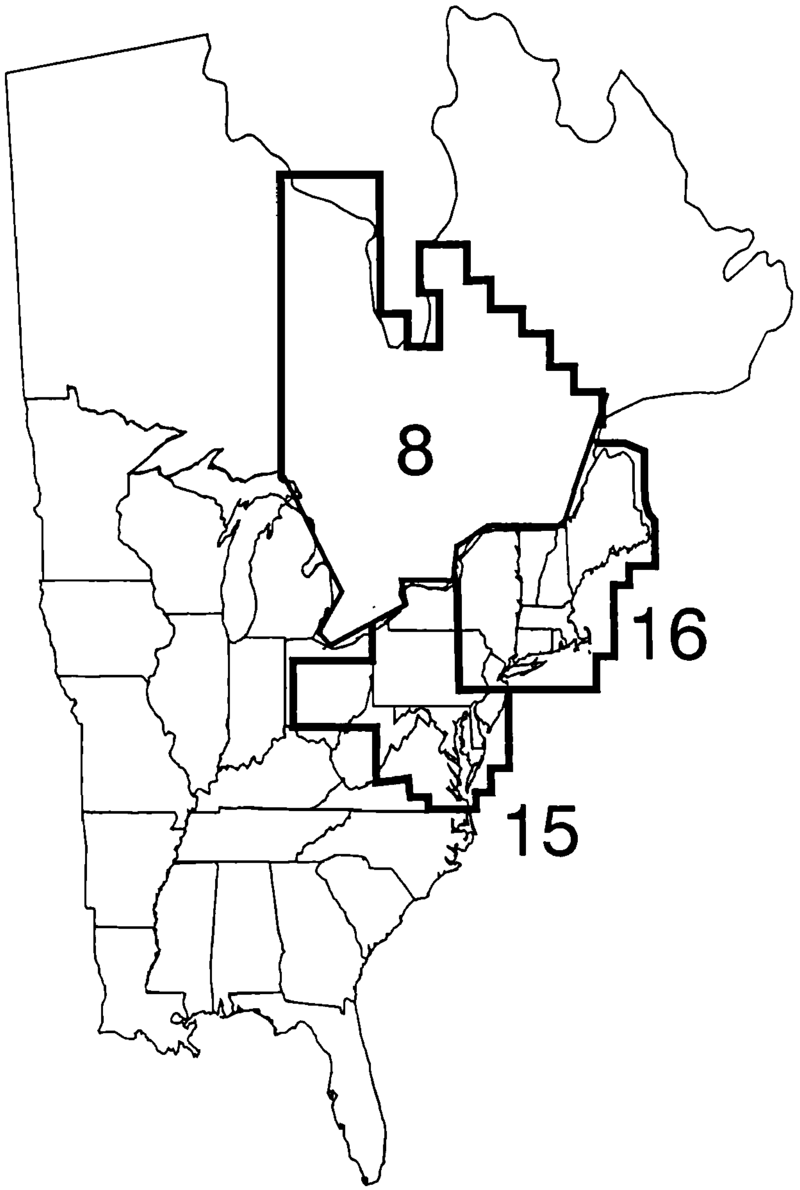

FIG. 1. Banding reference areas, as defined by Anderson and Henny (1972), representing breeding populations of Mallards in the Atlantic Flyway. Names of references areas are: (8) eastern Ontario / western Quebec, (15) mid-Atlantic, and (16) northeastern United States.

rates (young / adult) from young and adults banded in the eastern breeding reference areas and recovered in the United States harvest (Sheaffer and Malecki 1996). When estimating vulnerability to harvest, I assumed that band reporting rates did not differ between adult and young females. I converted $A_{pop,i}$ to the percentage of young in the fall population (Y_i) as:

$$Y_i = A_{pop,i} / (A_{pop,i} + 1). \qquad (3)$$

I used an arcsine-squareroot transformation that adjusted percentages to a normal distribution and improved the predictive ability of linear regression models (Zar 1984:239–241). The dependent variable in the recruitment models was Y_i, and predicted values from these models were transformed back to percentages as $Y_i = [\sin(Y_i)]^2$.

Monthly temperature means and precipitation totals during January, February, April, and May 1966 to 1994 were obtained from the Northeast Regional Climate Center, Cornell University, for six states (Connecticut, Massachusetts, New Jersey, New York, Pennsylvania, and Vermont). I selected these states because most of the harvest in the New England and mid-Atlantic states was derived from these regions (Sheaffer and Malecki 1998), and these states had regions of high densities of breeding Mallards estimated by ground surveys conducted from 1990 to 1994 (H. W. Heusmann unpubl. data). I selected January and February under the hypothesis that climate during severe winter months in the northeast would influence wetland conditions the following spring. I selected April and May because these months are peak times for nesting by Mallards in the northeast (Estel-Costanzo and Malecki 1994, Houston and Malecki 1994, Losito et al. 1995).

My objective was to construct models with a minimum of explanatory variables that adequately described variability in annual recruitment. The most thorough way to select the best model for a given set of variables is to examine all possible regression model subsets (i.e. all models with one regressor variable, with two regressor variables, etc.) and use some criteria to identify good predictive models within these subsets (Myers 1986, Neter et al. 1990). A limitation of this approach is that it assumes that the number of observations (sample size) exceeds the maximum number of potential parameters. Because the data spanned only 29 years, the number of potential predictor variables exceeded the sample size.

To reduce the number of predictor variables, I calculated a weighted precipitation total for each month (P_i) as:

$$P_i = \sum [(P_{i,j})(n_j)]/N, \qquad (4)$$

where $P_{i,j}$ was the total precipitation during month i in state j, n_j was the geographic area of state j, and $N = \Sigma\, n_j$. I calculated cumulative winter precipitation as the sum of the weighted precipitation totals for January and February, and cumulative spring precipitation as the total for April and May. I calculated a weighted mean temperature for each month (T_i) as:

$$T_i = [(T_{i,j})(n_j)]/N, \qquad (5)$$

where $T_{i,j}$ was the mean daily temperature during month i in state j. I calculated mean winter temperature as the average of the weighted means for January and February, and mean spring temperature as the average of the weighted means for April and May. The estimated number of ponds in the Canadian prairie during May (Canadian Wildlife Service [CWS] and USFWS 1996) was included as an additional predictor variable.

I also examined variables related to trends in population size. Unlike the situation in the prairie-parkland regions of North America, no annual breeding-ground surveys were conducted in eastern North America prior to 1990. Information on long-term trends in population size for eastern Mallards was available from two sources: the Midwinter Inventory (MWI) by the USFWS, and the North American Breeding Bird Survey (BBS) conducted by the CWS and USFWS. Both indices were available by state for 1966 through 1994. The MWI indexes the size of the winter population, and I combined state indices by summing the index values. Numbers from the BBS provide an index of annual changes in population size (Sauer and Geissler 1990). I calculated a regional BBS index as the weighted average of the state values using geographic area as weights. I examined different combinations of indices from the New England and mid-Atlantic states and selected the combination that demonstrated the highest correlation with the index of annual recruitment.

My model selection strategy was to fit all possible subset regressions from a group of variables and to identify the four models of each subset size that had the smallest error mean square. For each model I calculated Mallows' C_p as:

$$C_p = (\text{SSE}/\text{MSE}) - n + 2p, \qquad (6)$$

where MSE was the error mean square from the full model, SSE was the error sum of squares from the subset model, n was the sample size ($n = 29$), and p was the number of parameters in the subset model (including the intercept term; Mallows 1973, Neter et al. 1990). I compared values of C_p with the total number of parameters in a model (p) and identified parsimonious models as those with values of C_p close to p and $C_p < p$ (Mallows 1973, Hocking 1976).

I began model selection by examining single correlations between each predictor variable and the recruitment index. Multiple regression analysis was conducted using three variable sets: (1) spring and winter precipitation totals, spring and winter temperature means, and Canadian ponds; (2) precipitation totals, temperature means, and the MWI; and (3) precipitation totals, temperature means, and the BBS. When seasonal (spring, winter) variables exhibited poor correlation with the recruitment index, variables for individual months were substituted and selection procedures were repeated. Residuals from the selected models were plotted against cross products between the model parameters to identify interactions that potentially would improve the models (Henderson and Velleman 1981, Neter et al. 1990:128–129). Selection procedures were repeated to identify parsimonious models that included interaction terms.

I used a number of diagnostic statistics available in PROC REG (SAS 1990) to test for violations of model assumptions. I evaluated multicollinearity of independent variables and rejected models with variance-inflation factors greater than 10 and condition indices greater than 30 (Myers 1986:218–220).

TABLE 1. Regression models to predict annual recruitment of eastern Mallards using precipitation totals (P_{ij})[a] and mean temperatures (T_{ij})[a]. Models were fit using data from 1966 to 1994.

Variable	Parameter estimate	SE	R^2	PRESS
Intercept	0.783	0.053***	—	—
P_{winter}	0.011	0.008	0.056*	—
P_{May}	0.018	0.009*	0.154*	—
Model	—	—	0.210*	0.137
Intercept	1.395	0.300***	—	—
P_{winter}	0.015	0.007*	0.096*	—
T_{spring}	−0.011	0.006*	0.128*	—
$P_{April, NJ}$	0.031	0.009**	0.128*	—
$P_{April, PA}$	−0.028	0.012*	0.104*	—
Model	—	—	0.456***	0.109
Intercept	1.572	0.266***	—	—
P_{winter}	0.011	0.066	0.058*	—
T_{spring}	−0.011	0.005*	0.121*	—
$P_{April, PA}/P_{April, NJ}$	−0.014	0.031***	0.378***	—
Model	—	—	0.556***	0.093

[a] i = month (winter = January + February; spring = April + May); j = state.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

I examined partial regression leverage plots to assess model fit and identification of outliers, and normal residual plots for evidence of non-normality. I assessed the predictive ability of each model using the PRESS procedure (Neter et al. 1990). PRESS residuals (e_{i-1}) are defined as $e_{i-1} = y_i - y_{i-1}$, where y_i is the true value (i.e. the percentage of young) and y_{i-1} is the predicted value from the regression model fitted without data from year i. The PRESS procedure involves predicting the response variable for each year from the regression model fitted using data from the $n - 1$ remaining years. I calculated n PRESS residuals for each model, and the overall PRESS statistic as the sum of squares of the PRESS residuals (Myers 1986:105–111). The predictive ability of the models was assessed by comparing overall PRESS statistics; smaller values of PRESS indicated models with better predictive ability.

RESULTS

The MWI had the highest correlation with the recruitment index when I combined Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, and Vermont ($r = -0.442$, $P = 0.016$). The BBS index had the highest correlation with the recruitment index when I averaged indices from Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, Vermont, and New York ($r = -0.603$, $P < 0.001$). Both indices were negatively correlated with the recruitment index, suggesting that recruitment rates were lower at higher population sizes. The index to Canadian ponds was not highly correlated with the recruitment index ($r = 0.351$, $P = 0.062$). The Canadian pond index was negatively correlated with the Breeding Bird Survey index ($r = -0.437$, $P = 0.018$) but was not correlated with the New England MWI ($r = -0.255$, $P = 0.182$).

Precipitation totals for January, February, and both months combined were not correlated with the recruitment index ($P > 0.13$). Spring precipitation was correlated with the recruitment index ($r = 0.354$, $P = 0.06$); however, precipitation during May had a higher correlation with recruitment ($r = 0.392$, $P = 0.035$) than did precipitation during April ($r = 0.056$, $P = 0.775$). In contrast, the spring temperature mean was correlated with recruitment ($r = -0.357$, $P = 0.057$), but the weighted means for April and May were not ($P > 0.18$). Winter temperatures were not correlated with the recruitment index ($P > 0.50$).

Values of C_p indicated that the most parsimonious model, using winter and spring variables and Canadian ponds, contained P_{winter} and P_{spring} ($C_p = 2.03$; Table 1). Substitution of P_{May} for P_{spring} improved the model slightly; however, P_{winter} and P_{May} accounted for only 21% of the variation in the recruitment index ($P = 0.045$; Table 1). Precipitation totals for May were not correlated with precipitation totals for April (Table 2). Inspection of precipitation data for April revealed that P_{April} was not correlated with the recruitment index, but precipitation during April in New Jersey was ($r = 0.335$, $P = 0.076$). When I included state precipitation to-

TABLE 2. Correlation coefficients between mean temperature $(T_{ij})^a$, total precipitation $(P_{ij})^a$, and the Canadian pond index (CP).

	P_{winter}	P_{spring}	T_{winter}	T_{spring}	CP	$P_{April, NJ}$	$P_{April, PA}$
P_{winter}	—	0.052	−0.065	−0.171	0.347	−0.139	0.053
P_{spring}		—	0.380	−0.332	−0.146	0.538*	0.448*
T_{winter}			—	−0.118	−0.071	0.182	0.077
T_{spring}				—	−0.268	0.062	0.086
CP					—	−0.161	−0.179
$P_{April, NJ}$						—	0.730*
$P_{April, PA}$							—

[a] i = month (winter = January + February; spring = April + May); j = state.
*, $P \leq 0.05$.

tals for April, along with P_{winter}, P_{May}, T_{winter}, T_{spring}, and Canadian ponds, the most parsimonious model included P_{winter}, T_{spring}, $P_{April,NJ}$, and $P_{April,PA}$. Together, these four variables explained 46% ($P = 0.004$) of the variation in the recruitment index (Table 1).

Of interest was the positive coefficient for $P_{April,NJ}$ and the negative coefficient for $P_{April,PA}$ in the regression model (Table 1). To reduce collinearity between $P_{April,PA}$ and $P_{April,NJ}$ (Table 2), I combined them as a ratio ($P_{April,PA}/P_{April,NJ}$). This ratio of precipitation was negatively correlated with the recruitment index ($r = -0.622$, $P < 0.001$). I repeated the selection procedure including $P_{April,PA}/P_{April,NJ}$ along with P_{winter}, P_{May}, T_{winter}, and T_{spring}, and identified the three-term model P_{winter}, T_{spring}, and $P_{April,PA}/P_{April,NJ}$ as the most parsimonious model using climate ($C_p = 3.97$). These three variables explained 55.6% of the variation ($P < 0.001$) in the recruitment index (Table 1).

When I included MWI with the variables P_{winter}, P_{May}, T_{winter}, and T_{spring}, values of C_p identified the three-term model that included MWI and P_{May} ($C_p = 3.23$) as the most parsimonious model (Table 3). The most parsimonious model,

TABLE 3. Regression models to predict annual recruitment of eastern Mallards using combined USFWS Midwinter index (MWI) for New England and total precipitation $(P_{ij})^a$. Models were fit using data from 1966 to 1994.

Variable	Parameter estimate	SE	R^2	PRESS
Intercept	0.881	0.058***	—	—
MWI	−0.020	0.007*	0.196*	—
P_{spring}	0.014	0.007*	0.124*	—
Model	—	—	0.319**	0.112
Intercept	0.910	0.042***	—	—
MWI	−0.021	0.007***	0.196**	—
P_{May}	0.020	0.008*	0.163**	—
Model	—	—	0.358**	0.106
Intercept	0.990	0.040***	—	—
MWI	−0.022	0.007***	0.196*	—
$P_{April, NJ}$	0.031	0.009***	0.107	—
$P_{April, PA}$	−0.033	0.012***	0.168**	—
Model	—	—	0.471***	0.088
Intercept	1.116	0.037***	—	—
MWI	−0.019	0.006***	0.170**	—
$P_{April, PA}/P_{April, NJ}$	−0.139	0.031***	0.378***	—
Model	—	—	0.548***	0.074
Intercept	1.050	0.048***	—	—
MWI	−0.019	0.006**	0.170**	—
P_{May}	0.013	0.007*	0.062*	—
$P_{April, PA}/P_{April, NJ}$	−0.123	0.031***	0.378***	—
Model	—	—	0.610***	0.069

[a] i = month (winter = January + February; spring = April + May); j = state.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

TABLE 4. Regression models to predict annual recruitment of eastern Mallards using the combined Breeding Bird Survey Index (BBS) from New England and New York and total precipitation (P_{ij})[a]. Models were fit using data from 1966 to 1994.

Variable	Parameter estimate	SE	R^2	PRESS
Intercept	0.877	0.047***	—	—
BBS	−0.054	0.013***	0.364***	—
P_{winter}	0.013	0.006*	0.101*	—
P_{May}	0.014	0.007	0.069	—
Model	—	—	0.533***	0.094
Intercept	0.869	0.040***	—	—
BBS	−0.054	0.011***	0.364***	—
P_{winter}	0.018	0.005***	0.136**	—
$P_{April,\,NJ}$	0.027	0.007***	0.116*	—
$P_{April,\,PA}$	−0.021	0.010*	0.065*	—
Model	—	—	0.680***	0.069
Intercept	1.026	0.037***	—	—
BBS	−0.048	0.010***	0.237***	—
P_{winter}	0.015	0.005**	0.101**	—
$P_{April,\,PA}/P_{April,\,NJ}$	−0.120	0.026***	0.378***	—
Model	—	—	0.716***	0.057

[a] i = month (winter = January + February; spring = April + May); j = state.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

when state precipitation totals for April were added to the variable set, included MWI, $P_{April,PA}$, and $P_{April,NJ}$ ($C_p = 3.38$, $R^2 = 0.471$, $P = 0.001$). Substitution of $P_{April,PA}/P_{April,NJ}$ for $P_{April,PA}$, and $P_{April,NJ}$, improved the predictive ability of the model ($R^2 = 0.548$, $P < 0.001$). The most parsimonious model from the final variable set containing MWI included P_{May} and $P_{April,PA}/P_{April,NJ}$ ($C_p = 3.92$). This model explained 61% ($P < 0.001$) of the variation in the recruitment index (Table 3).

Models that included the BBS index generally exhibited better predictive ability than those constructed using the MWI (Table 4). The four-term model that included BBS, P_{winter}, and P_{May}, accounted for 53.3% of the variation in the recruitment index ($P < 0.001$). The final model incorporating BBS included P_{winter} and $P_{April,PA}/P_{April,NJ}$ ($C_p = 3.49$). This model explained 71.6% of the variation ($P < 0.001$) in the recruitment index (Table 4).

Interactions between population size and weather variables did not improve any of the models. PRESS statistics (Tables 1, 3, and 4) indicated that models containing MWI or BBS, along with winter precipitation, May precipitation, and $P_{April,PA}/P_{April,NJ}$, had the best predictive ability. Variance inflation factors and condition indices revealed no significant multicollinearity, and residual plots indicated no evidence of violation of model assumptions. Although models with BBS had higher R^2 and lower PRESS values than models with MWI, use of the BBS for harvest management presently is limited because the spring BBS is not available when harvest regulations are set in July (J. R. Sauer pers. comm.). Therefore, I selected the model containing MWI, P_{May}, and $P_{April,PA}/P_{April,NJ}$ as the most useful model. Predicted values from this model showed good correspondence to the percentage of young estimated from the harvest (Fig. 2). This model predicted that the percentage of young in the 1995 fall population was 49.8% (95% CI = 42.1 to 57.8%; age ratio = 1.021). The percentage of young, estimated from the 1995 Parts Collection Survey for the New England and mid-Atlantic states, was 51.0% (age ratio = 1.041).

DISCUSSION

The USFWS began to apply an adaptive resource management approach to the regulation of Mallard harvests in 1995 (Johnson et al. 1996). Adaptive resource management strategies (Holling 1978, Walters 1986) jointly consider the status of the resource and the uncertainty about the effects of management actions on resource dynamics. The role of quantitative models in adaptive harvest management is to provide a collective assessment of information from monitoring programs and to estimate changes in demographics and harvest rates based on alternate views about the relation-

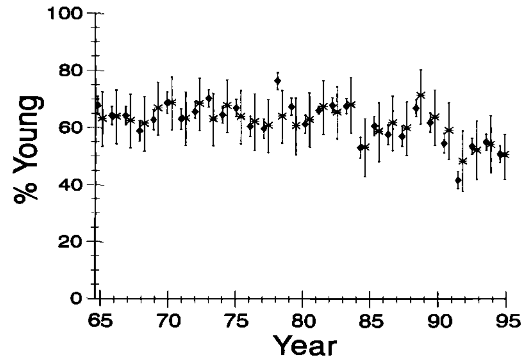

FIG. 2. Estimated (filled diamonds) and predicted (asterisks) values of the percentage of young female Mallards in the fall harvest in the New England and mid-Atlantic states, 1966 to 1995. Estimated values were calculated from the U.S. Fish and Wildlife Service Parts Collection Survey. Error bars on estimated values represent 95% confidence intervals. Error bars on predicted values represent 95% Bonferroni simultaneous prediction intervals. Predicted values are from the model $Y_i = 1.05 - 0.019(MWI) + 0.013(P_{May}) - 0.123(P_{April,PA} / P_{April,NJ})$, where Y_i *is the arcsine square root of the percentage of young, and* $P_{i,j}$ is the total precipitation during period i in state j.

ships among the factors that drive waterfowl population dynamics. Although alternative models can be constructed to provide adequate descriptions of the behavior of a system, models useful for management require an explicit causal structure in their formation (Holling 1978). My analyses demonstrate a correlation between climatic conditions and annual reproductive success of Mallards in eastern North America. Because of the observational nature of the data, these models do not support inference regarding cause and effect. However, they are useful because they provide insight into population and environmental factors that may influence the reproductive ecology of eastern Mallards, and because they provide an initial basis for the construction of recruitment models relevant to eastern Mallard populations.

Although the models do not reveal the mechanisms by which changes in climate affect reproductive success, the use of climatic conditions to predict trends in waterfowl recruitment is biologically relevant. Temperature affects the timing of nesting, and precipitation affects the quality of wetlands for brood rearing (Johnson et al. 1992). Models for eastern Mallards demonstrated that spring and winter precipitation were positively correlated with an index of recruitment. Models that included either MWI or BBS suggested that reproductive success declined as population size increased. Kaminski and Gluesing (1987) also demonstrated an inverse relationship between Mallard recruitment rates and population size and concluded that this relationship was significant during wet years but not during dry years or average years. My results did not suggest any difference in the effect of population size during wet and dry years (i.e. interactions between population size and precipitation were not significant). Although the empirical evidence indicates that Mallard recruitment rates are inversely related to population size, the lack of experimental data supporting density-dependent rates of recruitment underlies the uncertainty as to the mechanisms by which density dependence operates. It is not known whether the correlation between population size and recruitment will remain constant if the eastern Mallard population continues to increase, or if the population declines.

How the population indices (BBS and MWI) relate to the true size of the spring breeding population also is unknown. Breeding-pair surveys in eastern Canada and the Atlantic Flyway states have estimated the size of the breeding population annually since 1990. Comparison of the BBS and MWI with numbers of breeding pairs estimated from ground surveys in the northeastern United States suggests that the ground survey is positively correlated with the MWI ($r = 0.649$, $P = 0.163$) and with the BBS ($r = 0.628$, $P = 0.182$). However, the ability to detect a significant correlation was restricted due to the limited data base (1990 to 1994). As additional data are collected, the ability of the ground survey to monitor trends in the size of the breeding population should be evaluated and incorporated into models of recruitment for eastern Mallards.

My analyses demonstrate the potential to predict the percentage of young in the fall population of Mallards in eastern North America based on winter and spring precipitation and population size. The validity of these models depends on the representativeness of my estimate of annual recruitment. I attempted to minimize bias in the estimated percentage of young in the fall population by using age ratios from areas where more than 80% of the harvest was derived from eastern breeding stocks, and by adjusting age ratios in the harvest by the estimated differential vulnerability of young and adults to harvest. Direct estimates of annual recruitment, not presently available, are needed to test the validity of this index. In addition, because more than 80% of the harvest of female Mallards in the New England and mid-Atlantic states was derived from Mallards breeding the United States (Sheaffer and Malecki 1994), my index to recruitment did not represent Mallards breeding in eastern Canada.

In conclusion, the identification of factors that potentially influence recruitment of Mallards in the eastern North America is an important step in the adaptive management process. These factors provide a basis for the construction of meaningful hypotheses, and subsequently useful models, that capture the uncertainty about the reproductive ecology of this segment of the continental population. For example, uncertainty about future reproductive success could be modeled as structural uncertainty regarding the mechanism of density dependence (e.g. is it independent of environmental conditions?). Uncertainty about future recruitment also could be modeled as environmental uncertainty (i.e. random variation in annual precipitation). Future attempts to model the dynamics of Mallards in eastern North America should consider the effects of population size and precipitation on annual reproductive success.

ACKNOWLEDGMENTS

I thank F. A. Johnson, R. A. Malecki, and an anonymous referee for their suggestions. This study is a cooperative effort involving the New York Cooperative Fish and Wildlife Research Unit, the United States Geological Survey, Cornell University, and New York State Department of Environmental Conservation.

LITERATURE CITED

ANDERSON, D. R. 1975a. Optimal exploitation strategies for an animal population in a Markovian environment: A theory and an example. Ecology 56:1282–1297.

ANDERSON, D. R., 1975b. Population ecology of the Mallard. V. Temporal and geographic estimates of survival, recovery, and harvest rates. United States Fish and Wildlife Service Resource Publication No. 125.

ANDERSON, D. R., AND C. J. HENNY. 1972. Population ecology of the Mallard. I. A review of previous studies and the distribution and migration from breeding areas. United States Fish and Wildlife Service Resource Publication No. 105.

CAITHAMER, D. F., AND G. W. SMITH. 1995. North American ducks. Pages 34–37 *in* Our living resources (E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, Eds.). United States Government Printing Office, Washington, D.C.

CANADIAN WILDLIFE SERVICE AND U.S. FISH AND WILDLIFE SERVICE. 1996. Waterfowl population status, 1996. United States Government Printing Office, Washington, D.C.

ESTEL-COSTANZO, B., AND R. A. MALECKI. 1994. Nesting by dabbling ducks in western New York grasslands. Northeast Wildlife 51:13–20.

HEITMEYER, M. E., AND L. H. FREDRICKSON. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence Mallard recruitment? Transactions of the 46th North American Wildlife and Natural Resources Conference 46:44–57.

HENDERSON, H. V., AND P. F. VELLEMAN. 1981. Building multiple regression models interactively. Biometrics 37:391–411.

HOCKING, R. R. 1976. The analysis and selection of variables in linear regression. Biometrics 32:1–49.

HOLLING, C. S. 1978. International series on applied systems analysis. 3. Adaptive environmental assessment and management. John Wiley and Sons, New York.

HOUSTON, R. A., AND R. A. MALECKI. 1994. Habitat use and nest success of Mallards in bottomland hardwoods of western NewYork. Northeast Wildlife 51:21–28.

JOHNSON, D. H., J. D. NICHOLS, AND M. D. SCHWARTZ. 1992. Population dynamics of breeding waterfowl. Pages 446–485 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

JOHNSON, F. A., C. T. MOORE, W. L. KENDALL, J. A. DUBOVSKY, D. F. CAITHAMER, J. R. KELLEY, AND B. K. WILLIAMS. 1997. Uncertainty and the management of Mallard harvests. Journal of Wildlife Management 61:202–216.

JOHNSON, F. A., B. K. WILLIAMS, AND P. R. SCHMIDT. 1996. Adaptive decision-making in waterfowl harvest and habitat management. Pages 26–33 *in* 7th International Waterfowl Symposium (J. T. Ratti, Ed.). Memphis, Tennessee.

KAMINSKI, R. M., AND E. A. GLUESING. 1987. Density- and habitat-related recruitment in Mallards. Journal of Wildlife Management 51:141–148.

LARSSON, K., AND P. FORSLUND. 1994. Population dynamics of the Barnacle Goose *Branta leucopsis* in the Baltic area: Density-dependent effects on reproduction. Journal of Animal Ecology 63:954–962.

LOSITO, M. P., G. A. BALDASSARRE, AND J. H. SMITH. 1995. Reproduction and survival of female Mallards in the St. Lawrence River Valley, New York. Journal of Wildlife Management 51:23–30.

MALLOWS, C. L. 1973. Some comments on C_p. Technometrics 15:661–675.

MARTIN, E. M., AND S. M. CARNEY. 1977. Population ecology of the Mallard. IV. A review of duck hunting regulations, activity, and success, with special reference to the Mallard. United States Fish and Wildlife Service Resource No. Publication 130.

MARTIN, F. W., R. S. POSPAHALA, AND J. D. NICHOLS. 1979. Assessment and population management of North American migratory birds. Pages 187–239 *in* Environmental biomonitoring, assessment, prediction, and management—Certain case studies and related quantitative issues (J. Cairns, Jr., G. P. Pail, and W. E. Walters, Eds.). International Cooperative Publishing House, Fairland, Maryland.

MUNRO, R. E., AND C. F. KIMBALL. 1982. Population ecology of the Mallard. VII. Distribution and derivation of the harvest. United States Fish and Wildlife Service Resource Publication No. 147.

MYERS, R. H. 1986. Classical and modern regression with applications. Duxbury Press, Boston, Massachusetts.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models: Regression, analysis of variance, and experimental designs. Richard D. Irwin, Homewood, Illinois.

NICHOLS, J. D., AND J. E. HINES. 1987. Population ecology of the Mallard. VIII. Winter distribution patterns and survival rates of winter-banded Mallards. United States Fish and Wildlife Service Resource No. Publication 162.

POSPAHALA, R. S., D. R. ANDERSON, AND C. J. HENNY. 1974. Population ecology of the Mallard. II. Breeding habitat conditions, size of the breeding populations, and production indices. United States Fish and Wildlife Service Resource Publication No. 115.

ROTENBERRY, J. T., AND J. A. WIENS. 1991. Weather and reproductive variation in shrubsteppe sparrows: A hierarchical analysis. Ecology 72:1325–1335.

SAS INSTITUTE, INC. 1990. SAS/STAT user's guide, version 6, 4th ed., vol. 2. SAS Institute, Inc., Cary, North Carolina.

SAUER, J. R., AND P. H. GEISSLER. 1990. Estimation of annual indices from roadside surveys. Pages 58–62 *in* Survey designs and statistical methods for the estimation of avian population trends (J. R. Sauer and S. Droege, Eds.). United States Fish and Wildlife Service Biological Report No. 90(1).

SHEAFFER, S. E., AND R. A. MALECKI. 1996. Quantitative models for adaptive harvest management of Mallards in eastern North America. Report to the Atlantic Flyway Waterfowl Council Technical Section, New York Cooperative Fish and Wildlife Research Unit, Ithaca.

SHEAFFER, S. E., AND R. A. MALECKI. 1998. Distribution and derivation of the 1990–94 Mallard harvest in eastern North America. Northeast Wildlife 55: in press.

SHERRY, T. W., AND R. T. HOLMES. 1995. Summer versus winter limitation of populations: What are the issues and what is the evidence? Pages 85–120 *in* Ecology and management of Neotropical migratory birds (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

STRANGE, T. H., D. H. GORDON, AND J. A. TIMMERMAN, JR. 1989. Atlantic Flyway perspectives and expectations. Transactions of the 54th North American Wildlife and Natural Resources Conference 54:496–511.

WALTERS, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York.

WILLIAMS, B. K., F. A. JOHNSON, AND K. WILKINS. 1996. Uncertainty and the adaptive management of waterfowl harvests. Journal Wildlife Management 60:223–232.

ZAR, J. H. 1984. Biostatistics. Prentice-Hall, Englewood Cliffs, New Jersey.

Associate Editor: I. J. Ball