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Source: *Wildlife Monographs*, No. 150, Identification and Synthetic Modeling of Factors Affecting American Black Duck Populations (Oct., 2002), pp. 1-64

Published by: Wiley on behalf of the Wildlife Society

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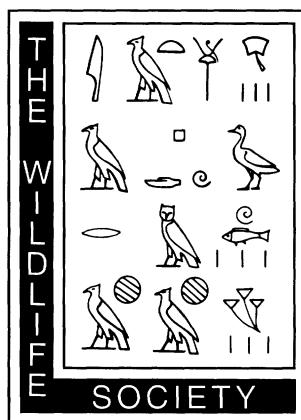
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Supplement to
The Journal of Wildlife Management
Vol. 66, No. 4, October 2002

WILDLIFE MONOGRAPHS

(ISSN:0084-0173)

A Publication of The Wildlife Society



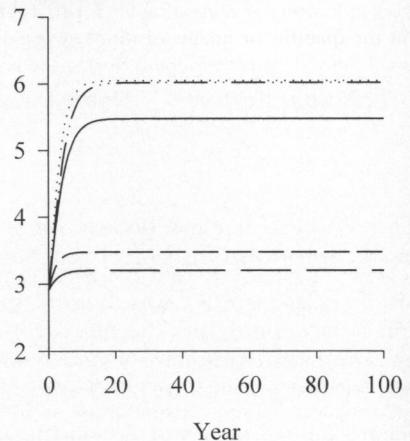
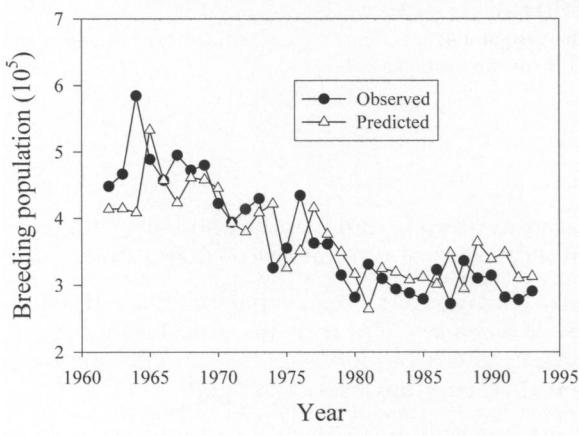
IDENTIFICATION AND SYNTHETIC MODELING OF FACTORS AFFECTING AMERICAN BLACK DUCK POPULATIONS

by

MICHAEL J. CONROY, MARK W. MILLER, AND JAMES E. HINES

NO. 150

OCTOBER 2002



FRONTPIECE. American black ducks during late migration in southern New Jersey. Comparison of predicted and observed abundances for the study period (1961–1993) and 100-year projections under model-averaged predictions (solid line) and 4 alternative models (Photo by Michael J. Conroy).

IDENTIFICATION AND SYNTHETIC MODELING OF FACTORS AFFECTING AMERICAN BLACK DUCK POPULATIONS

MICHAEL J. CONROY¹

U.S. Geological Survey, Biological Resources Division, Georgia Cooperative Fish and Wildlife Research Unit,
D. B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602

MARK W. MILLER²

D. B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602

JAMES E. HINES

U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, Laurel, MD 20708

Abstract: We reviewed the literature on factors potentially affecting the population status of American black ducks (*Anas rubripes*). Our review suggests that there is some support for the influence of 4 major, continental-scope factors in limiting or regulating black duck populations: 1) loss in the quantity or quality of breeding habitats; 2) loss in the quantity or quality of wintering habitats; 3) harvest, and 4) interactions (competition, hybridization) with mallards (*Anas platyrhynchos*) during the breeding and/or wintering periods.

These factors were used as the basis of an annual life cycle model in which reproduction rates and survival rates were modeled as functions of the above factors, with parameters of the model describing the strength of these relationships. Variation in the model parameter values allows for consideration of scientific uncertainty as to the degree each of these factors may be contributing to declines in black duck populations, and thus allows for the investigation of the possible effects of management (e.g., habitat improvement, harvest reductions) under different assumptions.

We then used available, historical data on black duck populations (abundance, annual reproduction rates, and survival rates) and possible driving factors (trends in breeding and wintering habitats, harvest rates, and abundance of mallards) to estimate model parameters. Our estimated reproduction submodel included parameters describing negative density feedback of black ducks, positive influence of breeding habitat, and negative influence of mallard densities; our survival submodel included terms for positive influence of winter habitat on reproduction rates, and negative influences of black duck density (i.e., compensation to harvest mortality). Individual models within each group (reproduction, survival) involved various combinations of these factors, and each was given an information theoretic weight for use in subsequent prediction. The reproduction model with highest AIC weight (0.70) predicted black duck age ratios increasing as a function of decreasing mallard abundance and increasing acreage of breeding habitat; all models considered involved negative density dependence for black ducks. The survival model with highest AIC weight (0.51) predicted nonharvest survival increasing as a function of increasing acreage of wintering habitat and decreasing harvest rates (additive mortality); models involving compensatory mortality effects received ≈ 0.12 total weight, vs. 0.88 for additive models.

We used the combined model, together with our historical data set, to perform a series of 1-year population forecasts, similar to those that might be performed under adaptive management. Initial model forecasts over-predicted observed breeding populations by $\approx 25\%$. Least-squares calibration reduced the bias to $\approx 0.5\%$ under prediction. After calibration, model-averaged predictions over the 16 alternative models (4 reproduction \times 4 survival, weighted by AIC model weights) explained 67% of the variation in annual breeding population abundance for black ducks, suggesting that it might have utility as a predictive tool in adaptive management.

We investigated the effects of statistical uncertainty in parameter values on predicted population growth rates for the combined annual model, via sensitivity analyses. Parameter sensitivity varied in relation to the parameter values over the estimated confidence intervals, and in relation to harvest rates and mallard abundance. Forecasts of black duck abundance were extremely sensitive to variation in parameter values for the coefficients for breeding and wintering habitat effects. Model-averaged forecasts of black duck abundance were also sensitive to changes in harvest rate and mallard abundance, with rapid declines in black duck abundance predicted for a range of harvest rates and mallard abundance higher than current levels of either factor, but easily envisaged, particularly given current rates of growth for mallard populations.

¹ E-mail: conroy@smokey.forestry.uga.edu.

² Present address: 336 S. Garfield Ave., Schuylkill Haven, PA 17972.

Because of concerns about sensitivity to habitat coefficients, and particularly in light of deficiencies in the historical data used to estimate these parameters, we developed a simplified model that excludes habitat effects. We also developed alternative models involving a calibration adjustment for reproduction rates, survival rates, or neither. Calibration of survival rates performed best (AIC weight 0.59, % BIAS = -0.280, $R^2 = 0.679$), with reproduction calibration somewhat inferior (AIC weight 0.41, % BIAS = -0.267, $R^2 = 0.672$); models without calibration received virtually no AIC weight and were discarded. We recommend that the simplified model set (4 biological models \times 2 alternative calibration factors) be retained as the best working set of alternative models for research and management.

Finally, we provide some preliminary guidance for the development of adaptive harvest management for black ducks, using our working set of models.

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Key words: Adaptive harvest management, American black duck, *Anas platyrhynchos*, *A. rubripes*, estimation, harvest, mallard, modeling, waterfowl.

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INTRODUCTION

For decades, cohesive management of American black ducks has been frustrated by a lack of agreement about the causes of and appropriate management response to declining populations. This is in spite of the fact that the species has been intensively monitored and studied over most of its range, and that basic information on life-history, distribution, and population dynamics is fairly well known (Rusch et al. 1989). Although it is generally accepted that black duck numbers have declined continentally, the decline has not been uniform across the range. Furthermore, fundamental disagreement exists about the relative importance of harvest, habitat change, and interspecific interactions in causing the decline in black ducks (Rusch et al. 1989, Conroy and Krementz 1990). Black duck populations may have stabilized (or at least decreased in rate of decline) concurrently with harvest restrictions, but they have not recovered in portions of the historical range where they have declined severely, as discussed below. To date, monitoring and research have left unresolved fundamental questions about the potential for improving the status of black duck populations through habitat and harvest management.

Our objective was to develop predictive models of population response to management activity, in the face of unresolved questions about the relative importance of proposed limiting or controlling factors. Herein, we have reviewed evidence in support of the major factors that have been invoked to explain the decline of American black duck populations. We then used this review as the basis for development of a population model which allows explicit predictions about the consequences of alternative management actions under competing hypotheses. Using available data, we performed a synthetic analysis to estimate model parameters and, where possible, to provide insights as to the relative importance of alternative explanatory factors and management actions; we also identify critical information needs.

Acknowledgments.—This work was supported by Cooperative Agreement 1434-HQ-97-RU-01551, Research Work Order 40 to the

Georgia Cooperative Fish and Wildlife Research Unit, with funding from the U.S. Fish and Wildlife Service; USGS Biological Resources Division, Patuxent Wildlife Research Center and Cooperative Research Units Center; and the Canadian Wildlife Service. We thank M. J. Petrie for providing compiled statistics on beaver harvest in Canada. J. D. Nichols, M. J. Petrie, J. T. Peterson, and M. C. Runge provided critical comments on earlier drafts, and their input has greatly improved the resulting manuscript. Model selection and model-averaged estimation was greatly facilitated by a SAS macro written by W. L. Thompson and J. T. Peterson. The final draft was greatly improved through critical comments by the consulting editors, F. A. Johnson and J. R. Longcore. The Georgia Cooperative Fish and Wildlife Research Unit is jointly sponsored by the Biological Resources Division, the University of Georgia, the Georgia Department of Natural Resources, and the Wildlife Management Institute.

EVIDENCE FOR THE BLACK DUCK DECLINE

Before reviewing factors that may have contributed to the black duck decline, we first consider the evidence for the decline itself. Although population surveys have been conducted in portions of the breeding range of black ducks (Fig. 1a) and are discussed below, there have not been continuous, range-wide surveys of black duck numbers over the period of apparent decline (1950s to present). Instead, the Midwinter Waterfowl Inventory (MWI) has constituted the primary evidence of a decline in the continental population. Wintering waterfowl populations and habitats are surveyed in each of the 48 conterminous states and Ontario (Crissey 1975, unpublished USFWS report, Laurel, Maryland); surveys have been conducted each year since 1955, usually in early January. The survey possesses numerous shortcomings for estimating population size: absence of an adequate sampling frame, non-stratification among habitat types, non-standardized sampling methodology within surveyed areas, and absence of correction factors for visibility bias (Conroy et al. 1988, Eggeman and

Johnson 1989, Rusch et al. 1989). Despite these shortcomings, the MWI may be useful

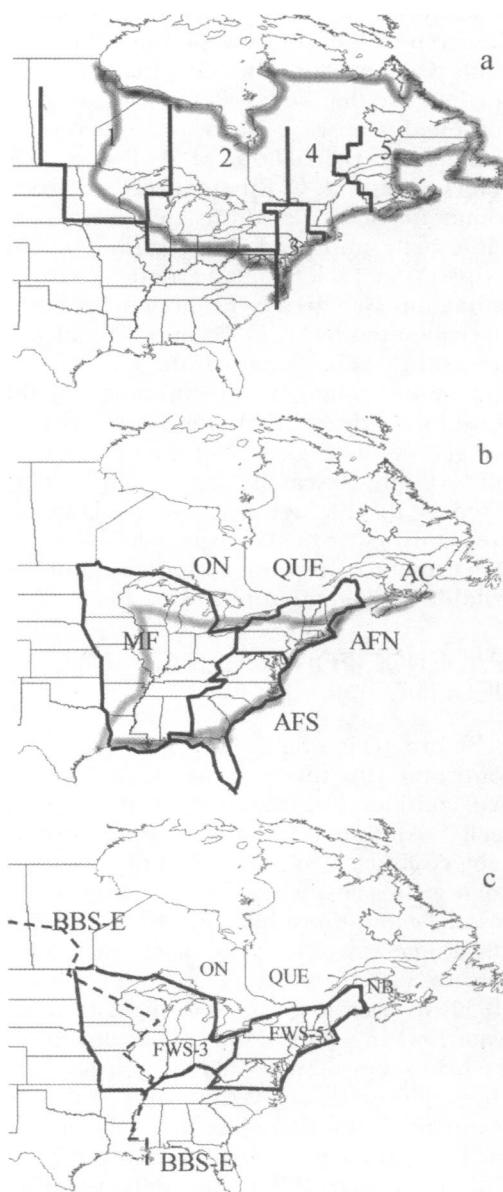


Figure 1. Geographic areas referenced in review and analyses. (a) Breeding range of American black ducks (gray outline, Blandin 1992) and pre-season banding reference areas 1–5 (Smith 1997). (b) Wintering range of American black duck (gray outline, Blandin 1992) and Administrative Flyways of the U.S. and regions in Canada; AFN = Northern Atlantic Flyway, AFS = Southern Atlantic Flyway, MF = Mississippi Flyway, AC = Atlantic Canada (Maritimes), ON = Ontario, QUE = Québec. (c) Eastern region of the Breeding Bird Survey (BBS-E, east of dashed line) administrative regions referred to in BBS analysis. FWS-3 = Region 3 USFWS, FWS-5 = Region 5 USFWS, ON = Ontario, QUE = Québec, NB = New Brunswick.

for detecting long-term population trends (Feierabend 1984, Eggeman and Johnson 1989). For example, Conroy et al. (1988) devised an experimental sampling protocol for estimating abundance of black ducks wintering in coastal habitats which generally agreed with the MWI over a 3-year period.

Data from the MWI suggest a steep decline in black duck numbers since 1955, although debate continues over the degree and geographic scope of the decline, and whether populations have recently stabilized or possibly increased (e.g., Alison 1976, Rogers and Patterson 1984, Dennis et al. 1989, Rusch et al. 1989, Nudds et al. 1996). The decline in winter black duck counts since 1955 is well known. However, the MWI actually began in 1935 (Crissey, W.F., 1975, unpublished USFWS report, Laurel, Maryland). Unpublished data from 1948–1954 (USFWS Office of Migratory Bird Management) suggests that black duck abundance was at a high in 1955, and that mean abundance during 1989–98 (287,410 birds) was 52% below mean abundance during 1948–57 (606,252 birds). Perhaps most surprising, the 1976 population estimate (434,350 birds) was higher than the 1948 estimate (411,999 birds), although improvements in survey procedures may have produced more reliable MWI estimates since 1955 than in earlier years.

To estimate rates of population decline and test for possible geographic heterogeneity in these rates, we analyzed MWI data for black ducks for the Atlantic and Mississippi Flyways, 1955–2001. We further stratified the Atlantic Flyway into a northern (AFN) and southern region (AFS; Fig. 1b) and for analysis combined the latter with the Mississippi Flyway (MF) because of similarity of harvest derivation for these 2 regions (Geis et al. 1971, N. L. Zimpfer, unpubl. data). We fit an exponential model to the stratified data using PROC GENMOD (SAS Institute 1999), specifying a log link function and a Poisson-distributed error. Our global model was

$$\log_e(\text{MWI}_t) = \beta_0 + \beta_1 X_1 + \beta_2 t + \beta_3 X_1 t,$$

where X_1 is a dummy variables for AFN vs. AFS-MF, and t is years elapsed since 1955. We developed 5 alternative models retaining various of the above effects, ranging from no

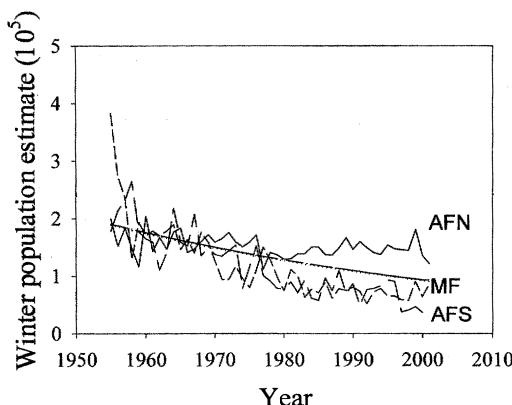


Figure 2. Trends by wintering in American black duck populations from the midwinter waterfowl inventory (MWI), 1956–2001, for northern Atlantic Flyway (AFN, Fig. 1b), southern Atlantic Flyway (AFS), and Mississippi Flyway. MWI observations superimposed on predictions from trend model (see text).

effects (β_0) to a global model ($\beta_0 - \beta_3$). We used a SAS (1999) model selection macro (W. L. Thompson and J. T. Peterson, personal communication) to rank these models by AIC weights and compute model-averaged estimates of ($\beta_0 - \beta_3$) (Burnham and Anderson 1998). The model-averaged estimates were used to provide predicted trajectories for AFN, AFS, and MF, along with the observed MWI values for these regions (Fig. 2). The analyses support overall similar rates of decline among regions, although there is an indication of moderation of the decline, particularly in the AFN, since 1980. We caution that inherent methodological problems of the MWI and possible changes in survey effort over time and between regions may make conclusion about trend based on the MWI suspect (Conroy et al. 1988, Eggeman and Johnson 1989).

We used online data and analytical tools at the Breeding Bird Survey (BBS; Robbins et al. 1986) website (www.mbr-pwrc.usgs.gov/bbs; Sauer et al. 2001) to compute rates of population change over 1966–2000 for breeding black duck populations range wide (approximated by BBS-E, Fig. 1c) and in selected geographic strata over the range (Table 1, Fig. 1c). Point estimates indicated declining populations over this period for 4 of 6 of these strata, with declines especially pronounced in Ontario and Québec; however, in all cases the 95% CI included zero,

Table 1. Estimates of breeding population trend, 1966–2000, from the Breeding Bird Survey American black ducks and sympatric species of waterfowl species.

Species	Region ^a	Number of routes	% Trend ^b	95% confidence interval	
				Lower	Upper
American black duck					
BBS-E	260	-1.480	-3.711	0.751	
ON	24	-2.770	-7.606	2.066	
QUE	35	-2.230	-8.172	3.712	
NB	23	1.100	-4.688	6.888	
FWS-3	16	2.300	-4.192	8.792	
FWS-5	131	-0.780	-3.082	1.522	
Mallard					
BBS-E	966	3.790	1.744	5.836	
ON	95	1.050	-2.831	4.931	
QUE	27	25.470	8.553	42.387	
NB	3	25.650	19.527	31.773	
FWS-3	434	2.250	0.720	3.780	
FWS-5	424	9.270	2.877	15.663	
Green-winged teal					
BBS-E	26	64.870	46.841	82.899	
ON	5	-0.060	-12.303	12.183	
QUE	5	80.130	77.508	82.752	
NB	4	0.500	-2.270	3.270	
FWS-3	9	-1.080	-5.972	3.812	
FWS-5	— ^c	—	—	—	—
American wigeon					
BBS-E	14	21.570	11.340	31.800	
ON	—	—	—	—	—
QUE	3	62.410	61.338	63.482	
NB	6	8.210	2.150	14.270	
FWS-3	—	—	—	—	—
FWS-5	—	—	—	—	—
Northern pintail					
BBS-E	17	14.800	-13.973	43.573	
ON	4	-4.500	-6.602	-2.398	
QUE	5	48.460	-17.688	114.608	
NB	—	—	—	—	—
FWS-3	19	-11.860	-25.020	1.300	
FWS-5	—	—	—	—	—
Wood duck					
BBS-E	823	5.060	3.469	6.651	
ON	55	8.660	4.682	12.638	
QUE	7	8.900	-16.685	34.485	
NB	3	8.040	5.624	10.456	
FWS-3	336	4.140	0.986	7.294	
FWS-5	257	7.970	2.560	13.380	
Ring-necked duck					
BBS-E	55	3.610	0.548	6.672	
ON	8	3.210	-1.311	7.731	
QUE	9	5.600	-14.998	26.198	
NB	3	10.110	-13.658	33.878	
FWS-3	23	12.130	-5.384	29.644	
FWS-5	5	3.240	-9.798	16.278	

(Continued)

^a See Figure 1c.

^b Average % annual change during 1966–2000. Data and analytical tools available at <http://www.mbr-pwrc.usgs.gov/bbs> (Sauer et al. 2001). Estimation via method of estimating equations (Link and Sauer 1994).

^c No estimate available at indicated level of stratification.

Table 1 (continued). Estimates of breeding population trend, 1966–2000, from the Breeding Bird Survey American black ducks and sympatric species of waterfowl species.

Species	Region ^a	Number of routes	95% confidence interval	
			% Trend ^b	Lower
Common goldeneye				
BBS-E	39	-3.110	-9.512	3.292
ON	16	-8.610	-19.433	2.213
QUE	7	20.940	-2.035	43.915
NB	5	-0.210	-8.681	8.261
FWS-3	3	-0.740	-27.595	26.115
FWS-5	3	-24.690	-77.945	28.565
Common merganser				
BBS-E	133	4.010	0.338	7.682
ON	23	0.360	-3.113	3.833
QUE	22	8.920	-5.954	23.794
NB	13	-2.170	-23.170	18.829
FWS-3	13	12.680	4.177	21.183
FWS-5	55	15.930	6.201	25.659
Red-breasted merganser				
BBS-E	20	-10.440	-20.057	-0.823
ON	3	9.000	-12.860	30.860
QUE	—	—	—	—
NB	3	-16.890	-30.080	-3.700
FWS-3	4	-9.500	-12.917	-6.083
FWS-5	—	—	—	—
Hooded merganser				
BBS-E	58	7.010	-6.265	20.285
ON	13	6.240	-9.966	22.446
QUE	3	19.800	12.196	27.404
NB	—	—	—	—
FWS-3	28	4.210	-5.019	13.439
FWS-5	19	18.530	11.800	25.260

^a See Figure 1c.

^b Average % annual change during 1966–2000. Data and analytical tools available at <http://www.mbr-pwrc.usgs.gov/bbs> (Sauer et al. 2001). Estimation via method of estimating equations (Link and Sauer 1994).

^c No estimate available at indicated level of stratification.

suggesting weak evidence for a decline. Positive trend estimates for New Brunswick were consistent with a general belief of stable to increasing black duck populations in that region. In contrast, the positive values for USFWS Region 3 seem contrary to evidence from aerial surveys that black duck populations have dramatically declined in that region (data on file, USFWS Off. Migratory Bird Management, Laurel MD). Again, these estimates are imprecise with CIs encompassing zero. Furthermore, there may be heterogeneity in the rates of population change within this stratum. For instance, the Great Lakes Transition Regions (Robbins et al. 1986:12), which includes northern Lower Michigan, Upper Michi-

gan, and northern Wisconsin, exhibited an apparent declining BBS trend over this same period (trend = -11.6, 95% CI = -21.3 – 21.0, n = 4 routes). We note that most BBS routes in Ontario and Québec are located in the southern half of these provinces and as such provide trend estimates potentially unrepresentative of these provinces as a whole. Finally, we caution that the BBS is uncorrected for imperfect and heterogeneous rates of detection, further confounding spatio-temporal inferences.

Fixed-wing aerial surveys of breeding black ducks have occurred in western Ontario most years since 1955, but methods have varied over time. Fixed-wing surveys also occurred throughout much of eastern Canada in the 1950s and 1960s (Kaczynski and Chamberlain 1968) and resumed in 1990 (USFWS Office of Migratory Bird Management, unpublished data). Helicopter plot surveys were also initiated during this later period (Memo. on file, Can. Wildl. Serv., Ottawa, 1999). Black duck populations have not declined in the boreal forest of western Ontario (Nudds et al. 1996). In eastern Canada comparison of estimated mean black duck density between early and recent surveys (M. W. Miller, unpublished data) provides no evidence of a change in the boreal forest of eastern Ontario (Area 2, Fig. 1a) but some indication of an increase in Québec and Labrador (Areas 4 and 5, Fig. 1a). However, absence of a valid statistical design, visibility correction, or variance estimate for the earlier surveys make comparisons over time and space of doubtful value, and we thus do not report statistical estimates of apparent changes.

Several possible explanations exist for the apparent inconsistency between wintering and breeding population trends since the mid-1950s. Either the midwinter or breeding ground surveys, or both, are unreliable for detecting trends; an increasing proportion of the black duck population may now winter in the Maritime, St. Lawrence or Great Lakes region of Canada; or black ducks wintering in the U.S. may have shifted their distribution such that larger numbers now settle in unsurveyed, or poorly surveyed areas away from coastal and riverine habitats typically used by this species in the past. However, Christmas Bird Count data

(Butcher 1990) also indicate a declining black duck population (J. R. Sauer, unpublished data, USGS Patuxent Wildlife Research Center, Laurel, Maryland), suggesting that wintering black ducks have not simply redistributed into areas not surveyed or poorly surveyed by the MWI. One possible explanation consistent with all available evidence is that declining winter counts reflect declines in breeding populations primarily outside the boreal forest (i.e., southern Ontario, southern New England, the Mid-Atlantic states, and the U.S. Midwest), while populations breeding primarily within the boreal forest have remained relatively constant or increased (i.e., western, central, and northern Ontario, Québec, the Atlantic Provinces, and northern New England).

We also examined BBS data for other waterfowl species that breed sympatrically with black ducks to look for community-level patterns in trend (Table 1). These other species included mallards, green-winged teal (*Anas crecca*), American wigeon (*A. americana*), northern pintail (*A. acuta*), wood duck (*Aix sponsa*), ring-necked duck (*Aythya collaris*), common goldeneye (*Bucephala clangula*), common Merganser (*Mergus merganser*), red-breasted merganser (*M. serrator*), and hooded merganser (*Lophodytes cucullatus*). Of these species only the common goldeneye and red-breasted merganser had negative BBS trends in large-scale regions where black ducks breed (Fig. 1c, Table 1). Indeed, 7 of these waterfowl species exhibited increasing BBS trends (i.e., 95% CI of trend did not encompass 0). These results are not consistent with common, large-scale phenomena affecting all sympatric waterfowl species. We recognize, of course, that niche specificity may have resulted in different species responding in a dissimilar manner to common factors. Finally, we reiterate that BBS data must be used with caution for estimating waterfowl trends, due to the roadside nature of the BBS, the relative paucity of BBS routes within much of the boreal forest, and the fact that the BBS is an uncorrected for incomplete detection (Sauer et al. 2001; J. R. Sauer, personal communication).

We conclude that substantial evidence exists that the continental black duck population has declined over several decades in at

least some portions of its range. In comparison to other waterfowl species, and particularly mallards, black ducks appear to have declined at greater rates than could be expected due to common factors affecting all species of waterfowl within the black duck's range. Again, we caution that several of the data sets we used are not directly comparable to one another, and that methodological problems exist to render comparisons over time, space, and between species problematic. In spite of these difficulties, it appears likely that the black duck's decline is real and not an artifact of survey design and data. In the next section we review potential causes of that decline.

REVIEW OF POPULATION FACTORS

We organized our review by the 4 major factors that have been proposed to explain the black duck decline: reductions in quantity or quality of 1) breeding or 2) wintering habitat, 3) effects of harvest, and 4) interactions (competition and hybridization) with mallards. Although other factors may have contributed to declining black duck populations, the above 4 involve broad (i.e., continental-scale) phenomena that logically could have had such an effect, and reasonably good reasons exist, both empirical and theoretical, for postulating each as a cause. Furthermore, at least the first 3 of these are potentially under the control of managers, so that identification of them as important limiting factors has bearing for future management actions. In Table 2 we summarize the scale at which each factor is examined.

Evidence for and against each of these factors has been reviewed periodically (Rusch et al. 1989, Conroy and Krementz 1990, Nudds et al. 1996), with inconclusive results. This state of affairs is, in part, the result of research approaches, which have tended to address single, potential causative factors, in a non-experimental context. Large-scale, manipulative experiments for testing importance of the above factors either one at a time (Anderson et al. 1987, Nichols 1991) or simultaneously (Nudds et al. 1996) have been proposed, but are logically difficult and expensive.

We discuss each factor to the extent possible, in the spirit of marshaling a "defense"

Table 2. Spatial scales at which factors potentially related to the black duck decline were examined.

Factor	Variable	Scale
Breeding habitat		
	Canadian forest	Banding regions (Fig. 1a)
	Beaver abundance	Québec
	Acidic precipitation	Total breeding range
Wintering habitat		
	Coastal emergent wetlands	AFN, AFS (Fig. 1b)
	Submerged aquatic vegetation	Chesapeake Bay
	Lead shot	Total wintering range
	DDT and DDE	Atlantic Flyway (Fig. 1b)
	Mercury	AFN, AFS (Fig. 1b)
	Prey species abundance	AFN, AFS (Fig. 1b)
	Winter climate	AFN (Fig. 1b)
Harvest		Rangewide
Mallards		Rangewide
	Hybridization	Rangewide
	Competition	Rangewide
Parasites and disease		Rangewide

of each as a plausible contributor to the black duck decline. We do this for two reasons. First, the purpose of our review is neither to support nor to reject any particular factor as a cause of the black duck decline, but instead to review objectively the evidence for each major, plausible factor. Second, we suggest that a strict hypothetico-deductive (Romesburg 1981) approach using single factors is almost certainly impossible, owing to our inability to control any of the factors under question. Instead of seeking to reject individual factors as hypotheses, we believe that it is more fruitful to direct efforts to determine the magnitude of influence of each for use in predictive modeling, which is the approach we have taken in SYNTHETIC POPULATION MODEL FOR AMERICAN BLACK DUCKS.

Breeding Ground Habitat

Reduced quality or quantity of breeding habitat may have caused a decline in the black duck population by affecting reproduction or survival rates. If reduced habitat quantity were responsible for the decline, one would predict that acreage of breeding habitat and some measure of abundance, survival or recruitment would correlate pos-

itively. Likewise, if reduced habitat quality were a significant cause of the decline, then one would predict that abundance, recruitment, or survival, and chemical or other indicators of wetland quality would correlate. We review the evidence for such relationships, after first describing general features of black duck habitats and habitat selection.

Breeding Habitats and Habitat Selection.—Habitat selection has been studied throughout the breeding season, generally in terms of the vegetation or water chemistry of occupied wetlands versus unoccupied wetlands. Black ducks are thought to prefer forested wetlands in boreal landscapes and coastal marshes farther south (Stewart 1958, Bellrose 1980), although they breed in a wide range of habitat types (Kirby 1988). Most studies that related habitat use to vegetation have been conducted in New England and the St. Lawrence Estuary (Area 4, Fig. 1a) and the Atlantic Provinces of Canada (Area 5, Fig. 1a). In these regions breeding black ducks prefer persistent emergent, deciduous forest and deciduous scrub-shrub wetlands (Ringelman et al. 1982, Dwyer and Baldassarre 1994) or palustrine emergent and tidal wetlands (Bélanger and Lehoux 1994, Seymour and Jackson 1996). Numerous studies have reported that breeding black ducks tend to be associated with forested beaver (*Castor canadensis*) ponds (Coulter and Mendall 1968, Ringelman and Longcore 1982, Diefenbach and Owen 1989, Merendino et al. 1995). Post fledging black ducks use riverine, palustrine emergent, and tidal wetlands in the northeastern portion of their range (Frazer et al. 1990).

We found no studies of habitat selection in terms of vegetation type in other portions of the black duck breeding range. However, breeding black duck occur throughout the boreal forest of Ontario (corresponding approximately with Area 1, Fig. 1a; Ross and Fillman 1990), in forested wetlands in the U.S. Midwest, in emergent marshes along the Great Lakes (Area 2, Fig. 1a, Peterjohn and Rice 1991, Brauning 1992), and in forested areas and coastal marshes in the Mid-Atlantic states (Area 3, Fig. 1a; Stotts and Davis 1960, Hess et al. 2000).

Studies of habitat selection in terms of water chemistry have found that breeding

black ducks prefer nutrient rich wetlands (McNicol et al. 1987, Merendino and Ankney 1994, Staicer et al. 1994). Experimental fertilization of wetlands has resulted in increased use by black ducks (Brylinsky 1993). Black ducks however are capable of breeding successfully on oligotrophic and mesotrophic forested wetlands (Seymour and Jackson 1996).

Habitat Quantity.—Long-term data on acreage of forested wetlands are available for the United States. Area of commercial forest by state and forest type generally is estimated every 13 years by the U.S. Forest Service. Each state has completed 3–4 such surveys since the early 1950s. Many of these data are available via the Internet from the Forest Inventory and Analysis Data Base Retrieval System (www.ncrs.fs.fed.us). We used these forest data for Maine, New Hampshire, Vermont, Massachusetts, New York, Rhode Island, Connecticut, New Jersey, Maryland, Delaware, Pennsylvania, Michigan, Wisconsin, and Minnesota. Three forest types were considered wetland forest: spruce-fir (*Picea* spp.–*Abies balsamea*), elm-ash-cottonwood (*Ulmus* spp.–*Fraxinus* spp.–*Populus* spp.) and oak-tupelo-bald cypress (*Quercus* spp. *Nyssa sylvatica*–*Taxodium distichum*). Gaps in data for a given forest type within a given state were filled using linear interpolation (i.e., missing years computed as the mean of adjacent years).

Unfortunately, forest classification varied among states and over time within a state. In particular, all red maple was apparently included in the elm-ash-red maple group in early surveys in some states. In later surveys a portion of red maple was classified separately in 1 or 2 upland forest types, and the remaining portion was included in the elm-ash-cottonwood group. Recent surveys reported data from the previous survey reclassified using the revised classification system. Data from the earliest surveys however were never revised. We estimated the proportion of lowland red maple in the elm-ash-red maple group in the earliest surveys by using the average of those proportions in later surveys derived by comparing data for the same year based on the revised and the older forest classification system. Annual estimates of spruce-fir, elm-ash-cottonwood and oak-gum-cypress forests in each state

were summed to obtain an annual total acreage of wetland forest within the U.S. portion of the black duck breeding range.

Similar data in Canada are not available. Area of forest is estimated by province every 5–10 years as part of the Canadian census (unpublished data, Statistics Canada). These data were used for all provinces from Ontario eastward, except Newfoundland, to estimate forest area within the Canadian portion of the black duck's breeding range. Estimates for Newfoundland were excluded because they showed extreme temporal fluctuations, suggesting sampling error rather than ecological trends. The Canadian land classification system has been revised several times, making comparison of land cover estimates among years suspect. Nevertheless, these data are the only known estimates of large-scale forest cover in eastern Canada. As above, interpolation was used to fill gaps in data within individual provinces. Recently, mapping of black duck habitat has been conducted in Québec using logistic regression models and remote sensing (Grenier et al. 1993, 1994) and appears to have utility for predicting abundance of black ducks breeding in the St. Lawrence Valley (Bordage, D., unpubl. report, Canad. Wildl. Serv.).

Acreage of forest wetlands in the northeastern U.S. decreased by 9%, or 891,000 ha, since the mid-1960s. The largest percent decreases occurred in the northeastern states (–25%, 1.1 million ha, corresponding approximately with Area 4, Fig. 1a) and the eastern states (–14%, 164,000 ha, Area 3, Fig. 1a). An 18% increase in area of forested wetland was detected in the northwestern states (511,000 ha, Region 1). During 1961–1996 the area of total forested land in Canada declined by 4%, or 4.25 million ha. The largest decline occurred in Ontario (9%, 4.0 million ha, Region 2); Québec (Area 4, Fig. 1a) lost 2%, or 0.93 million ha, of forest during this period; and area of forest increased by 6% (637,000 ha) in the Atlantic Provinces (Area 5, Fig. 1a).

Use of these data may not accurately portray black duck breeding habitat, as black ducks will nest in upland forests, as well as in freshwater and tidal marshes (Stotts and Davis 1960, Seymour 1984) and cut-over areas (Longcore et al. 1990). Furthermore,

our U.S. forest area data were restricted to commercial forests. An unknown portion of wetland forest in each state is considered unproductive or non-commercial forest or even non-forest land and was not included in the database used here. Under the U.S. Forest Service Forest Inventory classification system unproductive forest includes mostly state parks and other areas where timber harvest is banned by statute.

Some evidence suggests that loss of forest cover could cause a decline in breeding black duck abundance. Black ducks breeding in southern Ontario during 1971–1995 were 250% more abundant in heavily forested areas ($\geq 75\%$ forest cover) vs. largely unforested areas ($\leq 25\%$ forest cover) based on estimated forest cover in aerial photographs of plots surveyed by Dennis et al (1989; ANOVA, $F = 3.22$, $P < 0.001$, T. D. Nudds and M. W. Miller, unpublished data). Effects of timber harvest and urbanization, or their interaction, around wetlands on black duck abundance and production are unknown. Some biologists have suggested that, in some instances, clear-cutting may increase, rather than decrease black duck productivity, particularly in a boreal environment (J. C. Davies, Ontario Ministry of Natural Resources, personal communication; Longcore et al. 1990). Human disturbance alone may exclude black ducks from otherwise suitable breeding habitat (Morton 1998).

Beaver Populations.—If beaver populations have increased within the breeding range of the black duck, then quality of breeding habitat for broods may have improved. The price-adjusted beaver harvest in eastern Canada increased during 1961–1996, controlling for variation in the price of pelts adjusted for inflation ($t = 4.35$, $P < 0.01$; unpublished data, M. J. Petrie), suggesting that the beaver population in Québec may have increased. Alternatively, this could simply reflect an increase in number of trappers or trapper effort, rather than number of beaver. Furthermore, if beaver populations have increased mostly in urbanized areas, this may not reflect improved black duck breeding habitat (Morton 1998). Nevertheless, an increase in beaver populations in Québec (assuming that this translated into improved habitat conditions for black

ducks) would be consistent with an increase in abundance of black ducks in the boreal forest of Québec mentioned earlier. Unfortunately, mean number of beaver pelts harvested may not be a reliable index to either beaver populations or black duck breeding habitat quality.

Acidic Precipitation.—Acidic precipitation resulting from atmospheric pollution may have reduced black duck productivity on the breeding grounds, resulting in a population decline (Haines and Hunter 1981). This could occur if lowering pH reduces invertebrate biomass for black ducks, increases concentrations of heavy metals toxic to black ducks, or reduces black duck egg or duckling survival by reducing dietary calcium. Approximately 17% of the black duck's breeding range is vulnerable to acidic precipitation (Longcore et al. 1987b) and pH of lakes in northeastern North America apparently did decline between the 1930s and 1970s (reviewed in Haines and Hunter 1981, see also Kelso et al. 1992).

Studies that have tested for correlations between growth, survival and production of black duck duckling and wetland pH have provided conflicting results (DesGranges and Hunter 1987, Haramis and Chu 1987, Hunter et al. 1986, McNicol et al. 1987). In spite of possible negative effects of acidification, black ducks can be productive on nutrient-poor wetlands; likewise productivity can remain high on oligotrophic wetlands (Seymour and Jackson 1996, Longcore et al. 1998).

Acid rain might elevate levels of Al and Cd in wetlands by reducing pH (Nelson and Campbell 1991), and black ducks and mallards can accumulate Al, Cd and other metals in their tissue (DiGiulio and Scanlon 1984, Sparling 1991). Al and Cd are known to affect survival, production or behavior of captive mallards or black ducks (White and Finley 1978, White et al. 1978, Heinz et al. 1983, Sparling 1990, 1991, Silver and Nudds 1995). Scheuhhammer (1991) concluded, however, that wild omnivores were unlikely to experience significant health risks from exposure to levels of Cd and Al reached in acidified wetlands. That author believed that reduced availability of dietary Ca in acidified wetlands was a much greater health risk. Regardless, we could find no long-term

databases of water quality in wetlands on the breeding grounds with which to incorporate this factor in modeling efforts.

Summary of breeding ground habitat factors.—The data above suggest that circumstantial evidence exists for a linkage between declines in black duck populations, and declines in both the quantity and quality of breeding ground habitat. Virtually all of the evidence, however, is non-experimental and correlative. Although declines have been documented in the quantity, or in quality, or both of breeding habitats in some portions of the range, in other regions habitats appear stable. We believe that the evidence does not unequivocally support a breeding ground habitat hypothesis as explaining the decline in the black duck population. Conversely, we believe that the evidence is insufficient to rule out breeding habitat as an explanatory factor, and thus the hypothesis should be provisionally retained for further consideration in model development.

Wintering Ground Habitat

General Habitat Features.—Black ducks migrate and spend the winter at several latitudes, but the largest concentrations are contiguous with the eastern deciduous forest (Stewart 1958). Significant numbers of black ducks winter in the interior of the U.S. (Stewart 1958), but historically the largest numbers of black ducks have been along the Atlantic coast. Habitats used by Atlantic coastal birds vary annually among latitudes, depending on ice conditions (Lewis and Garrison 1984, Conroy et al. 1987). Emergent estuarine wetlands are preferred to other coastal wetland types (Morton et al. 1989). Mud flats receive heavy use north of Chesapeake Bay (Hartman 1963, Lewis and Garrison 1984, Jorde 1986, Longcore and Gibbs 1988; but see Lewis and Nelson 1988). In addition to the presence of emergent coastal wetlands or mud flats, wintering black ducks require adequate food, open water and shelter from low temperature and human disturbance (Lewis and Garrison 1984).

Habitat use by inland birds in winter has received additional study only recently. In far northern regions wintering black ducks apparently are restricted to areas of open

water by cold weather, typically large lakes and reservoirs (Winner 1959, Reed 1971), open stretches of large rivers (Reed 1971, Bellrose 1980, Brodsky and Weatherhead 1985) and wetlands kept open by natural springs or artificial means (Reed 1971). Female black ducks wintering in Tennessee selected palustrine emergent wetland, palustrine forested wetland, scrub-shrub wetland and lacustrine habitat, but avoided agricultural areas (Chipley 1995).

Food.—Black ducks wintering along the Atlantic coast feed on plant parts and aquatic organisms (Mendall 1949, Lewis and Garrison 1984). Eelgrass (*Zostera marina*), wigeon grass (*Ruppia maritima*), and smooth cordgrass (*Spartina alterniflora*) are important plant foods (Mendall 1949, Martin et al. 1951, Grandy 1972, Lewis and Garrison 1984). Mollusks, crustaceans, and insects are important animal foods (Mendall 1949, Grandy 1972, Lewis and Garrison 1984, Jorde and Owen 1988), particularly in mud flats (Hartman 1963). Of these, blue mussels (*Mytilus edulis*), soft-shelled clams (*Mya arenaria*), bent-nosed clams (*Macoma balthica*), snails (*Gastropoda*), particularly periwinkles (*Littorina* spp.), and amphipods such as gammarus (*Gammarus oceanicus*) seem to be most important (Mendall 1949, Hartman 1963, Grandy 1972, Jorde and Owen 1990). The proportion of animal matter in the diet increases with latitude (Lewis and Garrison 1984).

Habitat Quantity.—Destruction of winter habitat may have contributed to the black duck decline. If so, a positive correlation between acreage of available winter habitat and some measure of abundance, survival or recruitment of black ducks is predicted. Testing this prediction requires an estimate of winter habitat area over time. We did not test for trends in inland winter habitat largely because this habitat has received little study and no long-term databases of inland winter habitat could be located.

Periodic estimates of estuarine emergent coastal wetland area have been made for many states (Shaw and Fredine 1956; Tiner 1985a,b, 1989, 1990, 1991; Hefner 1986; Metzler and Tiner 1992; Smith and Tiner 1993; Tiner and Foulis 1993a,b,c; Fretwell et al. 1996; Hefner et al. 1994). We compiled these estimates made during 1961–1996 for

as many states as possible from Maine to Florida. Generally only 2–3 estimates of wetland area and 2–3 estimates of rate of wetland loss could be located for a given state. Most of these estimates were for the 1950s and the 1970s. Acreage for years with no published estimated were obtained by linear interpolation and extrapolation from published years, using published estimates of annual loss for the corresponding period, except that we projected rates of loss for the 1960s forward and for the 1970s backward to meet at 1972, a year in which several federal and state wetland protection laws were enacted.

Insufficient data were available to estimate trends in coastal wetland area for the Atlantic Provinces, Georgia, the Carolinas, New Hampshire and Maine. Furthermore, <5,000 black ducks have wintered annually in Florida since 1961. Therefore, we restricted the southern Atlantic region to Virginia, Maryland, and Delaware when examining temporal change in coastal wetlands. A total of 8% (21,900 ha) of estuarine emergent wetlands were lost since 1961 in the northern and southern Atlantic regions combined. Rate of destruction of coastal wetlands in our study area was high in the 1960s (approximately 1,900 ha/yr), but declined to an estimated 150 ha/yr in the 1970s after passage of federal and state wetland protection legislation. In the northern Atlantic states, 12% (17,200 ha) of coastal wetlands were lost during 1961–1996 vs. 4% (4,700 ha) in the southern Atlantic region. Thus, declining black duck abundance in the Atlantic Flyway may be partly explained by declines in available winter habitat.

Relatively few coastal emergent wetlands exist in New Hampshire and Maine (Jorde et al. 1989), and loss of this wetland type was minimal there during the mid-1970's to mid 1980's (Tiner 1991). However, wetland loss was high during portions of our study period in some southeastern states not included in our analysis, Florida in particular (Hefner and Brown 1984, Tiner 1991). Drainage of emergent estuarine wetlands has virtually stopped in Florida (memo on file, USFWS, Region 4, Atlanta, Georgia); however, 10,500 ha of wetlands of all types were drained annually in the state between the mid-1970's and mid-1980's (Fretwell et al. 1996).

Interestingly, 75,000 black ducks wintered in Florida in 1948 and 51,248 mallards and 215,160 pintails were counted in the state during the 1955 MWI survey. The 1998 Florida survey counted 0 black ducks, 559 mallards and 2,663 pintails.

Emergent estuarine wetlands are not the only wetland habitat type important to black ducks. As mentioned earlier, eelgrass is an important winter food in at least some portions of the black duck range (Lewis and Garrison 1984). Eelgrass and several other submerged aquatics have experienced periodic die-offs along the Atlantic coast or in Chesapeake Bay since the 1930s (Cottam and Munro 1954, Bayley et al. 1978, Orth and Moore 1983). These die-offs are capable of reducing diversity of invertebrate communities (Stauffer 1937), thereby potentially reducing both plant and animal food for black ducks. A decline in submerged aquatic vegetation in Chesapeake Bay may have been responsible for a decline in the wintering waterfowl population there (Bayley et al. 1978, Perry et al. 1981).

Large-scale monitoring of submerged aquatic vegetation in Chesapeake Bay began in 1971 (Orth and Moore 1981, Orth and Moore 1983, Orth et al. 1996). However, we know of no trend estimates for submerged aquatic vegetation outside of Chesapeake Bay. Some form of large-scale monitoring of submerged aquatic vegetation would have to be initiated along the Atlantic coast if this factor were to be included in modeling efforts like those developed in the next section.

Habitat Quality.—Numerous factors could be affecting quality of winter habitat. Mostly these involve environmental contaminants such as nutrient enrichment, organochlorines, lead shot, and other heavy metals. Other factors related to human activity, such as human disturbance, over-harvesting of shellfish and habitat fragmentation, could be important. We review several of these factors as they potentially relate to black duck populations in the following.

Environmental Contaminants.—Numerous studies have tested for the presence of various heavy metals and organic chemicals in waterfowl tissue, and for the possible effects of these contaminants on waterfowl reproduction and survival. The most frequently

studied of these contaminants are lead shot and the organochlorines (DDT, DDE). Others include cadmium and aluminum usually associated with acid rain, mercury, and various contemporary insecticides.

Lead shot was banned for use by waterfowl hunters in the United States over 1987–1992 and in Canada in 1997. Waterfowl ingest lead shot while feeding, perhaps for use as grit. This often leads to lead toxicosis and eventually death (Bellrose 1959). The percentage of black ducks ingesting lead shot has been estimated in several studies, but the number of black ducks dying annually from lead poisoning is more difficult to estimate. No evidence exists either that lead ingestion rates (Bellrose 1959:260, White and Stendell 1977, Stendell et al. 1979, Longcore et al. 1982, Moser 1983, U.S. Fish and Wildlife Service 1986, Daury et al. 1994) or toxicity of ingested lead are higher for black ducks than for mallards (Chasko et al. 1984), breeding populations of which apparently increased in the black duck breeding area during 1966–2000, based on Breeding Bird Survey data (www.mbr-pwrc.usgs.gov).

Commercial application of DDT began in the mid-1940's (Stickel 1968). Within 2 decades DDT residues were ubiquitous in birds throughout the world (Stickel 1968). Large-scale monitoring of DDT, DDE and DDD concentrations in mallard and black duck wings began in 1965 (Heath 1969). In 1972 the U.S. EPA banned most uses of DDT. Between the 1969–70 and 1979–80 surveys DDE levels in the Atlantic Flyway declined from 1.19 to 0.19 ppm in black duck wings and from 1.08 to 0.18 ppm in mallards (Heath and Hill 1974, Prouty and Bunck 1986). Thickness of black duck eggshells has increased to pre-DDT levels (Longcore and Stendell 1977, Hazeltine et al. 1980).

Of other contaminants, mercury has probably been studied most. Of 6 U.S. national surveys testing for contaminants in mallard and black duck wings, only Heath and Hill (1974) tested for mercury. Overall mercury levels in the Atlantic Flyway in 1969 were almost twice as high in black ducks ($\bar{x} = 0.20$ ppm, SE = 0.02) than in mallards ($\bar{x} = 0.11$ ppm, SE = 0.01). In northern Atlantic states the mean mercury level in black duck wings was 0.21 ppm, SE = 0.02 vs. 0.15 ppm, SE = 0.004 in southern Atlantic states. No

data were presented for black ducks in the Mississippi Flyway.

Winter Climate and Body Condition.—The extent to which severe winter weather may be responsible for the black duck decline is unknown. Nevertheless, severe winter weather can cause nutritional stress and periodic die-offs in at least some portions of the black duck's wintering range (Albright 1981, Reinecke et al. 1982, Conroy et al. 1989b). Black ducks will modify their activity to reduce energy expenditure on cold days (Albright et al. 1983, Brodsky and Weatherhead 1984, Longcore and Gibbs 1988), and high body mass in early winter may increase overwinter survival (Conroy et al. 1989b). Krementz et al. (1989, 1990), however, reported no relationship between late winter body mass and annual survival.

If body mass per se, or food availability, in winter do affect either black duck survival (Conroy et al. 1989b) or reproduction in the following spring (Hepp 1986, 1989), then a reduction in prey base may have repercussions at the population level. After black ducks select a wintering area they generally do not leave to escape periods of severe weather (Hartman 1960, 1963, Winner 1960, Conroy et al. 1989b, Morton et al. 1990). Ice formation during periods of prolonged low temperature can prevent access to coastal marshes (Hartman 1963, Morton et al. 1989) where energy-rich foods (e.g., *Gammarus*) are located (Hartman 1963, Jorde and Owen 1988). When this happens mud flats provide critical access to energy-poor invertebrate foods (e.g., blue mussels, periwinkles and soft-shelled clams [Hartman 1963, Jorde and Owen 1988]). Thus, reductions in the latter prey species may reduce emergency foods for black ducks.

Summary of wintering habitat factors.—Our review suggests a decline in quantity, quality, or both, of habitats for wintering black ducks. Field studies corroborate the importance of winter habitat quantity and quality in relation to black duck behavior and energetics, and some evidence exists of a linkage to demography (e.g., mortality rates, Conroy et al. 1989b). Because declines in habitat quantity and quality were contemporaneous with declines in continental black duck populations, at least circumstantial evidence exists for a causal linkage of the 2

phenomena. As with breeding habitats, however, this evidence is non-experimental and correlative, and declines in the quantity or quality or both of wintering habitats have not been uniform throughout the black duck range. The evidence neither strongly affirms nor rules out changes in wintering habitat as a causative factor in the black duck decline, and we conclude that wintering habitat should be considered as a factor in model development.

Harvest

Traditionally, 2 competing hypotheses have been stated regarding the effect of hunting on overall mortality rates of exploited populations: mortality from hunting is either additive to other sources of mortality, in determining total, annual mortality (additive mortality hypothesis, AMH), or is compensated by changes in natural mortality rates (compensatory mortality hypothesis, CMH) (Anderson and Burnham 1976). Numerous attempts either to distinguish between AMH and CMH, or to estimate the degree of compensation under CMH, have been conducted mostly for mallards (see Nichols et al. 1984). These questions also have been addressed for black ducks, notably by Geis et al. (1971), Blandin (1982, 1991), Krementz et al. (1987, 1988), and Francis et al. (1998). A review by Conroy and Krementz (1990) suggested conflicting evidence over time and among studies as to whether AMH or CMH applies to black ducks. These authors suggested that the compensatory threshold in black ducks might be temporally dynamic, and related to severity of winter weather. Recent evidence indicated that hunting mortality was additive for black ducks during the 1950s, 1960s and 1970s (Francis et al. 1998). Longcore et al. (2000) documented high rates of harvest mortality for black ducks radio-marked in Québec, Nova Scotia, and Vermont and suggested that harvest is responsible for depletion of local breeding populations. Additive harvest mortality could be partly responsible for the difference in population trajectories between mallards and black ducks, given the apparent high degree of compensation in mallards through the 1970's (Nichols et al. 1984). However, more recent evidence for mallards indicates that harvest mortality is at

least partly additive (Caswell et al. 1985, Smith and Reynolds 1992).

None of these analyses consider the impacts of illegal kill (Gray and Kaminski 1994), which may be substantial for some portions of the black duck range (e.g., Boyd and Wendt 1985), on black duck mortality. To the extent that illegal kill rates might increase as legal kill is restricted, this source of mortality could mimic compensatory, non-harvest mortality. This last point is worth considering in evaluating competing hypotheses about the impacts of harvest on total mortality (Anderson et al 1976, Nichols et al. 1984).

The influence of harvest on black duck population trajectories must be considered in the context of other population factors, such as habitat availability and interspecific and intraspecific competition. Even if the degree of compensation to harvest is identical for mallards and black ducks, their population trajectories could differ if the 2 species had different baseline survival and reproduction rates (Nichols et al. 1984, Conroy and Krementz 1990). Conversely, different degrees of compensation between the 2 species (e.g., more evidence of AMH for black ducks, and of CMH for mallards) alone cannot explain their differing population trajectories in the absence of control for other factors; e.g., under AMH density-dependent reproduction could nullify the effects of additivity on population growth.

Summary of harvest factors.—The role of harvest in reducing or limiting black duck populations has generated much contention, both within and outside of the scientific literature. It is not surprising that our review of the literature as to harvest effects reveals no consensus on the matter. Some evidence exists that harvest mortality may be, at least, partly additive to other mortality, but the evidence is not consistent among studies, or among areas or demographic strata in individual studies. Some of the conflicting results may be real, and others are likely statistical artifacts, or the result of differences in study designs. In the absence of experimentation, or possibly adaptive management, it may not be possible to separate the effects of harvest rates from those of mallard populations, habitat conditions, and other factors, all of which have varied over

the period of the black duck decline, and which may have interacted with harvest in affecting populations. We suggest that because harvest may affect black duck populations in an additive manner under some circumstances, and because harvest is one of the factors under the direct, regulatory control of managers, it is prudent to retain harvest as a factor for further consideration in parameter estimation and modeling. Finally, even under an assumption of complete compensation, harvest will have an effect if it exceeds a theoretical threshold (Anderson and Burnham 1976), and thus must be considered in any general population model of a harvested species.

Interactions with Mallards

Interspecific competition may limit the distribution or abundance of a species (Begon et al. 1990). Early in the last century black ducks may have expanded their range westward (Phillips 1922). In recent times, however, mallards are thought to have expanded their range eastward into the range of the black duck, perhaps as a result of human-induced habitat alteration on the breeding grounds (Heusmann 1974). At the same time, black duck populations are thought to have decreased. Several authors have suggested that the mallard may be causing the decline of black ducks through interspecific competition for habitat or genes (Merendino and Ankney 1994).

The Mallard Increase.—Evidence suggests that mallards have increased within the black duck's range, although by how much is unknown. Early reports considered the mallard rare in New England and southern Ontario (southern portions of Areas 2 and 4, Fig. 1a; reviewed in Heusmann 1974, Longcore et al. 1987a, Merendino et al. 1993). Mallard abundance increased during 1955–1996 in western Ontario (Areas 1 and 2, Fig. 1a; Nudds et al. 1996). Breeding mallards also increased during 1971–1987 in southern Ontario (Dennis et al. 1989), and possibly during 1965–1992 in the Atlantic Provinces (Area 5, Fig. 1a; D'Eon et al. 1995). Breeding Bird Survey indices also suggest that mallards have increased since 1966 throughout much of the breeding range of black ducks (Table 1, Figs. 1a and 1c) with the increases statistically supported

(i.e., the 95% CIs generally do not include zero; Table 1). Again, however, we caution that the Breeding Bird Survey may be unreliable as an index to breeding populations of waterfowl. Christmas Bird Count data during 1900–1974 also indicate an increase in wintering mallard abundance relative to black ducks (Johnsgard and DiSilvestro 1976), although population trend estimates were not computed for either species. No aerial surveys of breeding mallards occurred in the boreal forest of eastern Canada in the 1950s and 1960s with which recent estimates of mallard population size there can be compared. Recent ground plot surveys of breeding waterfowl in New England and the Mid-Atlantic region (Heusmann and Sauer 1997) have been conducted since the early 1990s and do not document earlier range expansion or population increases by mallards, augmented by the release of large numbers of hand-reared mallards since early last century (Heusmann 1987).

Hybridization.—Black ducks and mallards are closely related, and will hybridize in areas of sympatry, producing viable offspring (Johnsgard 1961, Heusmann 1974, Ankney et al. 1986). The frequency of hybrids increases from east to west (Johnsgard 1967), and the proportion of hybrids in the total mallard-black duck population is thought to be increasing (Heusmann 1974, 1988, Dennis et al. 1984, D'Eon et al. 1995, USFWS Office of Migratory Bird Management, unpublished data). Some authors have suggested the black duck may simply be a dark color morph of the mallard, and that a continued decline and eventual disappearance of the black morph through genetic swamping may be inevitable as eastward expansion of the mallard continues (Johnsgard 1961, Heusmann 1974, Ankney et al. 1986, 1987, 1989). Other authors have suggested that loss of habitat and harvest are plausible alternative explanations for the black duck decline (Conroy et al. 1989a). Hepp et al. (1988) argued that available information favored retaining mallards and black ducks as separate species.

Currently, hybrids are indistinguishable from black ducks in most abundance surveys (Barnes 1989, Johnsgard 1961, Kirby et al. 2000), and insufficient banding and other

data exist to separately estimate population parameters for hybrids, thus precluding the incorporation of a "hybrid effect" directly into a black duck model. For most management purposes, hybrids will continue to be treated like the taxon they most resemble. Therefore, for the remainder of this discussion, and the modeling to follow, we will focus on the population effects of mallards on "black ducks," which by implication include an unknown number of black duck-mallard hybrids. We do this without denying the existence of a "black duck-mallard complex" or of the long-term implications of introgressive hybridization on the status of black ducks as a distinct taxon. We argue, too, that if mallards are successfully competing with black ducks for genes, they probably are successful competitors for food and other resources, and these effects should be manifested in adverse effects on black duck reproduction or survival rates.

Competition.—Nudds (1990) reviewed 3 types of evidence for competition in waterfowl communities. We describe these kinds of evidence below, drawing heavily on Nudds (1990), then review mallard-black duck studies investigating each type of evidence. Type I evidence of competition typically consists of known differences among species (Nudds 1990). Although similarities between coexisting species also may suggest that competition occurs, Nudds (1990) concluded that Type I evidence by itself is of no value in determining whether species compete. Type II evidence consists of negative correlations in species abundance or between 2 species' traits such as habitat and diet (e.g., diet may be most different where habitat overlap is greatest; Nudds 1990). Type III evidence involves observed shifts in one species' abundance or distribution following the natural or experimentally manipulated appearance or disappearance of another species. Accepting Type III evidence from descriptive studies requires assuming that changes in one species were caused by changes in populations of the putative competitor (Nudds 1990). Generally this possibility cannot be distinguished from situations in which some third factor has induced changes in both species' abundance or distribution. Thus Type III evidence provides strong inference only

when arising from manipulative experiments, in which the researcher randomly assigns experimental units to treatments (presence of a factor) and controls (absence of a factor).

Type I Evidence of Competition.—Numerous studies have documented similarities between black ducks and mallards. The 2 species are similar biochemically (Morgan et al. 1978), genetically (Ankney et al. 1986, Avise et al. 1990), behaviorally (Bellrose 1980, Johnsgard 1960), and morphometrically (Bélanger et al. 1988, Bellrose 1980, Hanson and Ankney 1994). The most obvious morphological difference between the 2 species is that black ducks are sexually monochromatic whereas mallards are sexually dichromatic (Bellrose 1980).

Eggs of both species are similar in size, shape (Bellrose 1980) and in egg-white proteins (Johnsgard 1961). No differences have been detected in clutch size or nest success in sympatric populations (Coulter and Miller 1968, Laperle 1974, Krementz et al. 1992, Dwyer and Baldassarre 1993). Nor were mallard and black duck Class IIc-III brood sizes different for sympatric populations in Maine (Longcore et al. 1998). Dwyer and Baldassarre (1993) suggested that more persistent renesting efforts by mallards could have resulted in higher mallard than black duck production on their New York study area, although the number of nests in the study was small ($n = 18$ for mallards and $n = 9$ for black ducks). Furthermore, in Ontario hatch data of black duck and mallard broods appeared synchronous (Merendino et al. 2000).

No difference in breeding season survival has been detected for sympatric adult female mallards and black ducks (Dwyer and Baldassarre 1993). Nichols et al. (1987) concluded that annual survival of black ducks generally was not lower than for mallards banded in the same area.

Although mallards and black ducks are similar structurally and apparently have similar population dynamics, their breeding ranges overlapped little historically. Black ducks breed throughout the boreal forest of eastern Canada and the deciduous forest of the U.S. Midwest, northeast and mid-Atlantic regions. Mallards were found principally in the prairie-parkland region and

boreal forest of western Canada. The 2 species overlapped only in western Ontario and Minnesota (Stewart 1958, Heusmann 1974, Bellrose 1980).

Mallards and black ducks historically were segregated during winter along the coast, with black ducks making greater use of coastal estuarine wetlands (Heusmann 1974, 1988; but see Sanderson 1993). Mallards may now be making greater use of coastal areas in winter as a result of urbanization (Heusmann 1988). Whether winter habitat segregation occurs inland is unknown, but certainly mallards and black ducks occur in close proximity in many inland habitats (Chipley 1995).

Type II Evidence of Competition.—Increasing mallards and decreasing black ducks in areas of sympatry, as indicated by the Breeding Bird Survey, constitutes Type II evidence of competition. MWI counts suggest that abundance of wintering mallards and black ducks decreased in the Mississippi Flyway and in the southern Atlantic states during 1955–2000. This weakly suggests that competition, if it occurs, is more pronounced on the breeding grounds. Most black ducks wintering in the Southeast breed in the western part of their range (Geis et al. 1971). Aerial surveys on the breeding grounds suggest that mallards but not black ducks have increased in the boreal forest of western Ontario (Nudds et al. 1996).

Type III Evidence.—The only manipulative tests of the mallard hypothesis to date have involved interspecific dominance experiments using captive birds. Wild male mallards prefer female mallards to female black ducks, but can out compete male black ducks for unpaired female black ducks if no unpaired female mallards are available (Brodsky and Weatherhead 1984). Presumably this occurs because female black ducks select dominant males and will pair with dominant male mallards over subordinate male black ducks (Brodsky et al. 1988). Captive male mallards were dominant over male black ducks in one study (Brodsky et al. 1988), but not in another (Hoysak and Ankney 1996). In the field neither species was dominant during the breeding season (McAuley et al. 1998).

Nevertheless, Merendino et al. (1993) suggested that as mallards spread through

southern Ontario they displaced black ducks from the most fertile wetlands first. Black ducks in southern Ontario now appear to be restricted to wetlands with low fertility. Density of beaver colonies and wetland area increased after beaver trapping was experimentally stopped on a study area in Maine (McCall et al. 1996). Density of breeding mallards also increased, but breeding black ducks density remained constant or decreased, suggesting that black ducks were out-competed for the newly available habitat.

Summary of mallard effects.—Circumstantial evidence exists from both field and captive studies for a negative, competitive effect of mallards on black duck populations. The genetic similarity of black ducks and mallards provides additional concern about genetic “swamping” of black ducks by mallards. However, it remains unclear whether competition (for habitats, mates, or genes) is required as an explanation for relative increases of mallards and decreases of black ducks, or whether other factors, including habitat alteration, play an equal or greater role. In addition, there remain substantial differences in habitat selection between mallards and black ducks, particularly during winter. In the absence of controlled experimentation (e.g., involving habitat manipulation and the exclusion of mallards) these questions are unlikely to be resolved unequivocally. We conclude that, while unequivocal evidence for a “mallard hypothesis” does not exist, circumstantial evidence dictates the retention of this hypothesis for further consideration in model development.

Parasites and Disease

Parasite or disease organisms potentially may limit or regulate the abundance of their host (Anderson and May 1980, Begon et al. 1990). Both duck virus enteritis and avian cholera were first reported in North America <60 years ago (Leibovitz and Hwang 1967). Avian cholera is not known to have caused large-scale mortality in black ducks (Karstad and Lusis 1970, Locke et al. 1970). Some evidence suggests that black ducks may be particularly susceptible to duck virus enteritis. Mortality of black ducks averaged 86% vs. 0% for mallards

during outbreaks of duck virus enteritis in captive flocks on 2 game farms (Jacobsen et al. 1976, Montgomery et al. 1981). This disease, however, is difficult to monitor in the wild (Brand and Docherty 1984, 1988).

Typhlitis, caused by the digenean parasite *Cyathocotyle bushiensis*, was first reported in North America in 1961 and is fatal to black ducks (Gibson et al. 1972). The North American range of *Bythinia tentaculata*, the intermediate host for *C. bushiensis*, centers on the lower Great Lakes, the St. Lawrence River valley, and the Mid-Atlantic states (Hoeve and Scott 1988).

Summary of Effects of Disease.—Diseases and parasites commonly occur in black ducks and have resulted in severe morbidity and mortality in some local black duck populations, but we are unaware of evidence that supports disease as limiting the population. We suggest, for several reasons, that population level effects caused by diseases can be best described in terms of density feedback mechanisms instead of explicit modeling of diseases. First, to the extent that diseases have an effect on black duck populations an effect must be manifested through a direct or indirect influence on survival, reproduction, or both. More important, for disease to be regulatory, density feedback on survival, reproduction, or both must occur. Furthermore, many disease scenarios involve some type of concentration of birds in limited habitats, suggesting that habitat limitation may be the ultimate population limiting factor, with disease mediating as a proximate factor (we would use similar arguments in support of our decision not to explicitly consider predators or "predator hypotheses" in our models). Finally, although disease may be important, and may at times even be serve (at least proximately) to limit or regulate populations, it is not directly under the control of managers, at least in a practical sense, at scales of relevance to continental populations. Our further modeling and analytical work will thus not consider disease (or other factors such as predation) directly, but will incorporate potential density-dependent feedback on survival and reproduction, and habitat conditions (principally habitat quantity) that frequently may include disease as a proximate mechanism. Both density feedback (at

Table 3. Summary of major factors proposed as influencing American black duck population declines, and principal studies providing support.

Factor	Supporting studies
I. Breeding habitat	Kaczynski and Chamberlain (1968) Longcore and Stendell (1977) DesGranges and Hunter (1987) Dwyer and Baldassarre (1994) Sparling (1990, 1991) Kelso et al. (1992)
II. Wintering habitat	Bayley et al. (1978) Moser (1983) Orth and Moore (1983) Conroy et al. (1989b) Morton et al. (1989) Fretwell et al. (1996)
III. Harvest	Krementz et al. (1987, 1988) Francis et al. (1998) Longcore et al. (2000)
IV. Competition from mallards	Johnsgard (1961, 1967) Heusmann (1974) Brodsky and Weatherhead (1984) Ankney et al. (1987) Brodsky et al. (1988) Dennis et al. (1989) Merendino et al. (1993) McAuley et al. (1998)
V. Diseases and Parasites	Gibson et al. (1972) Jacobsen et al. (1976) Montgomery et al. (1981) Hoeve and Scott (1988)

least, on survival) and habitat are in turn related to management activities (harvest, and habitat restoration and management, respectively), and are thus subject to partial control by managers.

Conclusions from the Literature Review

The continental black duck population apparently declined greatly during the 1950s–1970s and has largely remained stable since the late 1970s. The review and data above suggest that at least circumstantial evidence exists for a linkage between declines in black duck populations and each of the factors examined (Tables 2 and 3). Virtually all of this evidence, however, is non-experimental and correlative. In our opinion, current evidence does not support any one factor as solely explaining the decline in the black duck population. Conversely, we

believe that the evidence is incapable of ruling out any of these factors, and thus all should be provisionally retained for further consideration in model development.

During the 1950s to 1970s breeding habitats were lost to forest clearing; acidic precipitation may have decreased pH and productivity of boreal wetlands; winter habitats were lost at a rapid rate, and some winter food supplies may have decreased; lead shot, mercury and organochlorine pesticides poisoned unknown numbers of birds; mallard populations increased, as did rates of hybridization; and new diseases and exotic parasites appeared.

Many of these trends are consistent with the apparent stabilization of the continental black duck population over the last 2 decades. Rates of acidic emissions have been reduced and pH of boreal wetlands has started to increase (Keller et al. 1992); loss of coastal wetlands has almost stopped; beaver populations appear to be increasing in many areas; lead shot and DDT have been banned in Canada and the U.S.; and harvest regulations have been restricted and the harvested proportion of the total black duck population has apparently stabilized.

Given the high degree of confounding among harvest regulations and historical waterfowl abundance, environmental conditions, and other factors, it is unlikely that a clear picture of the historical effects will emerge. It is also unknown whether current rates of harvest are capable of suppressing population growth in black ducks. Nonetheless, harvest regulations remain one of the few aspects of the black duck's "environment" under management control, and their potential for population effects remains an issue.

Major, broad-scale changes have occurred in the historical range of black ducks, with mallards increasing and black ducks declining precipitously in much of the western portion of the range. The degree to which competition from mallards (for habitats, genes, or both) has been one of many contributing factors to the decline of black ducks, or is the dominant factor, remains in dispute. Indeed, it is possible that mallards have simply filled a void left by black duck populations that have declined for other reasons. Finally, the degree to

which mallard effects may have interacted with other factors, such as habitat modification and harvest, in affecting black duck populations, remains unknown (Nudds et al. 1996).

Given this uncertainty, and the enormous cost and difficulty of field experiments to address these questions, we believe adaptive harvest management is the best, and perhaps only, viable approach to use for managing the continental black duck population. In the next section we develop a set of competing models of black duck population dynamics for use in an adaptive harvest management scenario.

SYNTHETIC POPULATION MODEL FOR AMERICAN BLACK DUCKS

Introduction

In this section we use our review of factors to develop a synthetic, research-management model of black duck populations. Our model is based on predictive relationships between quantity of (1) breeding habitat, (2) wintering habitat, (3) harvest rates, and (4) abundance of mallards, and population growth rates of black ducks, through effects on reproduction, survival, or both.

Model Formulation

We developed an annual life cycle model (e.g., Johnson et al. 1985), with accompanying submodels, to (1) provide a mechanistic description of annual population growth, (2) incorporate relevant hypotheses concerning factors that may be limiting black duck population growth, and (3) enable casting of these hypotheses in terms of parameter values that can be estimated from available data. The basic annual model describes discrete-time growth of the population of black ducks as

$$N_{t+1}^{(2)} = N_t^{(0)}(S_t + P_t S_t^y), \quad (1)$$

where

$N_t^{(0)}$ is abundance of adult (breeding) black ducks alive in spring of year t ,

S_t is annual (spring to spring) survival of adult black ducks,

S_t^y is fall-spring survival of young, and

P_t is annual, per-capita rate of reproduction

(young alive in fall per adult alive in spring of year t).

As discussed in the next section, P_t is difficult to observe directly; therefore we reparameterized the above modeled as

$$N_{t+1} = N_t(S_t + S_t^{(0,1)}A_t S_t^y), \quad (2)$$

where $A_t = P_t / S_t^{(0,1)}$ is the ratio of juveniles to adults in the fall population and $S_t^{(0,1)}$ is spring-to-fall survival of adults. Under the assumption that spring-to-fall survival is temporally constant ($S_t^{(0,1)} = S^{(0,1)}$), A_t is proportional to P_t by the factor $1/S^{(0,1)}$. As appropriate, $N_t^{(0)}$, S_b , S_t^y , and $S_t^{(0,1)}$ can be indexed by sex, so that, for example, $N_t^{(0)m}$ would denote the number of adult male black ducks during the breeding season in year t , and S_t^f would denote the spring-to-spring survival rate of adult female black ducks between year t and year $t+1$. We developed 2 basic submodels to separately handle reproduction and survival.

Reproduction Submodel.—Reproductive rates can be either density-dependent or density-independent. Density dependence can occur as a result of several factors, including disease, predation, competition, and environmental effects such as weather. Our purpose was to develop a model describing the influence of intrinsic and extrinsic factors on reproduction rates. We used an exponential model for fall age ratio as

$$A_t = A_{\max} \exp(\beta D_t^{(0)}), \quad (3)$$

where

$D_t^{(0)} = N_t^{(0)}/HAB_t^{(0)}$ is density on the breeding ground,

$HAB_t^{(0)}$ is a measure of the relative amount of breeding habitat (to be defined more specifically in the next section),

A_{\max} is an upper limit to fall age ratio, and β is a coefficient describing density dependent feedback on reproduction; both A_{\max} and β are model parameters, estimable from data (see next section).

The exponential functional form has 2 advantages over a linear model: (1) for $\beta \leq 0$, the maximum reproductive rate is determined by A_{\max} (either when $\beta = 0$, and thus

reproductive rates are independent of density, or when density is 0), and (2) for $\beta < 0$ reproductive rates decline exponentially, being bounded below by 0. These features preclude biologically inadmissible reproductive rates, i.e., negative or unreasonably large. The model also ignores the possibility of Allee (1931) effects, which a priori we thought unlikely for black ducks.

We distinguished habitat effects on reproductive rates (possibly acting the same regardless of abundance) from the effects of varying continental abundance levels (regardless of habitat availability) and abundance in relation to density per available habitat by reformulating Equation 3 as:

$$A_t = A_{\max} \exp(\beta_N N_t^{(0)} + \beta_X X_t^{(0)} + \beta_{NX} N_t^{(0)} X_t^{(0)}), \quad (4)$$

where $X_t^{(0)} = 1/HAB_t^{(0)}$. Finally, we incorporated the predicted effects of competition with mallards for breeding habitats by

$$A_t = A_{\max} \exp(\beta_N N_t^{(0)} + \beta_X X_t^{(0)} + \beta_{NX} N_t^{(0)} X_t^{(0)} + \beta_M M_t^{(0)} + \beta_{MX} M_t^{(0)} X_t^{(0)}), \quad (5)$$

where $M_t^{(0)}$ is mallard abundance on the breeding grounds, and β_N , β_X , β_{NX} , β_M , β_{MX} are coefficients (all ≤ 0) representing the effects of black duck abundance, habitat, density (per unit of habitat), mallard abundance, and mallard density (the latter under the assumption that black ducks and mallards are competing for the same habitat, $HAB_t^{(0)}$). Given an age ratio calculated according to Equation 5, we calculated fall abundance of black ducks as

$$N_t^{(1)} = N_t^{(0)} S_t^{(0,1)} (A_t + 1), \quad (6)$$

where $S_t^{(0,1)}$ is spring to fall survival for adults (initially assumed constant over time in our model, $S_t^{(0,1)} = S^{(0,1)}$).

Survival Submodel.—In our model, annual survival has 3 components: spring-to-fall $S_t^{(0,1)}$; survival during the hunting season, $S_t^{(1,2)} = (1 - K_t)$, where K_t is annual harvest kill rate; and survival following the hunting season, $S_t^{(2,0)}$, with annual survival modeled as

$$S_t = S_t^{(0,1)} (1 - K_t) S_t^{(2,0)}. \quad (7)$$

In practice the 2 components of non-harvest mortality, $S_t^{(1,0)}$ and $S_t^{(2,0)}$ usually cannot be estimated separately (see next section) and we modeled survival following the hunting season as

$$\log_e \left(\frac{\theta_t}{1-\theta_t} \right) = \alpha_0 - \alpha D_t^{(2)}, \quad (8)$$

where

$\theta_t = S_t^{(2,0)} S_t^{(0,1)}$ is survival from immediately following the hunting season to the subsequent fall.

$D_t^{(2)} = N_t^{(2)}/\text{HAB}_t^{(2)}$ is density of black ducks at the beginning of winter,

$N_t^{(2)}$ is abundance of black ducks at the beginning of winter,

$\text{HAB}_t^{(2)}$ is a measure of available winter habitat, and

α represents the slope of a density dependent effect on post-harvest.

Note that in the above (and subsequent) models we represent survival and harvest rates for a single age-sex class, but any of these can be stratified as appropriate for sex and age class (e.g., age- and sex-specific values for α_0 and α).

Given an initial (pre-harvest period) abundance of $N_t^{(1)}$, with harvest mortality K_t , abundance going into the winter period will be $N_t^{(2)} = N_t^{(1)}(1 - K_t)$ and density $D_t^{(2)} = D_t^{(1)}(1 - K_t)$, so that Equation 8 can be rewritten as

$$\log_e \left(\frac{\theta_t}{1-\theta_t} \right) = \alpha_0 - \alpha D_t^{(1)}(1 - K_t). \quad (9)$$

This basic model incorporates a density-dependent mechanism for compensation of harvest mortality.

As with reproductive rates, we hypothesized that competition from mallards for wintering habitats could influence black duck survival, and constructed an expression similar to Equation 5:

$$\begin{aligned} \log_e \left(\frac{\theta_t}{1-\theta_t} \right) &= \alpha_0 + \alpha_N N_t^{(2)} + \alpha_X X_t^{(2)} \\ &+ \alpha_{NX} N_t^{(2)} X_t^{(2)} + \alpha_M M_t^{(2)} \\ &+ \alpha_{MX} M_t^{(2)} X_t^{(2)}, \end{aligned} \quad (10)$$

where black duck, and mallard populations and habitat are described for the wintering populations and $X_t^{(2)} = 1/\text{HAB}_t^{(2)}$. From Equation 10 we can obtain an expression for θ_t in terms of a fall (pre-harvest) population size for black ducks, $N_t^{(1)}$. This form allows explicit incorporation of the compensatory (density-dependent) relationship into the annual life cycle model, and is also the form used in ultrastructural analysis when pre-harvest (rather than winter) abundance is used as a predictor, that is :

$$\begin{aligned} \log_e \left(\frac{\theta_t}{1-\theta_t} \right) &= \alpha_0 + \alpha_N N_t^{(1)}(1 - K_t) + \alpha_X X_t^{(2)} \\ &+ \alpha_{NX} N_t^{(1)}(1 - K_t) X_t^{(2)} + \alpha_M M_t^{(1)}(1 - K'_t) \\ &+ \alpha_{MX} M_t^{(1)}(1 - K'_t) X_t^{(2)}, \end{aligned} \quad (11)$$

where K_t and K'_t are the harvest mortality rates for black ducks and mallards, respectively. Finally, abundance in spring of the following year was modeled as

$$N_{t+1}^{(0)} = N_t^{(2)} \theta_t / S^{(0,1)}, \quad (12)$$

where again spring-summer-survival is assumed constant ($S_{t+1}^{(0,1)} = S^{(0,1)}$) but sex-specific (see next section). As with breeding habitat, additional components may require modeling. For example variation of winter habitat through time could be modeled as a function of previous amount of habitat and environmental variation through a simple autoregressive function with stochastic (e.g., weather) influences. However, because we were principally concerned with factors under potential management control, we placed less emphasis in the incorporation of "random" factors (e.g., weather).

Relation of Model Parameters to Population Factors.—Each of the major population factors we considered earlier relates to specific demographic parameters (i.e., reproductive and survival rates) within each of the sub-models previously considered (Table 4). In turn, we can describe each of the hypotheses above in terms of model parameter values or combinations of parameter values ($\beta_0, \dots, \beta_{MX}, \dots, \alpha_0, \dots, \alpha_{MX}$) that establish the hypothetical relationships among variation in intrinsic and extrinsic factors, and variation in demographic rates, as specified by

Table 4. Relationship of population factors (Table 3) to American black duck demographic model and submodels.

Factor	Demographic parameters	Submodels
I. Breeding ground habitat	P_t	Reproduction
II. Wintering ground habitat	S_b, S'_b	Harvest/winter survival
III. Harvest	S_b, S'_b	Harvest/winter survival
IVa. Breeding mallards	P_t	Reproduction
IVb. Wintering mallards	S_b, S'_b	Harvest/winter survival

Equations 5 and 10. These factors are described by specifying ranges of parameter values (Table 5). For each, 1 or more parameters are equal to 0 under a null hypothesis (i.e., the factor in question is hypothesized to have no effect on demographic rates), or to take on negative values under a 1-sided alternative. For example, parameters β_M and β_{MX} describe the presumed negative influence of breeding mallards on per capita reproductive rates of black ducks. One advantage of this approach is that it easily accommodates multiple, explanatory factors. For example,

$$\alpha_N < 0, \alpha_{NX} < 0, \beta_M < 0, \beta_{MX} < 0,$$

all other parameters = 0, corresponds to the combination of compensatory mortality (i.e., negative density dependence in survival), in conjunction with negative effect of mallards on reproductive rates.

Clearly, certain parameter ranges (Table 5) make no biological sense and need not be entertained further. For instance, we are aware of no reasonable scenarios wherein increasing densities of black ducks would positively influence either reproductive or

survival rates, except in the unlikely circumstance that black duck densities became so low that Allee (1931) effects came into play. Therefore we have constrained the "admissible" range for the associated parameters ($\alpha_N, \alpha_{NX}, \beta_N, \beta_{NX}$) to be bounded above by 0. Finally, the proposed model form and parameter relationships allow us (see next section) to develop statistical models to provide parameter estimates that will be interpretable in terms of the above factors singly and in combination, and which lead directly to models capable of forecasting future population status.

PARAMETER ESTIMATION AND MODEL EVALUATION

Philosophy and General Approach

In this section, we used historical data on black duck demographic parameters and relevant intrinsic (e.g., black duck abundance) and extrinsic (e.g., habitat conditions, weather) factors in an attempt to estimate parameters of the model and submodels developed in the previous section. We believe that this approach, in contrast to a purely exploratory analysis, is superior

Table 5. Relationship of American black duck model parameters to population factors (Tables 3 and 4) and range of logically admissible parameter values (see text).

Parameter(s)	Description	Factor	Parameter range
$\beta_0 = \log(A_{\max})$	intercept for reproduction	—	$[-\infty, +\infty]$
β_N, β_{NX}	Density dependence (reproduction)	—	$[-\infty, 0]$
β_M, β_{MX}	Mallard competition (breeding)	IV a	$[-\infty, 0]$
β_X	Breeding habitat	I	$[-\infty, 0]$
$\alpha_0 = \text{logit}[S_0/(1 - S_0)]$	intercept for winter survival	—	$[-\infty, +\infty]$
α_N, α_{NX}	Density compensation/ Harvest	III	$[-\infty, 0]$
α_M, α_{MX}	Mallard competition (wintering)	IV b	$[-\infty, 0]$
α_X	Winter habitat	II	$[-\infty, 0]$

because it (1) potentially allows direct interpretation of our data analyses in terms of the 4 major hypotheses of interest, and (2) it leads directly to a model set that can be used to make testable predictions, possibly under ARM (Walters 1986, Lancia et al. 1996).

We chose to emphasize parameter estimation, rather than hypothesis testing, for 2 reasons. First, we believe that for the most part hypothesis testing is inappropriate in the absence of controlled experimentation (Johnson 1999, Anderson et al. 2000). Using (as we are) retrospective analyses of data, it may not be logically possible to exclude *any* "reasonable" hypothesis as potentially explaining patterns in these data. Second, whereas 1 or more of the 4 major hypotheses (previous sections) are likely "true," to the extent that they may be said to have contributed to changes in black duck populations, we doubt that a single hypothesis would emerge as the sole "causative" factor, even if we were able to conduct a definitive, controlled experiment. We suspect that, assuming we have correctly identified the major factors affecting populations, historical (and future) effects on black duck demographics involve the interaction of several factors, operating either in an additive or non-additive fashion. Under these circumstances, an estimation approach seems most efficacious, where our parameter estimates provide measures of the relative strength or weakness of each factor. Thus, while we used statistical model selection procedures to "weed out" some clearly inferior explanatory factors, we generally included at least some parameters associated with each hypothesis, even if the estimated parameter values were statistically "nonsignificant."

Although many sources of data are potentially available for the estimation of some or all of the model parameters, we limited our analyses to data sources that met several criteria. First, because our model and analyses deal with a continental, migratory population, we required population, habitat, and other statistics at this scale. Second, we were interested in modeling the potential influence of factors such as harvest rates, habitat conditions, and mallard populations on a population that itself has exhibited various abundance levels and rates of change. To obtain estimates of the relationship of these

factors to population change, we needed a relatively long time series of data (at least 25–30 years). Unfortunately, these criteria eliminated a number of excellent but local or short-term studies. These studies, however, are incorporated in our comprehensive literature review and model development (previous sections) and thus are involved in specifying the structure of the model and hypotheses included, if not in the actual estimation of model parameters.

Methods

Breeding Period.—From the previous section, our breeding period submodel involves relationships between per-capita reproductive rates P_b and various intrinsic variables, such as black duck abundance ($N_t^{(0)}$) and density ($N_t^{(0)}X_t^{(0)}$), and extrinsic variables such as habitat conditions ($X_t^{(0)} = 1/HAB_t^{(0)}$) and mallard abundance ($M_t^{(0)}$) and density ($M_t^{(0)}X_t^{(0)}$). Because we had no direct estimates of P_b , we modeled population growth by Equation 3 based on fall age ratios, A_t . We predicted A_t from the above intrinsic and extrinsic variables by Equation 5 after log transformation to fit the model

$$Y_t = \hat{Y}_t + \varepsilon_t, \quad (13)$$

where

$$Y_t = \log_e(A_t),$$

and

$$\begin{aligned} \hat{Y}_t = & \log_e(A_t) - \beta_N N_t^{(0)} - \beta_X X_t^{(0)} - \beta_{NX} N_t^{(0)} \\ & - X_t^{(0)} - \beta_M M_t^{(0)} - \beta_{MX} M_t^{(0)} X_t^{(0)} \end{aligned}$$

with ε_t a residual error with expectation 0 and variance σ^2 . We used generalized linear models and maximum likelihood estimates (MLE) of the parameters of Equation 13, specifying normally distributed errors (ε_t) and a log link function (SAS Institute 1993, 1999). We used the U.S. harvest because these data were available over a longer time period than corresponding data for the Canadian harvest, and the U.S. harvest provides a sample of birds originating from both Canadian and U.S. breeding areas. The U.S. harvest statistics are based on a sample questionnaire of U.S. hunters to obtain an estimate of number of ducks of all species harvested by states and counties,

which is then stratified by species, age, and sex using a sample of wings obtained from a sub sample of hunters (Martin and Carney 1977). These data were used to obtain unadjusted estimates of the age ratio, H_t^y/H_t^a , in the harvest for each year t for all states in the Atlantic and Mississippi flyways during 1961–1996, where H_t^y and H_t^a are the estimated total numbers of immature and adult black ducks, respectively, harvested in year t . We initially attempted to estimate harvest age ratios separately for males and females, because of concerns about the effects of sex-specific spring–summer survival on interpretation of fall age ratios (see below). Our subsequent examination of the harvest data, however, revealed high proportions (>95%) of unknown sex immature black ducks in the samples in early years of the harvest surveys (before 1972), precluding the use of these data to estimate sex-specific ratios. We therefore obtained harvest age ratios as above, that is, pooled across sexes. These ratios were adjusted for differential vulnerability with direct (hunting season following banding) recoveries of normal, wild, known-age black ducks banded in the principal breeding range of black ducks (Areas 1–5, Fig. 1a; Smith 1997). Only recoveries of birds shot or found dead during the hunting season in the U.S. were used; this allowed matching of the harvest data with recovery data (both U.S. harvest) for vulnerability adjustment. We used these data to obtain a pooled estimate of the fall immature:adult age ratio for each year as

$$\hat{A}_t = \frac{H_t^y/H_t^a}{f_t^y/f_t^a}, \quad (14)$$

where

$$f_t^y = \frac{\sum_{j=1}^J m_{tj}^y}{R_t^y},$$

$$f_t^a = \frac{\sum_{j=1}^J m_{tj}^a}{R_t^a},$$

and m_{tj}^y , m_{tj}^a are direct recoveries in states $j = 1, \dots, J$ of R_t^y young and R_t^a adult birds banded preseason in reference areas 1–5

during year t . We also examined estimates in which the harvest age ratio and adjustment were computed separately (on a state or flyway basis) and then averaged (weighting by wing and banding sample sizes) to provide a composite estimate for each year. We found no substantial difference in these approaches, except that the pooled estimators appeared more stable (lower variances, fewer extreme estimates), probably because they were based on larger samples (estimated numbers harvested for each age and recoveries for each age). Therefore, we report only the results based on the pooled (year-specific) estimates. We then log-transformed these estimates to obtain $Y_t = \log_e(\hat{A}_t)$ for use in the log-linear model (Eq. 13).

We considered several possible data sources as candidate indices to black duck abundance for use in the reproductive model. More recent helicopter and fixed-wing surveys of black ducks in eastern Canada and the U.S. (Black Duck Joint Venture, 1997 Report, unpubl. report, Nepean, Ont.) were ruled out because these covered too short of a time span (<15 years). Also considered was the Breeding Bird Survey (Robbins et al. 1986). However, the BBS is more oriented toward terrestrial birds, and because of its roadside nature may not be appropriate for indexing waterfowl populations. Furthermore, most BBS routes in Canada are in the southern portion of the country, with few or none in the boreal forest region where much of the breeding black duck population occurs. We were left with no comprehensive, long-term survey of black duck abundance during the breeding period, and thus considered surveys at other times of the year that might provide a reasonable index to breeding abundances. We decided to use the MWI in the Atlantic and Mississippi Flyways, as providing a reasonable index to breeding populations of black ducks in the same calendar year ($N_t^{(0)}$). Analyses by John Sauer (USGS Biological Resources Division, unpublished data) support the use of MWI as indices to breeding black duck populations, finding high correlation between MWI, BBS, and, where available, more recent aerial surveys for black ducks. However, we recognize that substantial biases likely exist in MWI estimates (Conroy et al. 1988). In addition,

mortality and movement between the winter survey population and the referenced breeding populations of black ducks, may further detract from the utility of the MWI as an estimate of breeding black duck populations. These deficiencies will be considered further, when we discuss the interpretation of parameter estimates in ensuing sections.

We faced many of the same issues with respect to indexing the abundance of mallards for use in our predictive model. Although statistically based surveys are well established for western populations of mallards, only recently have similar surveys been instituted for eastern populations. Therefore, we again relied on MWI estimates of mallard abundance as the best available long-term index to subsequent breeding populations ($M_t^{(0)}$) in the area of sympatry with breeding mallards. However, many mallards wintering in the Mississippi Flyway breed in prairie habitats west of the black duck range. Consequently, we examined harvest derivation for states in the Mississippi and Atlantic Flyways via preseason band recoveries, and eliminated states which derived <75% of their mallard harvest recoveries from banded samples within the black breeding range (defined for these purposes as Ontario and the Great Lakes states eastward). Harvest derivation was computed according to Munro and Kimball (1982), with equal weighting for breeding population sizes because of the absence of reliable breeding population surveys for mallards in the black duck range prior to 1990. Based on these criteria, we included MWI data for mallards from Wisconsin, Michigan, Indiana, Ohio, Kentucky, and Alabama and the entire Atlantic Flyway, as representing breeding populations of mallards ($M_t^{(0)}$) roughly sympatric with black ducks. Again, as improved surveys of both species on the breeding grounds proceed, these data can and should be used in future analyses.

We considered separately 3 indices to the quantity of black duck habitat in the breeding range. Our first candidate was the total acreage of forest in eastern Canada. Unfortunately, available statistics for 1961–1996 did not include acreage by forest type. Thus, this measure is likely to be an imperfect index to the quantity of breeding habitat, and may reflect changes (e.g., because of

forest cutting) in upland, as well as those in lowland types favored by black ducks, such as peatlands (Bélanger et al. 1988). However, it was the only comprehensive data base available for Canada, and thus we incorporated it into our analyses, and thus we estimated $HAB_t^{(0)1}$ as the total forest acreage in eastern Canada in year t .

We also used the acreage of swamp forest in the northeastern and Midwestern U.S. as an index to black duck breeding habitat (see REVIEW OF POPULATION FACTORS). Again, this statistic is likely to be an imperfect indicator of black duck habitat quantity, given that this region includes only the southernmost portion of the black duck breeding range. Because the statistic includes only swamp forest types, it likely better characterizes habitat quantity for that portion of the black duck range. Thus we estimated $HAB_t^{(0)2}$ from the total swamp forest acreage in the northeastern U.S. in year t .

Finally, as mentioned earlier, we examined beaver harvest as a possible index to black duck habitat. We obtained data on the harvest of beaver in Canada for Ontario eastward for 1961–1996 (M. J. Petrie, unpubl. data), divided by the average annual price of beaver pelts (based on sales in Québec) each year in 1995 CDN\$ to obtain an index to beaver abundance (B_{tj}) for each province. Methods by which these data were collected were unavailable but we assume that these were different among provinces, making the computation of a pooled metric problematic. Therefore we standardized B_{tj} to provide a unitless indicator of relative (rather than absolute) change in abundance over time within each province

$$B'_{tj} = (B_{tj} - \bar{B}_j)/s_j,$$

where \bar{B}_j and s_j are the mean and variance across years for each province ($j = 1, \dots, J$). These province-specific, standardized values were then combined into a weighted average across provinces as

$$HAB_t^{(0)3} = \frac{\sum_{j=1}^J A_j B'_j}{\sum_{j=1}^J A_j},$$

where A_j was the geographic area (km^2) for each province. Because the Canadian data represented beaver harvest over most of the black duck breeding range, and because we were not confident of including comparable data from the U.S., we decided to exclude data on U.S. harvest of beaver in the above computations.

We also considered the effects of extrinsic, environmental factors on black duck reproductive rates. Specifically, we examined the effect of annual variation in precipitation, a factor also used in the development of a model for eastern mallard populations (F. A. Johnson, unpubl. data). We used total precipitation for March–May in each year, for the northern Atlantic Flyway (AFN, Fig. 1b; Northeast Regional Climate Center, available online at http://met-www.cit.cornell.edu/nrcc_home.html). To derive a precipitation index ($\text{PPT}_t^{(0)}$) for each year, we took the weighted average of each states' March–May precipitation, the weights being the geographic areas of the respective states. Unusually cold periods during brood rearing are thought to influence survival of black duck broods (Ringelman and Longcore 1982, Longcore et al. 1988). Therefore we also examined the effect of annual variation in minimum mean monthly May–July temperatures ($\text{TMP}_t^{(0)}$) as an index to this factor, using the same regional weather database cited above, likewise computed for each year as the area-weighted average over the states in AFN.

We fit several models representing combination of the plausible factors outlined earlier, all of which contained at least one term for density-dependence (β_N or β_{NX}). Additional terms representing habitat effects (β_X) and mallards (β_M , β_{MX}) were each added to represent the effect of the corresponding factor, resulting in 4 combinations. Models were evaluated following maximum likelihood estimation by computation of AIC as

$$\text{AIC} = -2\log_e(L) + 2K,$$

where L was the likelihood for a candidate model, evaluated at the MLE, and K was the number of estimated parameters (Burnham and Anderson 1998:46). Competing models

were ranked in increasing order by AIC score, which was used to compute a model weight as

$$w(i) = \frac{\exp(-\Delta_i/2)}{\sum_{m=1}^p \exp(-\Delta_m/2)}, \quad (15)$$

where $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$, and AIC_i and AIC_{\min} are the AIC scores for the i th model and the lowest-ranked model, respectively. These weights are approximately interpretable as the probability that the i th model is the “best approximating model” from among the plausible alternative models (Burnham and Anderson 1998:124). In this instance the respective models correspond to underlying biological hypotheses about the operation of combination of factors in influencing productivity rates, and we thus use the model weights as estimates of the probability that the corresponding model is “true.”

Harvest/Winter Period.—Several possible analyses and accompanying data structures exist that may be used to estimate parameters for the survival submodel, depending on availability and scope of data. All such analyses depend on time series of reproductive rates, annual or seasonal survival rates, kill rates, habitat conditions, and abundance estimates for black duck and (possibly) mallard populations. We review several of these with the idea that either current investigators who possess data of which we are unaware, or future investigators, may use the suggested methods in obtain independent estimates of key model parameters.

If mortality during the nonharvest period (θ_t) can be directly observed, then Equations 10–11 can be used in conjunction with estimates or projections of winter abundance to estimate the parameters of the survival submodel ($\alpha_0, \dots, \alpha_{MX}$). Estimates could be obtained via nonlinear regression, or by linear regression following logit transformation of estimates of θ_t , using as predictors the indices to black duck abundance ($N_t^{(2)}$), quantity of winter habitat ($X_t^{(2)} = 1 / \text{HAB}_t^{(2)}$), mallard abundance ($M_t^{(2)}$), and black duck and mallard density ($N_t^{(2)}X_t^{(2)}$, $M_t^{(2)}X_t^{(2)}$). Alternatively, a logit transform could be used directly in the statistical model used to estimate θ_t , e.g., using programs SURVIV

(White 1983) or MARK (White and Burnham 1999), thus bypassing the need for a 2-step process in which the θ_t are first estimated and then used as the response in a regression model. Advantages of the second approach include more efficient estimation, as well as proper estimation of variances.

Realistically, either approach may be difficult to apply to black duck populations, for several reasons. Direct estimates of winter, nonharvest mortality (θ_t) are difficult to obtain, requiring intensive efforts such as radio telemetry (e.g., Conroy et al. 1989b). We are aware of few examples of such estimates (e.g., the one just noted), and none where estimates occur for a substantial time series (e.g., >5 yr) and encompass a substantial portion of the black duck winter range (the cited study was for 3 years and involved black ducks marked in 2 locations in New Jersey and 1 location in Virginia). Even if local study estimates were available for a longer time series, difficulties would exist in deciding the appropriate spatial scale for matching these estimates with appropriate measures of black duck and mallard abundance and habitat conditions. For example, should θ_t for a coastal New Jersey study area be predicted from abundance and habitat conditions for that study area alone, all of coastal New Jersey, or coastal states New York and south (all potential wintering areas for black ducks originally captured in New Jersey)? Because of these difficulties, we chose to base our analyses on continental-scale estimates of survival from band recovery data to estimate survival and harvest rates, indices to abundance for black ducks and mallards from the MWI, and habitat indices, as described below in greater detail.

We obtained time-specific estimates of θ_t from a reparameterized band-recovery model (Brownie et al. 1985, Conroy et al. 1995, Pollock et al. 1995). From Equations 7 and 8, we reparameterized survival rates by separating annual survival into harvest ($1 - K_t$) and nonharvest (θ_t) components:

$$S_t = (1 - K_t)\theta_t.$$

Recovery rates are functions of annual kill rates (K_t), crippling loss rates (c_t) and band reporting rates (λ_t), such that

$$f_t = \lambda_t(1 - c_t)K_t. \quad (16)$$

Current, time-specific estimates of reporting rates and crippling rates do not exist for black ducks. If these rates can be assumed constant the above expression becomes

$$f_t = \lambda(1 - c)K_t.$$

and f_t bears a constant, proportional relationship to annual kill rate. We have no evidence of temporal changes in reporting rates (with the exception of the "1-800" issue, addressed below) since the Conroy and Blandin (1984) study, and have taken $\lambda = 0.3$ (Conroy and Blandin 1984) as the best value for a constant reporting rate. We are unaware of any large-scale studies to estimate crippling loss for black ducks, and thus have used the value of $c = 0.2$ from studies of mallards (Martin and Carney 1977) as our best estimate of crippling loss for black ducks in the above expression.

An additional consideration in modeling harvest and recovery rates is the occurrence of "band solicitation," in which law enforcement and other officials actively solicit the return of recovered bands from hunters. It is generally assumed that the reporting rate under these circumstances approaches 100%. Thus, to the extent that solicitation generates band recoveries, these recoveries must be parameterized differently in models, if unbiased estimation of kill rates is to occur. This can be accomplished by post-stratifying recoveries as voluntarily reported vs. solicited, based on "why reported codes." Thus, "ordinary" recoveries (i.e., those reported voluntarily, without solicitation) are parameterized by

$$f_{ht} = \lambda(1 - c)(1 - \gamma_t)K_t, \quad (17)$$

whereas solicited recoveries are parameterized by

$$f_{st} = (1 - c)\gamma_t K_t, \quad (18)$$

where γ_t is the annual rate of band solicitation (Conroy 1985, Conroy et al. 1995, Pollock et al. 1995). Combining these expressions with the partitioning of survival into harvest and nonharvest components, and using constants for reporting and crippling

loss allows us to use band recovery data to explicitly estimate K_t and θ_t . Using Equations 7, 17, and 18 we obtained general expressions for the probability π_{mij} of recovery of type m ($m = h$ [hunter] or s [solicited]) in recovery year j for birds banded in year i :

$$\pi_{mij} = \begin{cases} f_{mj}, & m = h, s \quad j = i \\ \prod_{t=i}^{j-1} (1 - K_t) \theta_t f_{mj}, & k = h, s \quad j > i \end{cases} \quad (19)$$

where

$$f_{hj} = \lambda(1 - c)(1 - \gamma_j)K_j,$$

$$f_{sj} = (1 - c)\gamma_j K_j;$$

see Conroy et al. (1995) and Pollock et al. (1995) for more details on this approach.

We used this basic approach, with extensions to a 2-age-class structure (i.e., banding of both juvenile [hatching year] and adult [after-hatching year] birds), and program SURVIV (White 1983) to estimate the parameters of primary interest (K_t and θ_t), and the nuisance parameter γ_t . We used pre-season (July–September) band releases of normal, wild, known age and sex black ducks and recoveries of black ducks shot or found dead during the hunting season, for the period 1961–1996, in Areas 1–5 (Fig. 1a). The model we developed allowed for variation in K_t , θ_t , and γ_t by age, sex, banding reference area, and year. Subsets of constrained models (i.e., parameters constant over combinations of the above dimensions) were examined using AIC (Burnham and Anderson 1998). For the purposes of the regression analyses (described below) we confined model selection to those models in which time-specific variation in θ_t was allowed. Preliminary results indicated that estimates for K_t and θ_t were unstable for reference area 1, because of small sample sizes; therefore subsequent analyses were based on reference areas 2–5. In addition, estimates for K_t based on assumed constant reporting rates increased after 1995, contemporaneous with implementation of a program for enhancing band reporting rates by means of toll-free (1-800) numbers. We thus considered only band recoveries through 1994 to

avoid possible biases in estimates because of recent, unestimated increases in reporting rates; these allowed estimation of θ_t for 1961–1993 (32 time-specific estimates).

We treated time-specific estimates of $\hat{\theta}_t$ from the above procedure as response variables in a least-squares regression to estimate the parameters of the survival submodel ($\alpha_0, \dots, \alpha_{MX}$). We fit the prediction equation:

$$Z_t = \hat{Z}_t + \varepsilon_t, \quad (20)$$

where

$$Z_t = \log_e \left(\frac{\theta_t}{1 - \theta_t} \right),$$

$$\hat{Z}_t = \alpha_0 - \alpha_N N_t^{(2)} - \alpha_X X_t^{(2)} \alpha_{NX} N_t^{(2)} X_t^{(2)} - \alpha_M M_t^{(2)} - \alpha_{MX} M_t^{(2)} X_t^{(2)},$$

where θ_t are estimates from the band recovery model, $X_t^{(2)} = 1/\text{HAB}_t^{(2)}$, $N_t^{(2)}$, $M_t^{(2)}$, are indices to winter abundance for black ducks and mallards, and $\text{HAB}_t^{(2)}$ is an index to the quantity of winter habitat, described later. Because these response variables are based on sample estimates with a sampling variance-covariance structure, we also considered using weighted least-squares regression (Myers 1990) to obtain estimates. As with the reproductive model, we computed AIC (Burnham and Anderson 1998) to compare among models incorporating subsets of the parameters $\alpha_0, \dots, \alpha_{MX}$ and additional coefficients α_{sex} and α_{age} representing sex- and age-specific winter survival, respectively, and α_{NM} representing the effects of interaction between black duck and mallard abundance ($N_t^{(2)} \times M_t^{(2)}$). However, we were unable to use maximum likelihood estimation because of problems encountered with unconstrained estimates assuming biologically inadmissible values (e.g., $\alpha_N, \dots, \alpha_{NX} > 0$), and instead used PROC NLIN (SAS Institute 1999) to perform least-squares estimation (LSE) with boundary constraints, i.e., we minimized $\sum_{t=1}^n (Y_t - \hat{Y}_t)^2 / n$ subject to $\alpha_0, \dots, \alpha_{MX}$ satisfying our biological constraints (Table 5). We then computed AIC as

$$\text{AIC} = n \log_e(\hat{\sigma}^2) + 2K, \quad (21)$$

where $\hat{\sigma}^2 = \sum_{t=1}^n (Y_t - \hat{Y}_t)^2 / n$ and K was the number of estimated parameters (Burnham

and Anderson 1998:48). Finally, we computed model weights as described above for the reproduction model corresponding to the combinations of factors (habitat, compensation, and mallards) under consideration for survival:

$$w(j) = \frac{\exp(-\Delta_j/2)}{\sum_{m=1}^s \exp(-\Delta_m/2)} \quad (22)$$

for the $j=1, \dots, s$ survival models under consideration.

The above approach requires a 2-step analysis, in which survival estimates are first obtained using SURVIV, and then used as the response variable in a regression analysis. An alternative to nonlinear regression, which was initially attractive, was to directly incorporate the hypothesized relationships into band-recovery models, and estimate parameters by ML methods using program SURVIV. This approach avoids the 2-stage analysis, and in theory is a more efficient use of data, because time-specific survival rates are no longer estimated, but instead are obtained via the predicted relationship between survival and the predictors (abundance, density, and habitat), given estimated values for $\alpha_0, \dots, \alpha_{MX}$ and other parameters.

We developed an ultrastructural model by substituting Equation 10 into 19 to obtain

$$\pi_{mij} = \prod_{t=i}^{j-1} (1 - K_t) \hat{\theta}_t f_{mj}, \quad k = h, s \quad j > i, \quad (23)$$

where $\hat{\theta}_t$ was defined in terms of the parameters of the survival model from Equation 20 as

$$\hat{\theta}_t = (1 + \exp(-\hat{Z}_t))^{-1}$$

with the remaining terms defined as in Equations 17–19.

To estimate parameters of the survival submodel, we required appropriate indices to winter abundance of black ducks ($N_t^{(2)}$) and mallards ($M_t^{(2)}$) and of winter habitat ($HAB_t^{(2)}$). We considered several alternative data sets for these indices, but few met our criteria of geographic scope and time frame. We are familiar with only 2: the MWI, and the Christmas Bird Count. We considered both of these as candidates, but decided to

focus our analyses on the MWI estimates, because unlike the CBC, this survey focuses on ducks vs. all birds, and because analyses by John Sauer (USGS Biological Resources Division, unpubl. data) and Butcher (1990) found close agreement between trends in these 2 surveys for black ducks. Thus, we estimated ($N_t^{(2)}$) from the Atlantic and Mississippi Flyway totals for the MWI, in January of year $t+1$ (i.e., in the biological year corresponding to the estimates of θ_t). Likewise for mallard abundance we estimated ($M_t^{(2)}$) from the MWI for mallards in the Atlantic and Mississippi Flyway, in January of year $t+1$. Because we were using the MWI to index wintering mallard populations we were not concerned about the breeding-ground derivation of these birds, but did wish to include mallards only to the extent of significant winter range overlap with black ducks, defined for our purposes as the average MWI for a state during the study period $>1,000$. Based on this criterion we excluded MWI totals for Minnesota, Iowa, Louisiana, and Missouri.

To index wintering habitat, we estimated $HAB_t^{(2)}$ from the total acreage of coastal wetland habitat along the Atlantic coast of the U.S. in year t . We also considered the potential for winter weather severity to explain annual variation in winter survival rates. We used mean December and January temperatures (Northeast Regional Climate Center, http://met-www.cit.cornell.edu/nrcc_home.html) for AFN (Fig. 1b) to compute a flyway index to winter severity as a weighted average of the state December–January temperatures, with the weights formed by the geographic areas of each state. In turn, we used this index as 1 of the predictors in the linear regressions (Eq. 20).

Model Synthesis.—After we obtained parameter estimates under the alternative reproductive and survival submodels, we combined the resulting prediction equations into the overall population growth model. We assumed that the model would be applied to projection of observable system states comprised of $N_t^{(0)}$ (estimates or indices of breeding black duck abundance), $HAB_t^{(0)}$ (ha of breeding habitat), and $M_t^{(0)}$ (estimates or indices of breeding mallard abundance). Sexes of black ducks cannot be observed from aerial surveys, so $N_t^{(0)}$ was

partitioned into male and female components according to

$$\begin{aligned} N_t^{(0)m} &= \alpha N_t^{(0)}, \\ N_t^{(0)f} &= (1 - \alpha) N_t^{(0)}, \end{aligned} \quad (24)$$

where α was assumed stable and estimated from average adult male (θ^{am}) and adult female (θ^{af}) survival rates (this study) by

$$\alpha = \theta^{am}/(\theta^{am} + \theta^{af}) = 0.545.$$

Using $N_t^{(0)}$, HAB $_t^{(0)}$, and $M_t^{(0)}$ as inputs, we obtained predicted fall age ratios $\tilde{A}_t(i)$ using Equation 13 under each alternative reproduction model (i). These in turn were used to project a fall population

$$\begin{aligned} N_t^{(1)am} &= N_t^{(0)m} S_t^{(0,1)m}, \\ N_t^{(1)af} &= N_t^{(0)f} S_t^{(0,1)f}, \\ N_t(i)^{(1)y} &= [N_t^{(1)am} + N_t^{(1)af}] \tilde{A}_t(i) \end{aligned} \quad (25)$$

for adult males (am) adult females (af) and juveniles (y) under each reproduction model, $i = 1, \dots, p$, where a spring-fall survival of $S_t^{(0,1)f} = 0.75$ was assumed for females (Ringelman and Longcore 1983, Dwyer and Baldassarre 1994). Given this assumed rate for females, an estimate of $\theta^{am}/\theta^{af} = 1.2$ (from our analyses), and assuming that the lower annual survival of females is accounted for by increased risk of predation during the breeding period, we obtain $S_t^{(0,1)m} = 0.75 \times 1.20 = 0.9$. This last assumption seems reasonable given that in the absence of sex-specific regulations or harvest rates for black ducks (Krementz et al. 1987), the reproductive period is the most likely period for differential mortality risk to occur. Finally, we assumed even sex ratios at hatching and equal hatching-to-fall survival rate to obtain

$$N_t(i)^{(1)ym} = N_t(i)^{(1)yf} = 0.5 N_t(i)^{(1)y}, \quad (26)$$

the projected number of juvenile males (ym) and females (yf) under each model, $i = 1, \dots, p$, to obtain a forecast for the fall population in year t .

Under our model (Eqs. 1–12) we assumed that all mortality between the post-reproductive period and winter is from hunting.

Based on radiotelemetry studies during the post-reproductive period (Conroy et al. 1989b, Chipley 1995) we believe this assumption to hold at least approximately. Thus, fall population size for each age and sex class was multiplied by the complement of kill rate ($1 - K_t$) for that class to determine the survivors to the post-harvest (winter) population, that is

$$\begin{aligned} N_t^{(2)am} &= N_t^{(1)am} (1 - K_t^{am}), \\ N_t^{(2)af} &= N_t^{(1)af} (1 - K_t^{af}), \\ N_t^{(2)ym}(i) &= N_t^{(1)ym}(i) (1 - K_t^{ym}), \\ N_t^{(2)yf}(i) &= N_t^{(1)yf}(i) (1 - K_t^{yf}), \end{aligned} \quad (27)$$

for adult males, adult females, young males, and young females, respectively, under each of the $i = 1, \dots, p$ reproduction models. Depending on the application, kill rates might either be determined *a posteriori* (known or estimated from historical data, e.g., for model calibration) or *a priori* (as management controls, e.g., under adaptive harvest management). In the latter case we would assume managers' ability to determine harvest rates, either as a fixed input, or as the outcome from specified probability distributions under alternative regulatory packages (Johnson et al. 1993). In either case, we assumed that harvest affects the different age and sex classes differentially. For model calibration based on historical data we used empirical estimates $1 - K_t$ from the survival estimation procedures described earlier. For forecasting of future scenarios we specified harvest rates (for instance, as might be realized under alternative sets of harvest regulations) in terms of adult males, and compute age- and sex-specific rates as

$$\begin{aligned} h_t^{am} &= h_t, \\ h_t^{af} &= h_t d^{af}, \\ h_t^{ym} &= h_t d^{ym}, \\ h_t^{yf} &= h_t d^{yf}, \end{aligned} \quad (28)$$

where d^{af} , d^{ym} , d^{yf} , are the differential harvest vulnerabilities of each of the other age-sex classes, relative to adult males. We estimated

d^{af} , d^{ym} , d^f from the ratios of average estimated band recovery rates for preseason-banded black ducks to obtain 0.94, 2.03, and 1.88, respectively. These rates represent the proportion of birds alive in the fall that are shot and retrieved in the legal harvest, and do not account for unretrieved kill (crippling loss). To adjust for crippling loss we computed harvest kill rates as

$$K_t^m = h_t^m / (1 - c), \quad m = af, am, yf, ym, \quad (29)$$

where $c = 0.2$ was used as the assumed rate of crippling loss (Martin and Carney 1977). Given our projected winter populations from Equation 28, we obtain a total, projected winter abundance as

$$\begin{aligned} N_t^{(2)}(i) &= N_t^{(2)am} + N_t^{(2)af} \\ &\quad + N_t^{(2)ym}(i) + N_t^{(2)yf}(i), \end{aligned} \quad (30)$$

$i = 1, \dots, p$. These values were then used as input, along with $HAB_t^{(2)}$ and $M_t^{(2)}$, to obtain predictions of winter survival $\hat{\theta}_t^{kl}(i,j)$, $k = a, y$; $l = m, f$ from Equation 20 under each reproduction model i , $i = 1, \dots, p$ and survival model, $j = 1, \dots, s$. The predictions were then used to project the winter populations to the subsequent breeding period according to

$$\begin{aligned} \hat{N}_{t+1}^{(0)}(i,j) &= \left[N_t^{(2)am} \hat{\theta}_t^{am}(i,j) \right. \\ &\quad \left. + N_t^{(2)ym}(i) \hat{\theta}_t^{ym}(i,j) \right] / S^{(0,1)m} \quad (31) \\ &\quad + \left[N_t^{(2)af} \hat{\theta}_t^{af}(i,j) + N_t^{(2)yf}(i) \hat{\theta}_t^{yf}(i,j) \right] / S^{(0,1)f} \end{aligned}$$

for each combination of reproduction and survival model, $i = 1, \dots, p$, $j = 1, \dots, s$. Finally, a weighted average projection was produced by

$$\bar{N}_{t+1}^{(0)} = \sum_{i=1}^p \sum_{j=1}^s wt(i) wt(j) \hat{N}_{t+1}^{(0)}(i,j), \quad (32)$$

where $wt(i)$, $wt(j)$, are the AIC weights for the reproduction and survival models, $i = 1, \dots, p$, $j = 1, \dots, s$.

In the above projections, mallard populations and habitat (breeding and wintering) are assumed to be known inputs. Again, depending on the application these would either be observed from surveys (e.g., of breeding or wintering mallards) or other sources (habitat inventories), projected via

models, or both. In particular, assumptions about the future trajectory of mallard populations and habitat conditions are potentially critical in modeling alternative management scenarios for black ducks, as discussed later.

Model Calibration and Prediction.—The methods used to estimate parameters for the reproduction and survival models should ensure that the separate models fit the respective data sets well, and produce biologically reasonable values. However, they do not ensure that the models will perform well in combination, particularly when used to forecast the future state of the system. Therefore, we evaluated model performance via a series of 1-year population forecasts using historical data for $N_t^{(0)}$, $HAB_t^{(0)}$, and $M_t^{(0)}$. Estimates of annual hunting season survival rates $(1 - K_t)$ for each age and sex for each year t were obtained from band recovery data (as a by-product of the data analysis used to fit our survival models), to project winter populations of black ducks. The projected population of black ducks was then used together with the year $t+1$ MWI estimates of $M_t^{(2)}$ and estimates of $HAB_t^{(2)}$ (acres of U.S. coastal wetlands in year t), to provide the inputs for the survival model and the model-specific (Eq. 31) and averaged projections (Eq. 32) of $N_{t+1}^{(0)}$. Finally, the model-averaged projections were compared to the observed index to $N_{t+1}^{(0)}$, and the agreement between these summarized by computing an estimate of relative bias as

$$\text{RBIAS} = \frac{\sum_{t=2}^n (N_t^{(0)} - \bar{N}_t^{(0)}) / (n-1)}{\sum_{t=2}^n N_t^{(0)} / (n-1)} \times 100\%. \quad (33)$$

Additionally, we computed a mean-square error loss function $\hat{\sigma}^2$ as

$$\hat{\sigma}^2 = \frac{\sum_{t=2}^n (N_t^{(0)} - \bar{N}_t^{(0)})^2}{n-1}, \quad (34)$$

and compared this to the total amount of variation of observed breeding abundance about the mean abundance to compute an R^2 statistic

$$R^2 = \frac{SS_T - SS_E}{SS_T}, \quad (35)$$

where

$$SS_E = \sum_{t=2}^n (N_t^{(0)} - \bar{N}_t^{(0)})^2,$$

$$SS_T = \sum_{t=2}^n (N_t^{(0)} - \bar{N}^{(0)})^2,$$

$$\bar{N}^{(0)} = \sum_{t=2}^n N_t^{(0)} / (n-1),$$

and $\bar{N}_t^{(0)}$ was computed for $t = 2, \dots, n$ from Equation 32. Note that Equation 35 potentially results in negative values, in situations where there exists pronounced bias in predictions. We recognize that this procedure does not constitute a validation of our model (*sensu* a comparison with independent data), because most of the model inputs were also involved in estimation of the parameters of 1 or both submodels. Instead, we suggest that large deviations or consistent errors of prediction could be diagnostic of parameter biases, flawed model assumptions, or both. An additional motivation for this analysis, discussed below, was to obtain an estimate of prediction error, for use in the development of a model updating procedure under adaptive harvest management.

Dynamic Behavior of Models.—To assess whether our models would perform well in a management context, we conducted a series of deterministic simulations, in which each of our alternative models was used to forecast future population growth, given initial conditions similar to those at the end of our analyses (1993). We used 1993 values for $N_0^{(0)}$, $M_0^{(0)}$, $X_0^{(0)}$, and $X_0^{(2)}$ parameter estimates under each of our $p \times s$ model combinations, Equation 31 to forecast $N_t^{(0)}(i,j)$, $t = 1, \dots, 100$ for $i = 1, \dots, p$, $j = 1, \dots, s$, and Equation 32 to forecast $\bar{N}_{t+1}^{(0)}$, $t = 1, \dots, 100$. For these simulations mallard abundance was held constant ($M_t^{(0)} = M_0^{(0)}$) and harvest rates were varied from zero to twice 1993 levels ($h_t = h_0 = 0, 0.055, 0.11$); effects of other combinations of harvest rates and mallard abundance are considered in the sensitivity analyses, below.

Sensitivity Analysis.—The parameters estimates of our models may reflect model uncertainty (Anderson and Burnham 1998),

statistical uncertainty, or both, and predictions (e.g., under management) from the model may be sensitive to errors in parameter estimation. We therefore conducted analyses to assess the relative sensitivity of population response to changes in parameter values Γ_i where Γ_i is a parameter under examination (e.g., $\alpha_0, \dots, \alpha_{MX}$; $\beta_0, \dots, \beta_{MX}$). First, we defined $N^*(\Gamma_i)$ as population size ($N_{t+1}^{(0)} \approx N_t^{(0)} = N^*$) after 100 generations, and examined $N^*(\Gamma_i)$ in response to variation in Γ_i over the estimated CI for Γ_i , constrained by the logical bounds on the parameter value (Table 5). To evaluate sensitivity we used elasticity, which measures proportional change in $N^*(\Gamma_i)$ given a proportional change in Γ_i (Caswell 2001:226), and is computed as

$$e(\Gamma_i) = \frac{\Gamma_i}{N^*(\Gamma_i)} \frac{\partial N^*(\Gamma_i)}{\partial \Gamma_i}. \quad (36)$$

Given initial values for $N_0^{(0)}$, $M_0^{(0)}$ HAB $_0^{(0)}$, and $h_t = h_0$, we evaluated Equations 13 and 20, projected population growth according to Equations 24–32, and used numerical differentiation to evaluate

$$\frac{\partial N^*(\Gamma_i)}{\partial \Gamma_i}$$

as

$$\frac{\partial N^*(\Gamma_0)}{\partial \Gamma_0} \approx \frac{N^*(\Gamma_0 + h) - N^*(\Gamma_0)}{h},$$

where Γ_0 is a specified value for Γ_i (e.g., the parameter estimate under model i) and h is a constant ($h = 10^{-14}$). For all parameters, we evaluated $N^*(\Gamma_i)$ and $e(\Gamma_i)$ over the range in the estimated confidence interval of Γ_i , constrained by biologically admissible values of Γ_i (Table 5), where estimates $\tilde{\Gamma}_i$ were obtained by averaging over the estimates across the p reproduction and s survival models, weighted by AIC model weights (Eqs. 15 and 22; Burnham and Anderson 1998:133), with approximate 95% confidence intervals computed by $\tilde{\Gamma}_i \pm 1.96 \times \tilde{SE}_i$, where \tilde{SE}_i is an estimate of unconditional standard error, and incorporated model selection uncertainty (Burnham and Anderson 1998:135). Given values for Γ_i from within these constrained confidence

intervals, and for all other model parameters $\Gamma_{j \neq i}$ at their model averaged values ($\tilde{\Gamma}_j$), projections were made using Equation 31, treating the resulting vector of parameters as the single model under consideration. As above we computed $N^*(\Gamma_i)$ and $e(\Gamma_i)$ assuming 1993 initial conditions, constant mallard abundance ($M_t^{(0)} = M_0^{(0)}$); we considered harvest rates from zero to 1993 levels ($h_t = h_0 = 0, 0.055$) since levels $h_t > 0.01$ resulted in exponentially decreasing abundance, with resulting numerical difficulties in computing elasticity (i.e., division by very small values of $N^*(\Gamma_i)$).

We also evaluated sensitivity of model predictions to variation in key model predictor variables that are potentially under the control of management. In this analysis we focused on 2 factors and their interaction that have proven especially contentious in the management of black ducks: harvest rates and mallard population size. We defined population response as above (i.e., $N_{100}^{(0)}$, but with the parameters of the reproduction (β) and survival (α) models fixed over the respective models. Given 1993 initial conditions and model-averaged estimates of β and α , as above we used the above procedure to project $N^*(\mathbf{x}; \alpha, \beta) = \bar{N}_{100}^{(0)}$ as a function of $\mathbf{x}' = \{x_1 \ x_2\}$, where x_1 is harvest rate of black ducks and x_2 is abundance of breeding mallards, under the assumption (subject to examination with our simulations) that all simulated populations would reach equilibrium (defined as $N_t = N_{t+1} = N^*$; Williams et al. in press) by 100 years. We then computed elasticity as

$$e(x_i) = \frac{x_i}{N^*(x_i; \beta, \alpha)} \frac{\partial N^*(x_i; \beta, \alpha)}{\partial x_i}, \quad i = 1, 2 \quad (37)$$

by numerical differentiation as above. These values represent the proportional change in $\bar{N}_{100}^{(0)}$ given a proportional change in the respective inputs (x_1, x_2) and thus may be viewed as the relative contribution of each input in determining the population's trajectory (Caswell 2001:233).

RESULTS

Reproduction Submodel

Estimated fall age ratios (\hat{A}_t) and predic-

tor values for black duck and mallard abundance ($N_t^{(0)}, M_t^{(0)}$), habitat quantity ($HAB_t^{(0)}$) and precipitation (PPT_t) are reported for 1961–1996 in Appendix 1. These data were used with Equation 13 to estimate the parameters of the reproduction submodel for subsets of predictor variables, with the proviso that abundance ($N_t^{(0)}$) or density ($N_t^{(0)} \times X_t^{(0)}$), were incorporated in every model so that population growth would be eventually density-limited. Models including beaver abundance ($X_t^{(0)3}$) as a predictor consistently scored lower (i.e., had higher AIC values and lower model weights) than did models including Canadian forest acreage ($X_t^{(0)1}$) or U.S. swamp forest acreage ($X_t^{(0)2}$). Because these last 2 habitat indices appeared in several of the top-ranked models, we conducted further combining these 2 indices to compute $X_t^{(0)4}$, where

$$X_t^{(0)4} = 1/HAB_t^{(0)4} = 1/(HAB_t^{(0)1} + HAB_t^{(0)2}).$$

Models based on this composite habitat predictor performed better than corresponding models using either component alone, and consistently were better (lower AIC, higher model weight) than any model based on $X_t^{(0)3}$. Also, models in which density-dependence was expressed by abundance ($N_t^{(0)}$) performed better than those based on density ($N_t^{(0)} \times X_t^{(0)}$). We therefore confined further model evaluation to 24 models involving the predictors $N_t^{(0)}, X_t^{(0)4}, M_t^{(0)}, PPT_t^{(0)}$, and $TMP_t^{(0)}$, all of which included density-dependence, and which spanned all 4 combinations of alternative assumptions regarding habitat and mallard effects on reproductive rates (Table 6). Of these, the model with the highest AIC weight (0.263) contained predictors $N_t^{(0)}, X_t^{(0)}$, and $M_t^{(0)}$. All 4 models containing both habitat and mallard effects were among the top-ranked models; likewise all models in which habitat was absent as a factor received low model weights (<0.03).

The parameter estimates for the model receiving the highest weight within each of the 4 factor combinations are reported in Table 7, along with AIC weights recalculated considering only these 4 models; none of the selected models incorporated either of the environmental predictors considered

Table 6. Model selection for American black duck reproduction submodel. Habitat predictors considered $X_t^{(0)} = 1/\text{HAB}_t^{(0)}$, where $= \text{HAB}_t^{(0)} = \text{HAB}_t^{(0)1} + \text{HAB}_t^{(0)2}$ and $\text{HAB}_t^{(0)1}$ was the total forest acreage in eastern Canada, $\text{HAB}_t^{(0)2}$ the total swamp forest acreage in the northeastern U.S. Black duck abundance ($N_t^{(0)}$), density ($N_t^{(0)} \times X_t^{(0)}$) or both common to all models, and mallard abundance ($M_t^{(0)}$), density ($M_t^{(0)} \times X_t^{(0)}$). Environmental predictors are March–May total precipitation ($\text{PPT}_t^{(0)}$) and minimum average May–July monthly temperature ($\text{TMP}_t^{(0)}$) for northeastern U.S. (Maryland and north).

Factor ^a		Predictor variables	ΔAIC	Model weight
Habitat	Mallards			
1	1	$N_t^{(0)} X_t^{(0)} M_t^{(0)}$	0.000	0.263 ^b
1	1	$N_t^{(0)} M_t^{(0)} X_t^{(0)} \text{PPT}_t^{(0)}$	1.498	0.124
1	1	$N_t^{(0)} M_t^{(0)} X_t^{(0)} \text{TMP}_t^{(0)}$	1.549	0.121
1	1	$N_t^{(0)} M_t^{(0)} X_t^{(0)} N_t^{(0)} \times M_t^{(0)}$	1.886	0.102
1	0	$N_t^{(0)} X_t^{(0)}$	2.478	0.076 ^a
1	0	$N_t^{(0)} X_t^{(0)} \text{PPT}_t^{(0)}$	3.489	0.046
1	1	$N_t^{(0)} X_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)} \text{TMP}_t^{(0)}$	3.701	0.041
1	0	$N_t^{(0)} X_t^{(0)} \text{TMP}_t^{(0)}$	3.731	0.041
1	1	$N_t^{(0)} X_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)} \text{PPT}_t^{(0)}$	4.056	0.035
1	1	$N_t^{(0)} X_t^{(0)} M_t^{(0)} \text{PPT}_t^{(0)} \text{TMP}_t^{(0)}$	4.140	0.033
0	1	$N_t^{(0)} M_t^{(0)}$	5.012	0.021 ^a
0	0	$N_t^{(0)}$	5.781	0.015 ^a
0	1	$N_t^{(0)} M_t^{(0)} \text{PPT}_t^{(0)}$	5.827	0.014
1	0	$N_t^{(0)} X_t^{(0)} \text{PPT}_t^{(0)} \text{TMP}_t^{(0)}$	5.890	0.014
0	0	$N_t^{(0)} \text{PPT}_t^{(0)}$	6.145	0.012
1	1	$N_t^{(0)} X_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)} \text{PPT}_t^{(0)} \text{TMP}_t^{(0)}$	6.804	0.009
0	1	$N_t^{(0)} M_t^{(0)} \text{TMP}_t^{(0)}$	6.822	0.009
0	1	$N_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)}$	7.467	0.006
0	0	$N_t^{(0)} \text{TMP}_t^{(0)}$	8.146	0.004
0	1	$N_t^{(0)} M_t^{(0)} \text{PPT}_t^{(0)} \text{TMP}_t^{(0)}$	8.621	0.004
0	1	$N_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)} \text{PPT}_t^{(0)}$	8.684	0.003
0	0	$N_t^{(0)} \text{PPT}_t^{(0)} \text{TMP}_t^{(0)}$	8.770	0.003
0	1	$N_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)} \text{TMP}_t^{(0)}$	9.425	0.002
0	1	$N_t^{(0)} M_t^{(0)} N_t^{(0)} \times M_t^{(0)} \text{PPT}_t^{(0)} \text{TMP}_t^{(0)}$	11.658	0.001

^a 0 = absence, 1 = presence of habitat and mallard effects, respectively on age ratios of black ducks.

^b Model with highest weight within combination of factors (habitat, mallards).

($\text{PPT}_t^{(0)}$ and $\text{TMP}_t^{(0)}$). Model-averaged estimates of the parameters ($\log(A_{\max})\beta_N, \beta_M, \beta_X$) were also calculated following Burnham and Anderson (1998), except that averaging was across all 4 models for all parameters, with estimates and standard errors set to zero for absent parameters. All parameter estimates were within biologically admissible constraints except for $\hat{\beta}_N = 0.0268$ for model 2 (habitat = 0, mallards = 1). This model received low AIC weight (0.057) and the 95% CI included negative values; as discussed later we substituted the model-averaged estimate of $\hat{\beta}_N = -0.0205$ for use in our integrated population model. These results suggest support for a positive effect of habitat quantity on black duck reproductive rates, and negative density effects from mallards.

Survival Submodel

Using program SURVIV and AIC, we selected a model based on time-, location-(band reference area), and age-specific annual kill rates (K_t), time- and location specific band solicitation rates (γ_t), and time-, age-, and sex-specific non-harvest survival rates (θ_t). Estimates for winter survival rates were of primary interest, being the response variable in our regression models, and are reported in Appendix 2; estimates of area- and year-specific harvest rates for each age-sex class also were calculated, and are included in Appendix 3, and predictor variables of black duck and mallard abundance ($N_t^{(2)}, M_t^{(2)}$), and weighted January–February temperatures ($\text{TMP}_t^{(0)}$) are reported in Appendix 4. These predictors were used with the estimates to fit linear regression

Table 7. Final model selection and parameter estimates for American black duck reproduction submodel.

Model	Factors ^a		Predictors	Coefficient estimate	SE	95% Confidence Interval		ΔAIC	$w(i)$
	Habitat	Mallards				Lower	Upper		
1	0	0	$\log(A_{\max})$	0.1960	0.1549	-0.1075	0.4996	5.781	0.039
			β_N	-0.0126 ^b	0.0418	-0.0945	0.0694		
2	0	1	$\log(A_{\max})$	0.4235	0.2123	0.0074	0.8396	5.012	0.057
			β_N	0.0268 ^b	0.0449	-0.0613	0.1149		
			β_M	-0.1040 ^b	0.0559	-0.2136	0.0056		
3	1	0	$\log(A_{\max})$	2.2821	0.8087	0.6970	3.8671	2.478	0.203
			β_N	-0.0600 ^b	0.0481	-0.1542	0.0343		
			β_X	-0.0227 ^c	0.0085	-0.0394	-0.0059		
4	1	1	$\log(A_{\max})$	2.5698	0.7172	1.1642	3.9755	0.000	0.701
			β_N	-0.0229 ^b	0.0462	-0.1135	0.0677		
			β_M	-0.1160 ^b	0.0505	-0.2150	-0.0171		
Model averaged			β_X	-0.0227 ^c	0.0074	-0.0373	-0.0082		
			$\log(A_{\max})$	2.2963	0.8920	0.5480	4.0445		
			β_N	-0.0272 ^b	0.0501	-0.1253	0.0710		
			β_M	-0.0873 ^b	0.0652	-0.2150	0.0405		
			β_X	-0.0205 ^c	0.0092	-0.0385	-0.0025		

^a 0 = absence, 1 = presence of habitat and mallard effects, respectively on age ratios of black ducks.

^b Coefficient for predictor variable ($N_t^{(0)}$ or $M_t^{(0)}$; Appendix A1.) $\times 10^{-5}$.

^c Coefficient for predictor variable ($X_t^{(0)4}$; Appendix A1, text) $\times 10^{-9}$.

models after logit transformation, which were grouped into combinations of factors (habitat, compensation, and mallard effects) in Table 8. As with the reproduction submodel, the environmental predictor $TMP_t^{(0)}$ did not add to the predictive capability of these models, as judged by AIC. Furthermore, although we used sex- and age-specific survival estimates as response variables (after logit transformation), neither sex nor age effects contributed to model prediction; therefore, the parameters associated with these effects were not considered further. For each of these factors (groups of models) we computed a weight by summing across the model weights for the models in the group, to obtain a weight for the 8 factor combinations ranging from no habitat effects, no compensation, and no mallard effects (0, 0, 0) to all 3 factors operating (1,1,1). As noted in Table 8, however, in all instances where either black duck abundance or density ($N_t^{(2)}$, $N_t^{(2)} \times X_t^{(2)}$) or mallard abundance or density ($M_t^{(2)}$, $M_t^{(2)} \times X_t^{(2)}$) were involved as predictors, the estimates of the corresponding model parameters (α_N , α_{NX} , α_M , α_{MX}) either had biologically inadmissible values (i.e., < 0) or, under constrained optimization, took on the

imposed boundary values (10^{-14}). We took the overall AIC weights for these models as evidence of some type of density-dependence or mallard effect on survival, but did not use the parameter estimates under these models, because these were clearly either biologically unreasonable, or arbitrary (in the case of the constrained estimates).

Instead, we re-estimated parameters and model weights under the top models in the factor groups not involving these coefficients, that is, involving only an intercept term ($\alpha_0 = \text{logit}(\theta_0)$) or the intercept and a habitat effect (α_0 , α_X), but no mallard or compensation terms; the weights for the associated models were 0.42 and 0.58, respectively. This approach, however, leaves a critical alternative hypothesis, that of additive harvest effects, without a balancing competitor (compensation). Although we have no empirical evidence of compensation via density-dependence in this study, it is possible that our methods were simply not precise enough to detect a real, though likely small, compensatory effect. We examined the effect in our survival submodel of including various coefficient values for α_N , and found that values of $\alpha_N \approx 10^{-6}$ resulted in strong (i.e., nearly complete) compensation

to changes in harvest mortality, for ranges in $N_t^{(2)}$ of 300,000 (near the current level) and higher; higher values for α_N resulted in unreasonably low predicted values for θ_b , while lower values produced a negligible compensatory effect. We therefore constructed 2 additional models in Table 9, which were simply the first 2 models of the table, to each which was added $\alpha_N = 10^{-6}$. Finally, in lieu of direct, empirical weights for these models, we summed over the models involving compensatory effects in Table 8, to obtain a "marginal" value of $w(\text{comp}) = 0.119$ for compensatory models (i.e., involving α_N , α_{NX} , or both) and $w(\text{add}) = 0.881$ for non-compensatory models (not involving these parameters). These values were used with the weights for models 1–2 (Table 9) to derive new model weights for the 4 combinations of habitat effect/no effect with compensation/no compensation of

$w(1)' = w(1) \times w(\text{add})$ (No habitat effect, no compensation),

$w(2)' = w(2) \times w(\text{add})$ (Habitat effect, no compensation),

$w(3)' = w(1) \times w(\text{comp})$ (No habitat effect, compensation),

$w(4)' = w(2) \times w(\text{comp})$ (No habitat effect, compensation)

(see Table 9).

Because mallard effects are already included in the reproduction submodel, we did not include a corresponding term in the survival submodel for possible mallard effects. However, we note that to the extent there is literature support for such an effect, a mallard effect is postulated to occur mainly during the reproductive period, either by direct displacement of black ducks from breeding habitats, competition for mates, or both. Thus in excluding mallards from the survival portion of the model, we have still retained a "mallard effect" in the overall model; whereas exclusion of a compensatory effect from the survival model by definition excludes this effect from the overall model. We of course caution readers that our parameter values for compensatory "effects" are set arbitrarily by us, and not supported by data. Although these values may be reasonable, their lack of empirical support means that one must be especially aware of

the model's sensitivity to errors in these values, particularly as these may influence management decisions.

As noted earlier, we also attempted to use the data structure and SURVIV to directly obtain estimates of model parameters, via ultrastructural analysis, using Equation 23. However, we found these analyses to be numerically unstable (e.g., convergence to parameter estimates was difficult; near singular variance-covariance matrices), and have based all subsequent model analysis on the estimates from the regression models in Table 9.

Model Calibration and Prediction

We used our model estimates and weights and Equations 24–32 to develop model-specific and averaged predictions, and Equations 33–35 to evaluate model performance, using historical data for $N_t^{(0)}$, $HAB_t^{(0)}$, and $M_t^{(0)}$ and age and sex-specific estimates of $(1 - K_t)$ (Appendix A) as input, to evaluate the model's predictive ability. Using the parameter estimates and model weights and equations and constants in Equations 24–32, our model predictions on average overpredicted by 92,124 (RBIAS = 24.58%); this pronounced bias resulted in a negative estimate of $R^2 = -0.62$. We used the following procedure in an initial effort to reduce this bias and provide better model fit, for our subsequent evaluation of parameter and management sensitivity; later we revisit the model recalibration issue, for a simplified set of models. We examined residuals from the model predictions, and found no evidence of temporal trends in these biased predictions. We then fit a linear regression model

$$N_t^{(0)} = \zeta \bar{N}_t + \varepsilon_t, \quad (38)$$

where $N_t^{(0)}$ was the observed, historical abundance of black ducks and \bar{N}_t was the model-averaged prediction from Equation 32. This resulted in an estimate of $\zeta = 0.7976$ (SE = 0.0183), which we then applied as a constant multiplier to our population projections (Eq. 31) in an effort to reduce prediction bias. The results from the recalibrated prediction models agree well with the historical data (RBIAS = 0.46%, $R^2 = 0.67$; Fig. 3).

We do not claim that this approach is a real solution to the problem of biased

Table 8. Model selection for American black duck survival submodel. Predictors considered include $X_t^{(2)} = 1/\text{HAB}_t^{(2)}$ where $\text{HAB}_t^{(2)}$ was total hectares of Atlantic coastal wetlands in U.S. in year t , black duck abundance ($N_t^{(2)}$) during winter as estimated by the midwinter inventory, density ($N_t^{(2)} \times X_t^{(2)}$), and weighted average of December-January temperatures for Atlantic coastal states from Maine to Maryland ($\text{TMP}_t^{(2)}$).

Habitat	Factor ^a		Predictor variables ^b	ΔAIC	Weight	
	Density	Mallards			Model	Factor ^c
0	0	0	None	0.647	0.169	0.327
0	0	0	Sex	2.479	0.068	
0	0	0	Age	2.621	0.063	
0	0	0	Sex Age	4.240	0.028	
0	0	1	$M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$	4.739 ^d	0.022	0.042
0	0	1	$M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex	6.571 ^d	0.009	
0	0	1	$M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Age	6.713 ^d	0.008	
0	0	1	$M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex Age	8.332 ^d	0.004	
0	1	0	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)}$	4.662 ^d	0.023	0.044
0	1	0	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)}$ Sex	6.494 ^d	0.009	
0	1	0	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)}$ Age	6.636 ^d	0.008	
0	1	0	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)}$ Sex Age	8.255 ^d	0.004	
0	1	1	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$	8.755 ^d	0.003	0.006
0	1	1	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex	10.586 ^d	0.001	
0	1	1	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Age	10.728 ^d	0.001	
0	1	1	$N_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex Age	12.347 ^d	0.000	
1	0	0	$X_t^{(2)}$	0.000	0.233	0.453
1	0	0	$X_t^{(2)}$ Sex	1.828	0.093	
1	0	0	$X_t^{(2)}$ Age	1.973	0.087	
1	0	0	$X_t^{(2)}$ Sex Age	3.584	0.039	
1	0	1	$X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$	4.065 ^d	0.031	0.059
1	0	1	$X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex	5.893 ^d	0.012	
1	0	1	$X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Age	6.038 ^d	0.011	
1	0	1	$X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex Age	7.649 ^d	0.005	
1	1	0	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)}$	4.004 ^d	0.032	0.061
1	1	0	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)}$ Sex	5.833 ^d	0.013	
1	1	0	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)}$ Age	5.977 ^d	0.012	
1	1	0	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)}$ Sex Age	7.588 ^d	0.005	
1	1	1	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$	8.069 ^d	0.004	0.008
1	1	1	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex	9.898 ^d	0.002	
1	1	1	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Age	10.042 ^d	0.002	
1	1	1	$N_t^{(2)} X_t^{(2)} N_t^{(2)} \times X_t^{(2)} M_t^{(2)} M_t^{(2)} \times X_t^{(2)}$ Sex Age	11.654 ^d	0.001	

^a 0 = absence, 1 = presence of habitat, compensatory, and mallard effects, respectively on survival of black ducks.

^b Excluding , which was eliminated early in the model selection process.

^c Total weight across all models with same combination of factors.

^d Indicates boundary constraint(s) invoked.

prediction, but we note that this problem is not unique to black ducks, and has been encountered in other attempts to model populations (e.g., mallards; F.A. Johnson, pers. commun.). While there exist several “suspects,” including overestimation of age ratios from wing surveys (F. A. Johnson, personal communication) and underestimation of crippling loss (N. L. Zimpfer, unpubl. data), there are at present no objective means of assigning a correction to one or

several model parameters. Furthermore, attempts to do so would potentially result in predictions skewed toward 1 or more alternative models (e.g., adjustment of crippling losses upward would accentuate additive mortality effects) and should be undertaken only with strong empirical support. Rather, our approach adjusts predictions under all models by the same factor. Our rationale for doing so is based on our application of these models to forecasting and AHM. Given that

Table 9. Final model selection and parameter estimates for American black duck survival submodel. Mallard competition factor excluded. Top-ranked models selected from within factors 000 (no habitat, compensation, or mallard effects) and 100 (habitat effect only) in Table 8. Additional compensation models constructed by setting value for parameter $\alpha = 10^{-6}$ (see text).

Model (j)	Factor ^a			Parameter	Estimate	SE	95 % Confidence interval		ΔAIC	Weight	$w(j)^b$
	Habitat	Density					Lower	Upper			
1	0	0		logit(θ_0)	1.033	0.197	0.647	1.420	0.647	0.420	0.370
2	1	0		logit(θ_0)	14.887	8.539	-1.850	31.624	0.000	0.580	0.511
				α_X	-3.473 ^c	2.140	-7.668	0.722			
3	0	1		logit(θ_0)	1.033	0.197	0.647	1.420			0.050
				α_N	-1.000 ^d						
4	1	1		logit(θ_0)	14.887	8.539	-1.850	31.624			0.069
				α_N	-1.000 ^d	—	—	—			
				α_X	-3.473 ^c	2.140	-7.668	0.722			
Model-averaged				logit(θ_0)	9.071	9.370	-9.294	27.436			
				α_N	-0.119 ^d						
				α_X	-2.015 ^c	2.348	-6.618	2.588			

^a 0 = absence, 1 = presence of habitat, and compensatory effects, respectively, on survival of black ducks.

^b Model weights recalculated including compensation models (models 3 and 4); see text.

^c Coefficient for predictor variable ($X_t^{(2)}$; Appendix 1.) $\times 10^{-6}$.

^d Coefficient for predictor variable ($N_t^{(2)}$; Appendix 1, text) $\times 10^{-6}$.

uncalibrated models consistently overpredicted historical population sizes in 1-year projections, it is fair to assume that long-range projections would be even worse. Although we cannot be certain that a model that empirically fits the historical trajectory will do a good job of forecasting under future conditions, we think it is fair to assume that it will do a better job than one that does not fit the historical data. However, we revisit this issue in the context of parameter sensitivity, below.

Dynamic Behavior of Models

In the absence of harvest, projected populations stabilized quickly (<20 years). Under most models, projected equilibrium abundance in the absence of harvest was < 1,000,000, but there was extreme variation in the range, from 165,356 (reproduction model 2, survival model 4; Tables 7 and 9) to > 4,000,000 (reproduction model 1, survival model 1); equilibrium under model-averaged projections was 972,569 (Fig. 4a). For harvest levels similar to 1993 levels model-averaged projections stabilized at <500,000; however under extreme models (reproduction model 1, survival model 1) stabilized at >2,000,000 (Fig. 4b). Under higher levels of harvest (approximately twice 1993 levels) populations declined dramatically ($N_{100}^{(0)} = 9,345$ and still declining, for model-averaged projections), again with some exceptions (reproduction model 1, survival model 1, $N_{100}^{(d)}$ stabilized at $\approx 630,000$) (Fig. 4c).

Sensitivity Analysis

Projected abundance after 100 years ($N_{100}^{(0)}$) and elasticity $e(\Gamma_i)$ varied widely among the model parameters, and depended to varying degrees on the parameter's value and to a lesser degree on harvest rates (Fig. 5–7). Abundance projections increased exponentially, as β_N (coefficient of density

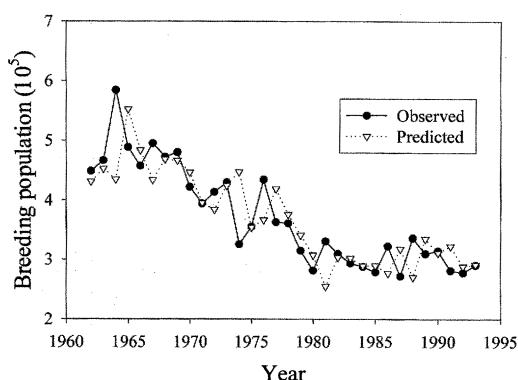


Figure 3. Predictions under model-averaged forecasting model (predicted, $\bar{N}_t^{(0)}$), and breeding abundance of black ducks as indexed by midwinter waterfowl inventories (observed, $N_t^{(0)}$) for American black ducks, 1962–1993. Averaging using AIC model weights over alternative biological models and bias-adjustment factors (see text).

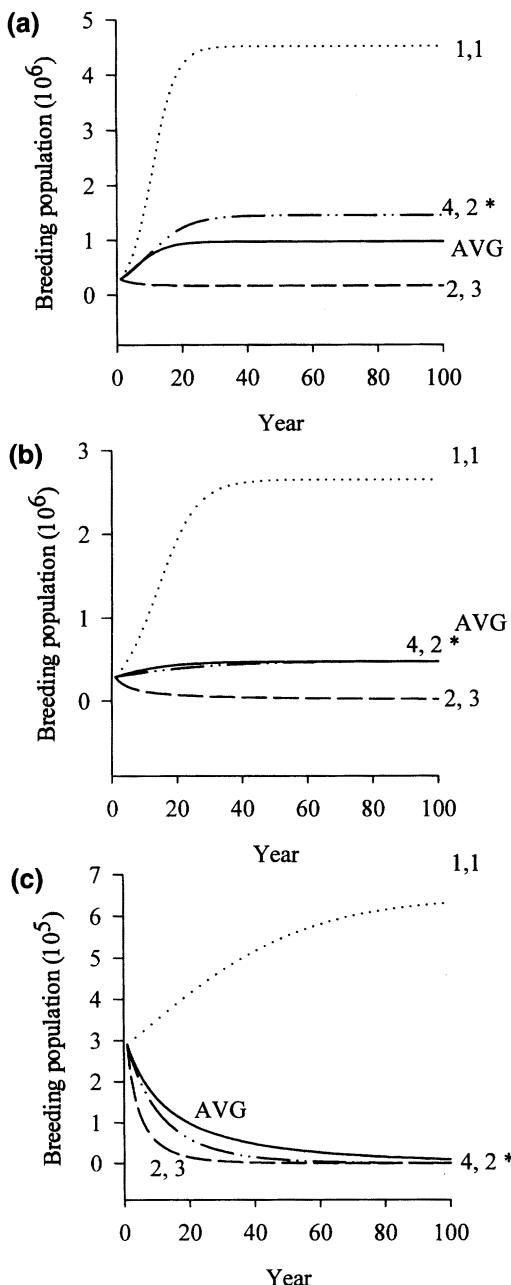


Figure 4. Equilibrium population projections using parameter estimates and model weights in Tables 7 and 9. AVG—model-averaged predictions under Equation 2 using the above weights; 3 other predictions for models providing a range of equilibrium conditions, where in each case full weight is given to the indexed production (Table 7) or survival (Table 9) models; model-averaged estimate of β_N substituted for production model 2 estimate (Table 7), which is outside biologically admissible range for this parameter (Table 5). * denotes model with highest AIC weight. Harvest rates (a) zero; (b) 0.055, and (c) 0.11 for adult males; harvest rates for other age-sex categories obtain by differential vulnerability correction (see text).

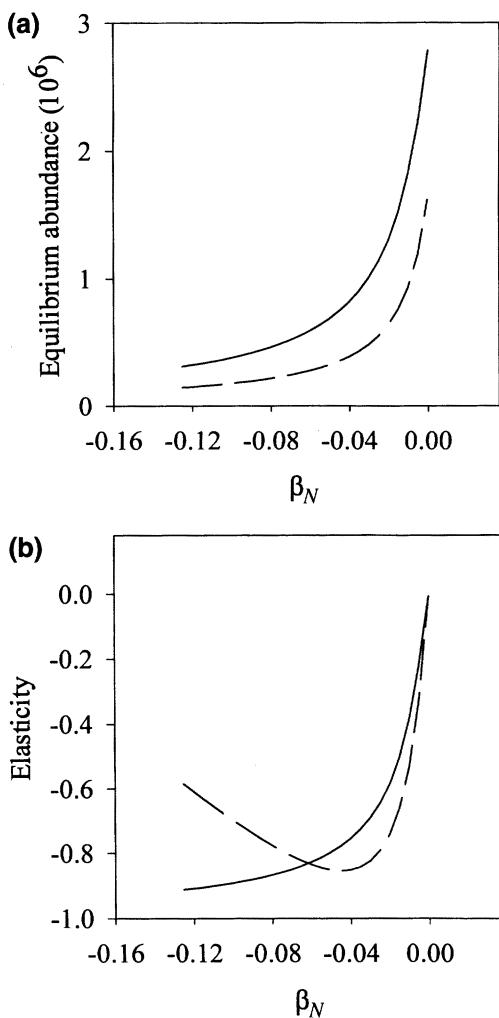


Figure 5. Equilibrium population projections and elasticity versus values of β_N (coefficient of density-dependence for black duck age ratios); harvest rates (h) of 0 (solid lines) and 0.055 (dashed lines) for adult male black ducks; harvest rates (h) of 0 (solid lines) and 0.055 (dashed lines) for adult male black ducks.

dependent reproduction) approached the boundary condition of zero; nevertheless, projections were relatively insensitive to this parameter ($|e(\beta_N)| < 1$) over the entire range of the constrained confidence interval (Fig. 5). By contrast, projections were extremely sensitive to β_X (habitat influence on reproductive rates), with both equilibrium abundance and elasticity varying by several orders of magnitude over the range examined (Fig. 6). Of particular concern was high sensitivity in the range of the model-averaged MLE ($\hat{\beta}_X = -0.0205$), suggesting that even

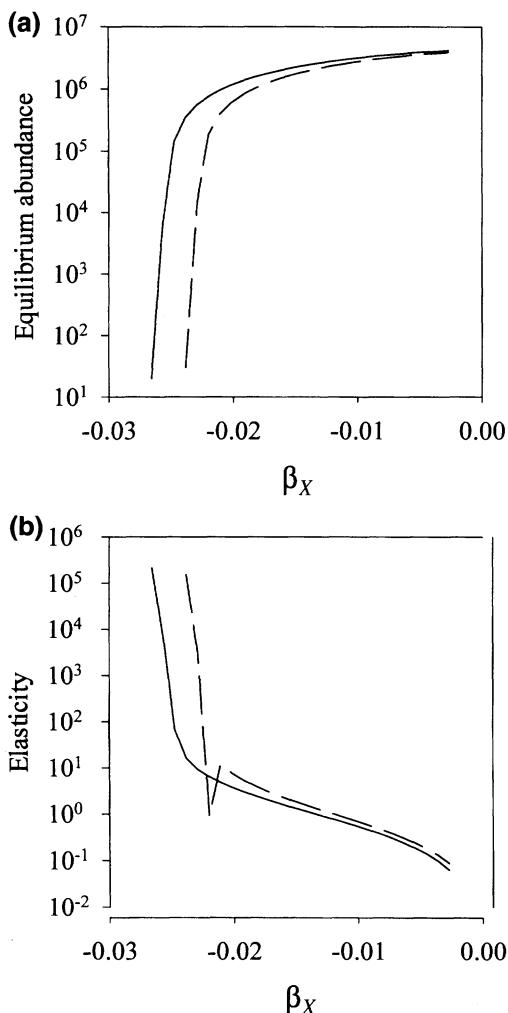


Figure 6. Equilibrium population projections and elasticity versus values of β_X (coefficient of habitat effects for black duck age ratios); harvest rates (h) of 0 (solid lines) and 0.055 (dashed lines) for adult male black ducks.

moderate statistical uncertainty in this parameter could have profound effects on model predictions. Likewise, projections were sensitive to values of β_M , although much less so in the vicinity of the model-averaged MLE ($\hat{\beta}_M = -0.08$) than for β_X (Fig. 7). Also, over the range of β_M the effects of variation in this parameter on equilibrium abundance were much less pronounced than corresponding changes in β_X (200,000 to $<2,000,000$ vs. 10^1 to 10^7).

In lieu of statistical estimates for α_N (coefficient of compensation) we varied the value of this parameter by $\pm 10^3$ and observed $N_{100}^{(0)}$ and $e(\alpha_N)$. Model projections were relatively

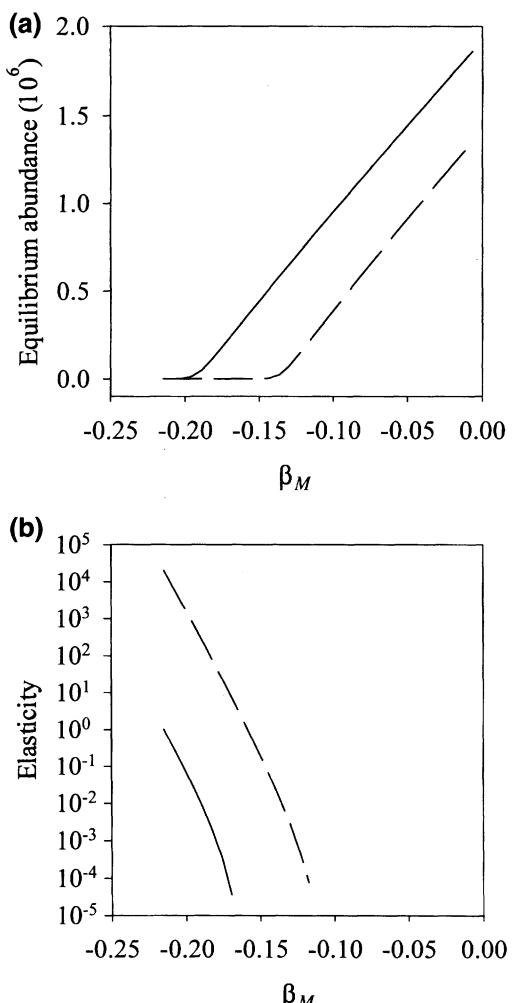


Figure 7. Equilibrium population projections and elasticity versus values of β_M (coefficient of mallard effect for black duck age ratios); harvest rates (h) of 0 (solid lines) and 0.055 (dashed lines) for adult male black ducks.

insensitive to this parameter, with $|e(\alpha_N)| < 1$ for this broad range of values (Fig. 8). In contrast, model projections were extremely sensitive to values of α_X (influence of winter habitat), with sudden increases in sensitivity in the vicinity of the model-averaged MLE ($\hat{\alpha}_X = -2.02$; Fig. 9).

Our examination of the sensitivity of black duck population growth, averaged over our survival and reproduction models, to combinations of harvest rates and mallard abundance (Fig. 10) reveals several patterns of relevance to management. First, under low to moderate harvest rates ($h < 0.1$), black duck populations can be expected to stabilize at or

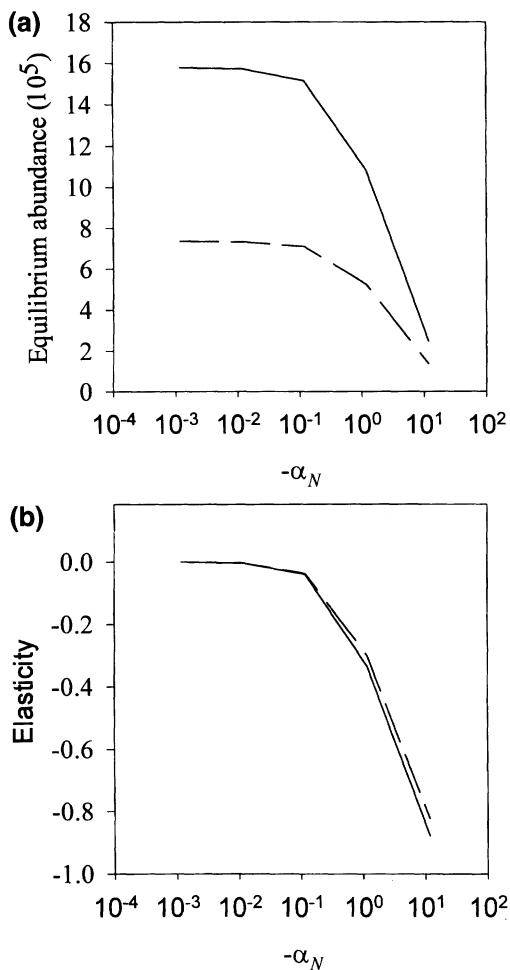


Figure 8. Equilibrium population projections and elasticity versus values of α_N (coefficient of density compensation for black duck survival rates); harvest rates (h) of 0 (solid lines) and 0.055 (dashed lines) for adult male black ducks.

near 1993 levels (~300,000) (Fig. 10a). However, if mallard populations continue to increase beyond 1993 levels (400,000+) (e.g., doubling to 800,000), our projections are that black ducks will stabilize at lower levels (<200,000 black ducks), even given further reductions in harvest rates on black ducks (Fig. 10a). Second, our sensitivity analysis suggests a fairly abrupt transition in sensitivity to harvest at $0.10 < h < 0.15$, with elasticities sharply increasing thereafter (Fig. 10b). Third, projections were even more sensitive to changes in mallard abundance than to harvest rates, and the sensitivity increased in response to both increasing harvest rates and increasing mallards (Fig. 10c). This pro-

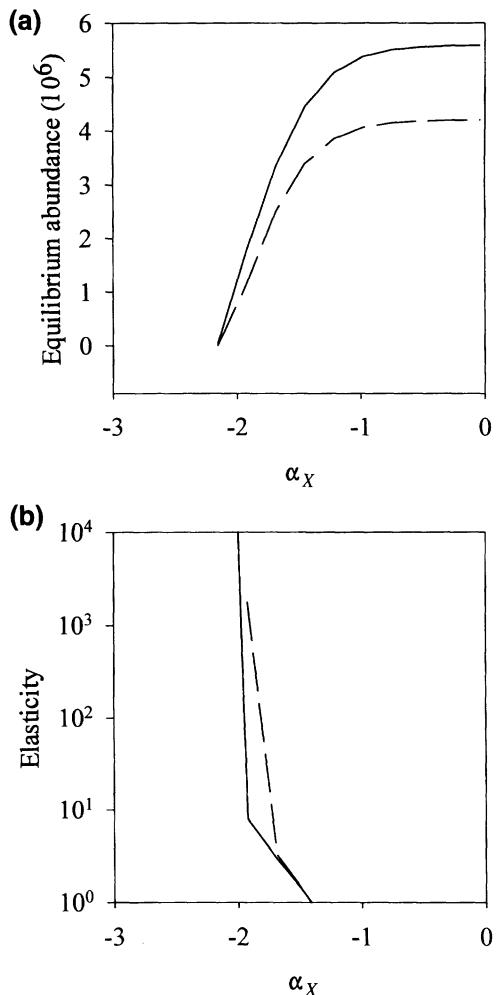


Figure 9. Equilibrium population projections and elasticity versus values of α_X (coefficient of winter habitat effect for black duck survival rates); harvest rates (h) of 0 (solid lines) and 0.055 (dashed lines) for adult male black ducks.

vides the potential for harvest and mallards to operate synergistically, in accelerating population decline, in that combinations of high harvest rates and mallard populations are projected to lead to rapid declines in black duck abundance. Furthermore, increasing mallards and harvest rates imply that these 2 factors interact so that sensitivity to mallards is most pronounced at both higher harvest rates for black ducks and higher abundance of mallards (Fig. 10c). If true, it would be advisable to avoid management scenarios that placed black duck populations in combinations of high harvest rates and increasing mallard populations,

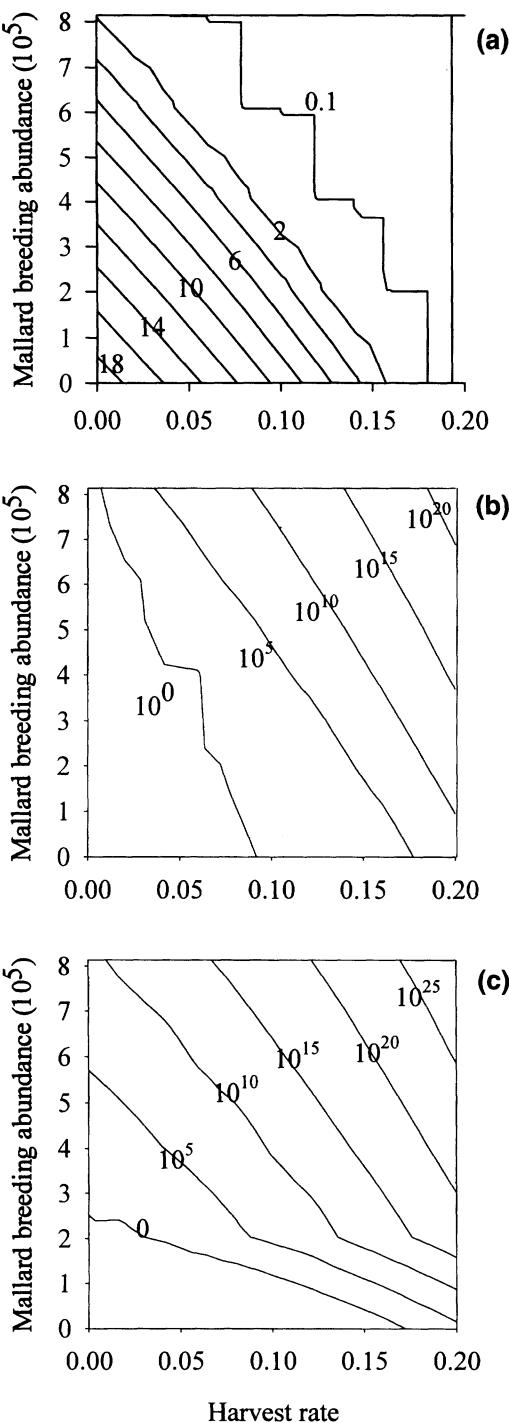


Figure 10. Equilibrium, model-averaged population projections (N^*) and elasticity in relation to mallard abundance and harvest rates of black ducks. (a) contours of breeding population abundance (10^5 breeding black ducks); (b) elasticity to harvest rate changes for levels of harvest rate; (c) contours of elasticity to mallard population changes for combinations of mallard abundance and black duck harvest rate.

because these may be inherently unstable conditions.

The degree of sensitivity to the model coefficients for habitat effects, β_X and α_X , is of great concern, given both the inaccuracy of these estimates, and questions about the reliability of the underlying habitat data, particularly for the breeding range. Because of these concerns, we developed an alternative set of models excluding habitat effects in both the reproduction and survival models. Examination of residuals from this model revealed increasing prediction error over time, suggesting the need for inclusion of a temporal factor in the prediction model. Therefore we fit several models including linear and quadratic terms in t , number of years elapsed since 1961. Models with linear time effects were uniformly superior (i.e., had lower AIC scores) than comparable models without this effect, or with those also including a quadratic term. We thus included linear time effects in each of the alternative reproduction models retained (Models 1 and 2, Table 7), with resulting AIC model weights of 0.0006 and 0.9994, respectively. These estimates and model weights were combined with the non-habitat survival models (1 and 3, Table 9) to form a revised set of reproduction-survival estimates, with weights normalized so as to sum across the model set (Table 10). These alternative models produce a combination of 2 alternative reproduction models (mallard effects absent or present) with 2 survival models (compensation absent or present). Although these models include an estimated negative trend in age ratios ($\hat{\beta}_T = -0.0129$, SE = 0.00342), we are unable to infer a specific mechanism for the apparent decline in productivity, nor can we eliminate the possibility that trends may be partly an artifact of changing methodologies in the harvest surveys.

We initially repeated the model calibration that had been used with the 16-model set, this time obtaining a better average agreement of the model with historical data (RBIAS = -0.28%, $R^2 = 0.68$), after inclusion of a calibration factor of $\zeta = 0.798$. However, after further discussion (F.A. Johnson, pers. commun.) we realized that our model calibration based on Equation 38 arbitrarily has its principal effect on the survival portion of the model. That is, a constant correction on the

Table 10. Parameter estimates of models retained for use in forecasting and optimal management, after elimination of models involving habitat effects because of parameter sensitivity.

Factor	Mallards ^a	Density ^b	Submodel	Parameter	Estimate	SE	95 %Confidence interval		Model weight
							Lower	Upper	
0	0	Reproduction	$\log(A_{\max})$	0.97578	0.2192	0.54615	1.40541	0.001	
			β_N	-0.1627	0.04492	-0.2508	-0.0747		
			β_T	-0.0129	0.00342	-0.0195	-0.0062		
	1	Survival	$\text{logit}(\theta_0)$	1.0333	0.1971	0.6469	1.4197		
			$\log(A_{\max})$	0.97578	0.2192	0.54615	1.40541	0.000	
			β_N	-0.1627	0.04492	-0.2508	-0.0747		
1	0	Reproduction	β_T	-0.0129	0.00342	-0.0195	-0.0062		
			$\log(A_{\max})$	1.23519	0.21299	0.81774	1.65264	0.880	
			β_N	-0.1336	0.04327	-0.2184	-0.0488		
	1	Survival	β_M	-0.0959	0.02473	-0.1444	-0.0474		
			β_T	-0.0144	0.00338	-0.021	-0.0078		
			$\text{logit}(\theta_0)$	1.0333	0.1971	0.6469	1.4197		
1	1	Reproduction	α_N	-1.0000	—	—	—		
			$\log(A_{\max})$	1.23519	0.21299	0.81774	1.65264	0.11893	
			β_N	-0.1336	0.04327	-0.2184	-0.0488		
	0	Survival	β_M	-0.0959	0.02473	-0.1444	-0.0474		
			β_T	-0.0144	0.00338	-0.021	-0.0078		
			$\text{logit}(\theta_0)$	1.0333	0.1971	0.6469	1.4197		
			α_N	-1.0000	—	—	—		

^a 0 = absence, 1 = presence of effects of mallard competition on reproductive rates of black ducks.

^b 0 = absence, 1 = presence of effects of compensatory effects on survival rates of black ducks.

prediction equation modifies Equation 31 as

$$\hat{N}_{t+1}^{(0)}(i, j)^{\text{adj}} = \hat{N}_{t+1}^{(0)}(i, j)^{\text{adj}} \times \zeta$$

for $i = 1,.., 2$ reproduction and $j = 1,.., 2$ survival models. In turn, this is equivalent to adjusting each of the survival rates in Equation 25 as

$$\hat{\theta}_t^{\text{as}}(j)^{\text{adj}} = \zeta \hat{\theta}_t^{\text{as}}(j).$$

As noted above, we cannot identify the true source of model prediction bias, and thus cannot assume that it primarily involves survival. Therefore, we also performed adjustments on the reproduction portion of the model by modifying Equation 25 as

$$N_t^{(1)y \text{ adj}} = [N_t^{(1)am} + N_t^{(1)af}] \tilde{A}(i) \times \zeta'.$$

We selected values for ζ , ζ' to minimize prediction error (Eq. 34) by varying each parameter separately over the range (0.5, 1) while holding the other constant at 1, and compared these as alternative models to unadjusted prediction ($\zeta = 1$, $\zeta' = 1$).

Our inability to attribute model over-pre-

diction to a specific portion of our model (in this case, survival versus reproduction submodels) represents an additional component of model uncertainty. We represented this uncertainty by considering prediction under 3 alternative model adjustments: survival (ζ) and reproduction (ζ') factors, estimated as above, and no adjustment ($\hat{\zeta}' = \zeta = 1$). We then used Equations 21 and 22 to compute model weights, with $K = 1$ for the 2 adjustment models and $K = 0$ for the unadjusted model. The reproduction adjustment provided $\hat{\zeta}' = 0.588$, $\hat{\sigma} = 47,517$ (%RBIAS = -0.267, $R^2 = 0.672$), whereas the survival adjustment provided $\hat{\zeta} = 0.798$ (identical to that produced by the simple regression approach, above) and $\hat{\sigma} = 46,982$ (%RBIAS = -0.28, $R^2 = 0.68$); the unadjusted model produced $\hat{\sigma} = 105,263$. These error estimates produced AIC weights of 0.41, 0.59, and <0.0000001 for the reproduction, survival, and no adjustment models, respectively. Based on these results we discarded the “no adjustment” option. This results in 8 prediction models: the 4 reproduction-survival combinations described above, combined with adjustments on reproduction or survival as

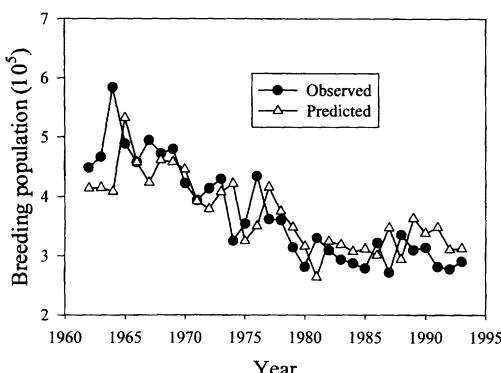


Figure 11. Predictions under model-averaged forecasting model (predicted, $\hat{N}_t^{(0)}$), and abundance of breeding black ducks as indexed by midwinter waterfowl inventories (observed, $N_t^{(0)}$) for American black ducks, 1962–1993, using parameter estimates and model weights in Table 10. Projections averaged (weighted by AIC model weights) over models in which a bias-reducing adjustment factor was included for either the reproduction or survival sub-model; see text.

above; comparison of model-averaged predictions to observed abundance over 1961–93 is provided in Fig. 11. We simulated population projections from 1993 conditions under these 8 models, and present projections under each of the 4 biological models (averaged over the adjustment options weighted by above), and averaged across all 8 models (weighted both by the AIC weights from Table 10, and the adjustment weights, above) in Fig. 12. For the purposes of these projections we set $t = 32$ in the reproduction models, equivalent to assuming that 1993 environmental conditions influencing reproductive rates persist into the future. Although we have no empirical evidence to support this assumption, we believe that it is unlikely that environmental factors, if any, influencing reproductive rates, would continue to change linearly through time. Inclusion of a negative linear term in time in a dynamic model would, of course, lead to population extinction ($A_t = 0$) in all cases.

Model-averaged projections stabilized at ~525,000 black ducks in the absence of harvest, at ~360,000 with harvest rates held constant at approximately 1993 levels (0.055), and declined to and stabilized at approximately 190,000 black ducks at harvest rates twice this level. This set of 4 models and the model-averaged projection appears to capture most of the breadth of population behavior exhibited by the full set of 16 models (Fig. 4). However, predicted, equilibrium

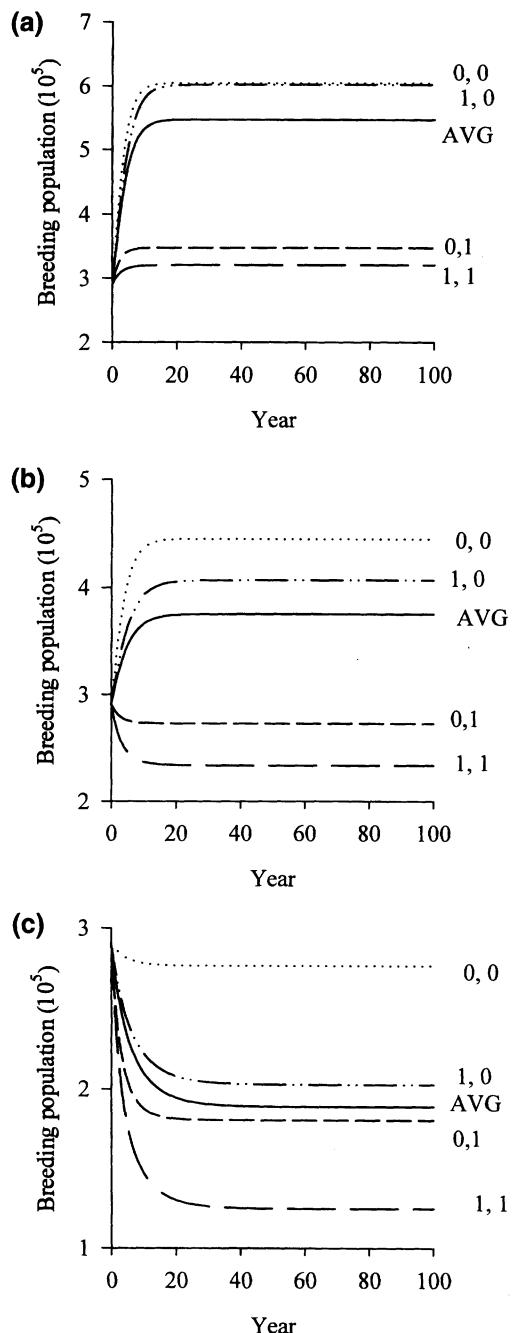


Figure 12. Equilibrium population projections using parameter estimates and model weights in Table 10. AVG—model-averaged predictions (Eq. 32) and predictions under combinations of absence (0) or presence (1) of mallard effects and survival compensation, where full weight is given to the indexed model. Harvest rates (a) 0.0; (b) 0.055, and (c) 0.11 for adult males; harvest rates for other age-sex categories obtain by differential vulnerability correction (see text). Projections averaged (weighted by AIC model weights) over models in which a bias-reducing adjustment factor was included for either the reproduction or survival sub-model; see text.

abundance was in all cases lower for the revised models, in some cases by nearly an order of magnitude. These divergent projections forcefully illustrate that models that are empirically similar (i.e., fit the data nearly equally well) may provide quite different long-term projections (Runge and Johnson 2002). We believe that the revised projections (Fig. 12) are more biologically reasonable than those in Fig. 4, being in the range of 0.7 to 2 times recent MWI figures (276,000 for 2001; data on file, Office of Migratory Bird Management, USFWS). Our revised projections should be viewed as provisional, and require validation through a forecasting and updating procedure as described in the next section.

DISCUSSION

Our model development, parameter estimation, and model evaluations constitute a major new synthesis of information about black ducks. In particular, all major areas of uncertainty about factors responsible for declines in continental black duck populations are incorporated into the model structure. Furthermore, our estimates of parameters under these alternative models is the most comprehensive treatment of the data in a prediction framework to date. Finally, our use of information-theoretic methods in model selection, parameter estimation, and hypothesis weighting should be robust and repeatable, and leads naturally into a Bayesian updating approach under AHM (next section).

Our study, nonetheless, was plagued by difficulties and assumptions that necessarily make many of our conclusions provisional. First and most obvious, our analyses were, by definition, retrospective, without the controls of an experimental design. Our parameter estimates are based on observed associations among many variables, and may, or may not, be indicative of causation. By beginning with reasonable, *a priori* models, based on alternative biological hypotheses of population processes, we have reduced but not eliminated the possibility that our results are artifacts of "data dredging." Second, we were forced to rely on several data sets that were unsatisfactory in our analyses. In particular, our long-term data on habitat quan-

tity, especially for breeding habitats, almost certainly do not capture changes in black duck habitats in a meaningful way. Because our analysis of parameter sensitivity indicated high sensitivity to changes in habitat coefficients, we removed habitat factors from our reduced set of predictive models. Further work is needed, using appropriate measures of habitat, to develop empirical relationships between habitat factors and demographic parameters. Our efforts to develop predictive relationships between habitat factors and demographic rates were further hampered by an inability to directly associate these variables at relevant scales of spatial resolution. For example, rates of habitat loss have undoubtedly been heterogeneous over the black duck's breeding range, but neither our estimates of abundance (based on the MWI) nor of recruitment (based on fall age ratios) could reliably be associated with specific portions of that range. Improved technology for measuring habitat conditions, together with advances in methods for direct estimation of abundance and reproductive rates on the breeding grounds, offer promise that data will soon exist to allow better prediction of recruitment, survival, and other vital rates as functions of habitat conditions. If so, our modeling framework will allow incorporation of this new information.

Finally, even if we take our data at face value, many of our parameters were estimated with poor precision, so that predictions under alternative models may be difficult to distinguish, and may be unreliable. Depending on the parameter, statistical uncertainty can be critical in determining model behavior, and to predictions under management. Our results offer insights into setting priorities for data gathering, in that these should be directed at reducing uncertainty in parameters that induce the highest proportional response in model output (e.g., as modeled by elasticity). Additionally, high priority needs to be given to collecting data that allows for reduction in uncertainty among the alternative reproduction and survival models. We explore this latter issue in more depth in the section below.

Our models also make no attempt to explain spatial (vs. temporal) variation in important factors. We recognize that a full

spatial modeling and analysis of the black duck population may be especially important in developing strategies for managing the species in different portions of the range. We believe that fundamental challenges remain, including severe data limitations, to parameterizing a spatial model of black ducks, and thus have chosen to limit our study to the development of model for a single, continental population. The first author and collaborators are now engaged in extending these efforts to multiple stocks of black ducks, taking into account heterogeneous factors influencing each stock, especially mallards, and developing models that incorporate movement and other dependencies among stocks.

Finally, we repeat our plea to readers not to use our model selection and estimation process, and computed model weights, either to discriminate among the alternative models, or to "reject" any proposed biological hypotheses. As discussed earlier, we believe that the evidence marshaled to date, including from this study, is simply incapable of rejection of any of these major explanatory factors; in addition, in all likelihood these factors operate simultaneously to varying degrees. Instead, these results may be useful as an initial step in an adaptive management process. In the next section we describe some issues that should be considered in the development of an adaptive management process for black ducks, and how our modeling and analytical efforts may contribute.

SUMMARY

We selectively used available, historical data on the black duck populations (abundance, annual reproductive rates, and survival rates) and possible influential factors (trends in breeding and wintering habitats, harvest rates, and abundance of mallards) to estimate the parameters of our model. Our resulting models included parameters describing positive influence of breeding habitat and negative influence of black duck and mallard densities on reproductive rates, and negative influence of both black duck density (indicating compensation to harvest mortality) and mallard density (suggesting negative competitive effects). We used these

parameter estimates to investigate the effects of statistical uncertainty in parameter values on predicted population growth rates for the combined (annual) model. We then investigated the effects of various combinations of factors (breeding habitat, harvest rates, and mallard densities) for fixed parameter values, on predicted growth rates, in an effort to understand how these factors might interact in determining population response. We used the combined model, together with our historical data set, to perform a series of 1-year population forecasts, similar to those that might be performed under adaptive management. The combined model explained approximately 67% of the variation in annual breeding population abundance for black ducks, suggesting that it might have utility as a predictive tool in adaptive management. Because essentially the same data were used in the forecasting exercise, as were used to estimate model parameters, true forecasting ability awaits confirmation through independent data. We examined the sensitivity of model predictions to variation in parameter values and in factors under potential management control. Population projections were especially sensitive to variation in the coefficients for habitat effects, in both the reproductive and survival submodels. Stable or increasing populations were projected for combinations of mallard abundance and harvest rates similar to those now experienced. However, population projections were extremely sensitive to increases in harvest or mallard levels, with foreseeable combinations of these factors resulting in precipitous declines in black duck abundance. A simplified model, eliminating habitat effects in both submodels, explained approximately 68% of black duck variation from 1961–1993. This model includes 4 alternative models, representing combinations of presence and absence of a mallard effect on reproductive rates, with presence and absence of harvest compensation; the model with presence of a mallard effect but no harvest compensation received the highest weight (AIC weight = 0.88). Model-averaged projections stabilized at just above 500,000 black ducks in the absence of harvest, at above 350,000 at harvest rates held constant at approximately 1993 levels (0.055), and declined to and

stabilized at approximately 190,000 black ducks at harvest rates twice this level.

DEVELOPMENT OF AN ADAPTIVE MANAGEMENT PROTOCOL FOR AMERICAN BLACK DUCKS

Adaptive Resource Management (ARM; Walters 1986, Lancia et al. 1996) is a process for making a decision, in the face of uncertainty, which results in an optimal value for some resource objective while reducing uncertainty through time. More narrowly defined, adaptive harvest management (AHM) (Johnson et al. 1993, 1997; Williams and Johnson 1995) seeks to reach a long-term harvest objective, with the decisions being annual harvest regulations. In the discussion below we emphasize AMH, that is, the objective and the management decisions revolving around harvest. A broader discussion of ARM that explicitly includes both nonharvest objectives as well as management decisions other than harvest regulations for reaching those objectives, certainly may be appropriate, as discussed below.

Objective Function

Formulation of a suitable objective function is essential to the ARM process; it is also a matter for resolution among managers and policy makers and not a scientific issue per se. Scientific resource management principles and theory do, however, provide guidance for an AHM objective in that the concept of "sustainability" is central to renewable resource management. We define a sustainable harvest as one that does not, over an infinite time horizon, result in a loss of a stock's ability to replenish itself. Presumably, the harvest of this resource (e.g., annual take of black ducks) has inherent economic and other value; thus, it seems reasonable to formulate the objective in words as "the maximum harvest (number of black ducks), over the long term that can be killed while not diminishing the stock." In fact, harvest theory (e.g., Caughley 1977) permits us to express our harvest objective as

$$V^* = \max \sum_{t=0}^{\infty} H_t, \quad (39)$$

where H_t is size of the harvest in year t .

Because of the infinite time horizon, population persistence is necessary to provide harvest opportunity in future years; short-term harvest at the expense of these later harvest opportunities is precluded. It is evident, however, that this maximum could in theory be achieved while allowing the population to decline in some years to levels unacceptable to stakeholders. For this reason, we consider objective functions of the form in Equation 39, but constrained so as to penalize the objective if mallard populations fall below North American Waterfowl Management Plan (NAWMP; USFWS and CWS 1986) population objectives.

A harvest objective as stated above (possibly constrained by NAWMP goals) would be straightforward to implement as part of AHM. Several additional considerations, however, may result in modification of this objective. First, is the issue of *harvest allocation*. In theory, it would be possible to attain an objective such as Equation 39, with strikingly different distribution among countries, states or provinces within each country, or other administrative/political units. For instance, the same maximum, long-term harvest (V^*) could be obtained with 50% of V^* occurring each in Canada and the U.S., or with 100% in one country or the other. Given the international nature of this shared resource, there would likely be great dissatisfaction if one of the latter results were to occur over any significant time horizon, or perhaps even for any year. Of course, such a result is very unlikely to occur, given the migratory nature of the species, unless hunting seasons were closed in either country. Nevertheless, to secure stakeholder support for AHM in both countries, it might be desirable to impose a "parity constraint" on harvest allocation, so that the objective would be penalized if the distribution of harvest were to deviate substantially from recent historical distributions (approximately equal between countries). Similar constraints could be imposed at finer levels of resolution, but might prove either impractical, highly suboptimal (from the overall objective standpoint), or both. Before any type of harvest allocation constraint is imposed on a harvest objective, we would strongly advise thorough investigation of the implications and costs (monetary and political) of such an approach.

An additional issue, tending to complicate the objective, is that of *multiple species* under management. For black ducks, mallards are obviously an important consideration, because of the potential that the state of mallard populations could directly influence the expected harvest of black ducks. Under various of our alternative models, it would certainly be important to model mallard populations, and to incorporate this influence into the models predicting the harvest of black ducks under different black duck regulatory options. It seems a fair question, however, to ask whether black ducks and mallards should be considered jointly in the objective function as well, which has interesting and important implications that should be examined through simulation trials. For instance, if mallards and black ducks were equally valued in the harvest, a composite objective might be expressed as

$$V^* = \max \left[\sum_{t=0}^{\infty} (H_t^b + H_t^m) \right], \quad (40)$$

where H_t^b, H_t^m are the annual numbers of black ducks and mallard, respectively, harvested in each year t . Conversely, if black ducks were deemed twice as valuable (e.g., because of a tradition for hunting black ducks) then the objective might be expressed as

$$V^* = \max \left[\sum_{t=0}^{\infty} (H_t^b + 0.5H_t^m) \right].$$

The decision problem also could be expanded to include harvest regulations for mallards as well as black ducks. Again, the consequences of including multiple species in a common objective, together with the effects of differing weighting factors, should be thoroughly evaluated.

Finally, although we have emphasized a harvest objective, the objective could be expanded to include nonharvest population objectives, or even to explicitly include a value for habitat (e.g., for nongame waterbirds). Difficulties could arise, however, in deciding how to value these objective components (e.g., what is the equivalence between numbers of harvested ducks, and acreage of wetland habitat?), and thus what

objective weights to use. Irrespective, non-harvest and nonharvest objectives may be worth considering.

Decision Alternatives

Under AHM for black ducks, harvest rates are at least partly controllable by means of harvest regulations set in the U.S. and Canada. The decision is not the rate of harvest (which is a partly random outcome), but instead some set of fairly complicated regulatory options. In practice, these regulations can and probably should be grouped into discrete sets thought to have similar effect on harvest rates, and describable generically as "restrictive" (e.g., relatively short seasons and lower bag limits), "moderate," and "liberal" (longer seasons, higher bag limits), basically the approach taken with mallard AHM. To translate these regulatory options into harvest rates, an empirical relationship must be established that predicts an expected (average) harvest rate for each; inclusion of "partial controllability" also requires the modeling of a statistical distribution about that expected value. Historical data on harvest regulations and subsequent harvest rates (estimated through band recoveries) could be used to construct these relationships (e.g., see Johnson et al. 1997).

Again, this relatively simple approach is complicated because the U.S. and Canada each currently set harvest regulations independently. In addition, within each country regulations are set on a flyway or regional basis, but are implemented at the state or provincial or even finer spatial scale of administration. Any AHM process developed for black ducks must consider this complexity and negotiate a compromise between overly coarse- or fine-resolution management.

As alluded to above, it may be desirable, even necessary, to link the harvest decision process for black ducks, with those of other species, especially mallards. For instance, a joint black duck-mallard objective as in Equation 40 would require joint consideration of harvest regulations for each species (e.g., restrictive for both species, liberal for both, restrictive for one and liberal for the other). Under the simple scheme of 3 harvest levels for each species, this would result in 9 possible joint harvest strategies.

We also alluded to the inclusion of non-harvest decisions, such as habitat management, into an ARM decision space. If habitat decisions were included, many issues would have to be dealt with, such as (1) the spatial scale at which to describe (or summarize) habitat decision making, and (2) the different temporal scale at which habitat decisions tend to occur, compared to harvest decisions (longer term, vs. annual). We believe that an eventual, integrated harvest-habitat approach will prove valuable for waterfowl management in general, but that questions such as those posed above create logistical and technical challenges. As with the development of an objective, we recommend beginning with a simple decision space (e.g., an overall low, medium, or high rate of harvest), and then exploring the implications of geographic, multiple species, and harvest-habitat decision spaces through simulation.

Definition of State Space

By "state space" we mean the array of state variables (principally, population size and habitat conditions) and the spatial and temporal resolution at which these are considered measured and represented in models. To make rationale decisions about how to manage the resource, we must know the current system state (e.g., numbers of breeding black ducks, acres of breeding habitat). Given knowledge (or an estimate) of this state, a decision (e.g., a liberal harvest) and a dynamic model such as the one we have developed, we can then predict the future state of that system (e.g., next year's numbers of breeding black ducks and acres of breeding habitat), and ultimately, of the expected return (e.g., long-term harvest) for a series of decisions through time.

Our modeling effort should make clear that certain state variables are key components of AHM for black ducks. These include:

- Abundance of breeding (or wintering, or both) black duck populations.
- Habitat conditions on breeding areas.
- Abundance of breeding (or wintering, or both) mallard populations.

In our models we described each of these with range-wide estimates or indices,

because of the relative lack of long-term, finer resolution data, as well as to the need to simplify modeling at this stage of model development. As with the objective function and decision space, however, finer resolution may be needed to adequately represent the dynamic behavior of black duck populations, and may be possible as more reliable information becomes available (e.g., from continued surveys of black ducks and mallards in eastern Canada and the U.S.). Differences in black duck densities and the influence of mallards in western vs. eastern Canada suggest a possible need for modeling 2 breeding stocks of black ducks, with distinct responses to mallards, habitat conditions, and harvest. In addition, it may be desirable to model distinct wintering (e.g., coastal vs. interior) populations of black ducks, to the extent that reliable surveys of these populations are feasible. As with the objective function and decision space, investigations should be conducted into the extent to which spatial or other model stratification produces better decisions, and whether the gain in objective return (i.e., long-term harvest) is worth the cost of model complexity (and the concomitant increase of cost and loss of reliability, for states that are measured at too fine a scale).

Population, habitat, and other state variables obviously can and will be collected at some arbitrary levels of spatial and temporal resolution and aggregated as needed for model states. The process cannot work in the other direction, i.e., if the decision is made to collect survey data at an aggregated spatial scale or at >1 year intervals, it will not be possible to re-create disaggregated data for later modeling use. We suggest, therefore, that modeling and monitoring efforts work in concert to achieve the best tradeoff.

Alternative Models and Model Updating

Our work makes clear that managers must continue to make management decisions for black duck populations in the face of considerable uncertainty as to how fundamental biological processes will translate these decisions into future harvest opportunity. AHM allows for the explicit incorporation of this uncertainty through the delineation of alternative models, which are

thought to encompass the range of uncertainty. Our work has resulted in a general modeling framework that encapsulates multiple, alternative hypotheses about factors that may be influencing black duck populations, in particular habitat conditions, competition with mallards, and harvest. After discarding alternative models involving habitat effects (because of concerns about unreliability of these models, together with extreme sensitivity to parameter uncertainty) we were left with 4 competing models, representing the interaction of presence or absence of mallard effects, with presence or absence of compensation (Table 10). Under AHM, decisions about harvest, habitat, and other management are made in the face of uncertainty among these alternatives.

Updating of Model Weights.—Our selection of model parameters and parameter values was based on our assessment of the most parsimonious (i.e., best fitting, with fewest parameters) models, from our separate analyses of the reproduction and survival submodels, together with analysis of model behavior and parameter sensitivity. However, we were interested in taking our modeling process a further step, by addressing how the models might be used in an adaptive management context. Under AHM, forecasts are obtained under each model, following decisions about harvest regulations and subsequent observations of the population in year $t + 1$. To illustrate how model updating might work, we used model projections from 1994–1995 as input to provide predictions for 1995–1996 under each model, using Equation 31. These in turn were used to compute updated model probabilities with a form of Bayes' Theorem

$$P_{t+1}(H_{ijk}) = \frac{P_t(H_{ijk})L_{ijk}}{\sum_{m=0}^1 \sum_{n=0}^1 \sum_{w=r}^s P_t(H_{mnw})L_{mnw}}$$

where $P_t(H_{ijk})$ is the weight for model i,j,k prior to each year's updating (year t), and is the weight for reproduction submodel $i = 0, 1$, survival submodel $j = 0, 1$ (Table 10), and reproduction (r) or survival (s) adjustment. $P_{t+1}(H_{ijk})$ is the corresponding weight following Bayesian updating, subsequent to each year's updating. The predictions were

used to compute likelihoods under each submodel as

$$L_{ijk} = \exp \left\{ \frac{[N^B - \hat{N}(i,j,k)]^2}{2\sigma^2} \right\},$$

where N^B is the observed breeding populations size, $\hat{N}(i,j,k)$ is abundance predicted under each model combination, and σ^2 was estimated from the historical data by Equation 34. $P_{t+1}(H_{ijk})$ then becomes the new prior for the next round of updating ($t + 2$), and so on. We calculated updated model probabilities under 2 scenarios: first with model weights taken as equal (1/8) in 1994 (Fig. 13), and second with the model weights for 1994 set equal to the AIC weights

$$P_t(H_{ijk}) = w(i)w(j)w(k)$$

where $w(i), w(j)$ were obtained from Equation 15 and 22 (see Fig. 14) and $w(k)$ were the AIC weights for the model calibration factors (0.41 and 0.59 for reproduction and survival, respectively). In either case the results show a relatively slow rate of "learning." In particular, there was little change to the relative weights given to the 2 models with the highest a priori (AIC-based) weights: 1, 0 (mallard effects on reproduction combined with no compensatory effects on survival) and 1,1 (mallard effects combined with compensation). These values are only for illustration, because the data used for "updating" are a portion of the data used for estimation (although survival estimation ended with 1994); nevertheless, they are illustrative of the procedure, and of how "learning" may proceed slowly when large errors of prediction exist, as in this instance. We recommend that further emphasis be devoted to initiating a simple (e.g., single population, single decision variable) AHM model, and exploring the consequences of finer vs. coarser resolution in objective, decision space, and state space, and of alternative model weighting (e.g., equal vs. empirically derived) in reaching optimal decisions. We suggest that these steps will, in the earliest stages, be most useful as heuristic devices for familiarizing stakeholders with AHM, and for mapping out a more detailed, eventual implementation of AHM/ARM for American black ducks.

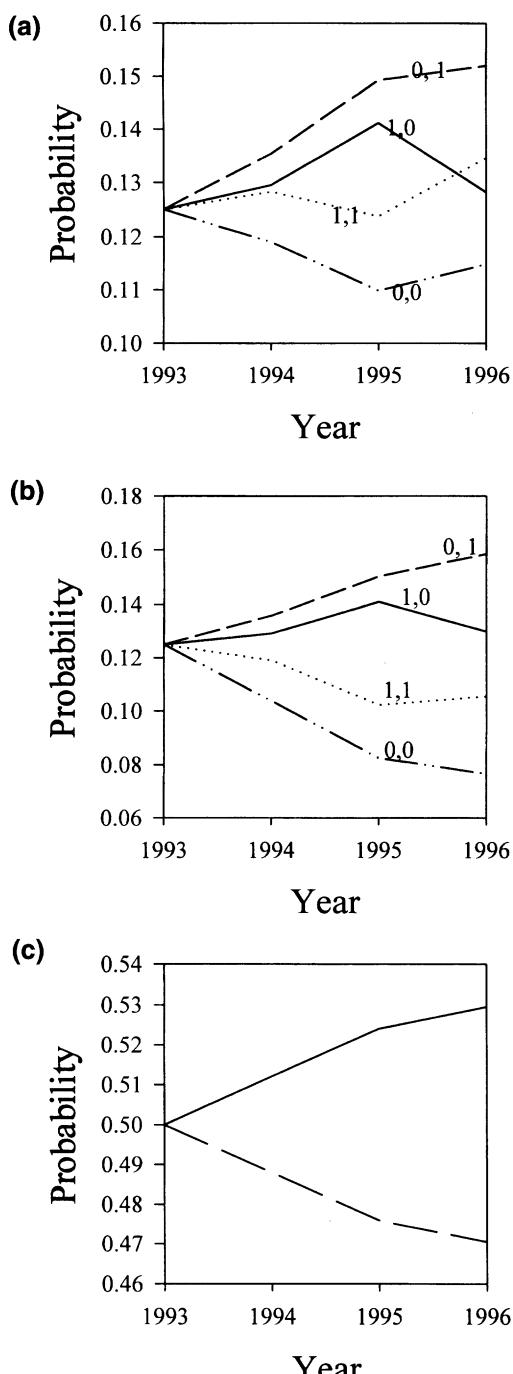


Figure 13. Evolution of model weights from forecasting and updating process for 1993–96. Equal prior (1993) probabilities of reproduction \times survival model \times bias adjustment combinations. Posterior (1994–94) probabilities with (a) bias-reducing adjustment factor applied to reproduction submodel (b) bias-reducing adjustment applied to survival model. (c) Marginal prior and posterior probabilities for adjustment factors (summed across alternative biological models): solid line = reproduction adjustment, dashed line = survival adjustment.

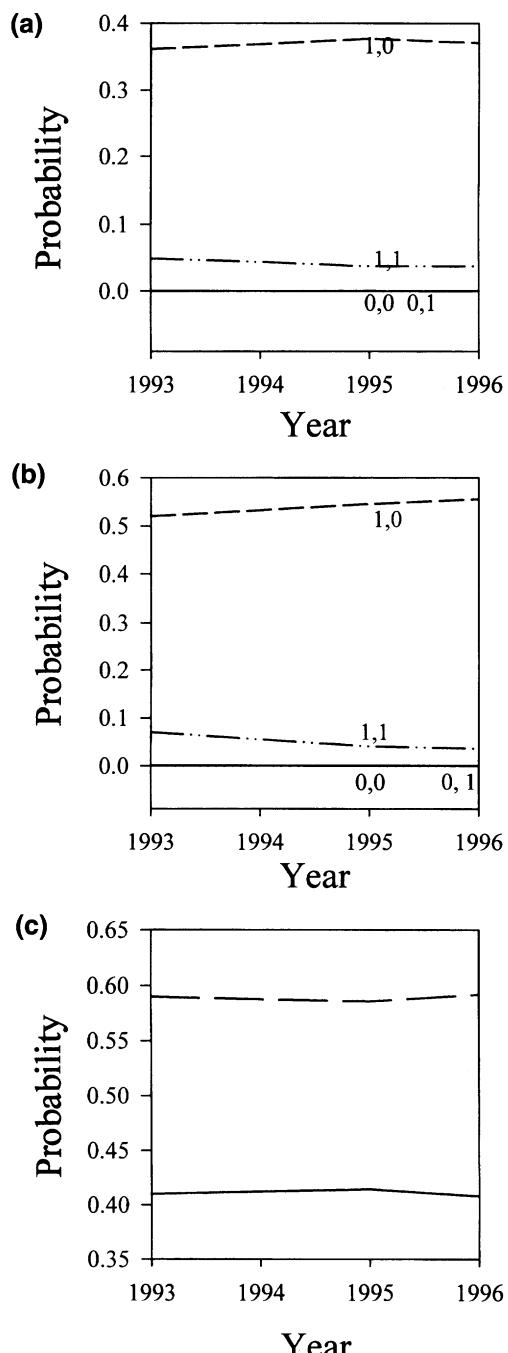


Figure 14. Evolution of model weights from forecasting and updating process for 1993–96. Prior (1993) probabilities of reproduction \times survival model \times bias adjustment estimated using AIC model weights. Posterior (1994–94) probabilities with (a) bias-reducing adjustment factor applied to reproduction submodel (b) bias-reducing adjustment applied to survival model. (c) Marginal prior and posterior probabilities for adjustment factors (summed across alternative biological models): solid line = reproduction adjustment, dashed line = survival adjustment.

Other Data Needs

Although not explicitly part of the state space of our models, our estimates of annual reproductive rates, harvest rates, and annual and seasonal (i.e., winter) survival rates were fundamental to model construction. Continued monitoring of these parameters is needed, both to enable revised projections of population growth rates, and to revised estimates of the functional relationships between demographic parameters and extrinsic and intrinsic variables. Again, our modeling effort was forced by the paucity of data to estimate these parameters and relationships on a range-wide basis. Finer scale information, e.g., corresponding to western vs. eastern black duck populations, is needed to establish whether significant spatial heterogeneity in functional relationships occurs, and to adjust models accordingly. These will require 1) continued banding efforts on population segments, to estimate harvest and survival rates; 2) harvest derivation analyses, to link harvest age ratios to breeding population segments, and 3) continued monitoring of black duck abundance, mallard abundance, and habitats rangewide.

GENERAL CONCLUSIONS AND RECOMMENDATIONS

Our review, modeling, and estimation resolve neither the uncertainty about which factors have contributed to black duck declines, nor what management actions may lead to stable or increasing populations of this resource. Our analysis, however, formalizes the degree of uncertainty for both questions, and leads to testable predictions about the effects of management alternatives. Further improvements in monitoring, experimental studies, and modeling may reduce some of this uncertainty, but we are convinced that uncertainty will remain, and more important, must be systematically considered in managing this international resource. We suggest that the best way to accomplish this is through ARM.

We recommend that black duck managers continue, and refine where necessary, population and habitat surveys for black ducks and sympatric mallards, to provide the necessary state information to allow deci-

sion making. These estimates should be obtained annually from surveys conducted following rigorous statistical sampling designs. Estimates must be of sufficient geographic scope to provide inferences on trends in the continental breeding population, as opposed to regional or local populations, and sufficiently precise so as to enable discrimination among predictions under alternative management models. If management is to be based on geographically subdivided management units then survey intensity must be sufficient to provide precise, annual estimates at the level of these smaller units.

In addition to reliable estimates of black duck and mallard populations and habitat conditions, continued and refined estimates of annual survival, reproductive rates, and harvest rates must be available. Reliable data are needed to estimate parameters and calibrate the models, as well as to establish relationships between regulatory options and harvest intensity. Again, estimates must be available on the basis of management units for stocks if these smaller units (rather than the continental population) are to be the basis for management.

We recommend that our model sets be implemented into a provisional AHM protocol, and that AHM decision making be evaluated, including linkages between harvest management of black ducks and mallards, and between harvest and habitat management. An important part of this evaluation should be to explore alternative forms for the objective functions, decision space, and state space formulations. We also encourage linked efforts for the development of an integrated, international management strategy for black ducks following ARM principal, including:

- Objective-driven decision making
- Explicit consideration of uncertainty in decision making
- Reduction of uncertainty through adaptive feedback

Finally, we encourage ongoing and future efforts to explore the technical, logistic, and political challenges of an AHM-ARM approach for managing American black ducks on a continental basis.

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Received 1 February 2001

Accepted 7 June 2002

Appendix 1. Estimated fall age ratios for American black ducks, and predictor variables for development of reproduction submodel.

Year	\hat{A}_t^a	$N_t^{(0)}$	$M_t^{(0)}$	$HAB_t^{(0)}$	$HAB_t^{(0)2}$	$HAB_t^{(0)3}$	$PPT_t^{(0)}$	$TMP_t^{(0)}$
1961	1.201	479,400	667,300	109,967,000	9,776,512	-0.729	12.076	53.464
1962	1.093	448,200	373,100	109,924,000	9,887,443	-0.353	8.512	58.390
1963	1.006	466,400	469,300	109,881,000	9,964,315	-0.230	9.092	54.726
1964	0.873	584,400	479,200	109,159,000	10,041,187	-0.204	9.634	58.719
1965	0.882	488,600	304,400	108,437,000	10,111,597	-0.386	6.969	59.301
1966	0.846	457,000	394,300	107,715,000	10,163,569	-0.224	8.022	53.175
1967	1.203	494,900	354,100	106,994,000	10,128,407	-0.568	11.481	49.648
1968	1.596	472,100	249,000	106,272,000	10,093,245	-0.648	11.283	53.306
1969	1.047	479,800	341,200	109,659,000	10,039,141	-0.312	8.686	55.938
1970	1.332	422,300	389,400	113,045,000	9,985,036	-0.615	10.018	58.300
1971	0.967	393,900	405,600	116,432,000	9,930,931	-0.633	8.767	54.430
1972	1.267	413,700	375,400	119,818,000	9,856,110	-0.659	11.862	57.062
1973	1.722	429,600	359,443	123,205,000	9,778,687	-0.502	13.330	53.661
1974	1.743	325,500	223,055	121,305,000	9,715,183	-0.532	12.093	53.904
1975	1.175	355,000	329,511	119,404,000	9,651,679	-0.664	10.082	60.106
1976	1.205	434,300	388,542	117,504,000	9,588,175	-0.584	9.994	54.293
1977	1.163	362,500	412,171	115,603,000	9,534,461	-0.087	10.183	58.974
1978	1.416	360,800	445,855	113,703,000	9,526,878	-0.475	9.606	56.454
1979	1.244	314,600	397,988	111,803,000	9,507,537	-0.501	11.842	57.096
1980	1.371	281,500	393,400	109,902,000	9,488,197	0.061	11.608	57.171
1981	0.921	330,500	465,275	108,002,000	9,490,175	0.824	8.920	56.572
1982	1.123	309,600	327,125	106,101,000	9,492,154	0.668	9.055	58.698
1983	1.153	293,800	292,437	104,201,000	9,468,749	-0.667	16.575	53.849

(Continued)

^a \hat{A}_t = estimated fall age ratio (young per adult in fall population; $N_t^{(0)}$ = breeding population of black ducks (indexed by MWI count in previous January); $M_t^{(0)}$ = breeding population of mallards (indexed by MWI count in previous January); $HAB_t^{(0)1}$ = ha of forest area in eastern Canada.; $HAB_t^{(0)2}$ = ha of forested wetlands in northeastern U.S.; $HAB_t^{(0)3}$ = index to beaver abundance in eastern Canada; $PPT_t^{(0)}$ = weighted average March–May precipitation (in), $TMP_t^{(0)}$ = minimum mean monthly May–July temperatures (°F), for U.S. Atlantic coastal states Maryland and north.

Appendix 1 (continued). Estimated fall age ratios for American black ducks, and predictor variables for development of reproduction submodel.

Year	\hat{A}_t^a	$N_t^{(0)}$	$M_t^{(0)}$	$HAB_t^{(0)}$	$HAB_t^{(0)2}$	$HAB_t^{(0)3}$	$PPT_t^{(0)}$	$TMP_t^{(0)}$
1984	1.061	287,800	271,833	102,300,000	9,452,998	0.632	14.944	53.942
1985	1.770	278,900	246,500	100,400,000	9,437,247	0.415	8.903	57.550
1986	1.106	322,500	306,444	100,883,000	9,421,496	0.652	8.466	58.686
1987	1.038	272,000	306,033	101,367,000	9,405,745	1.830	9.790	57.615
1988	1.246	335,900	295,065	101,850,000	9,389,993	1.760	8.648	57.243
1989	1.415	310,000	342,974	102,333,000	9,374,586	1.236	13.182	56.252
1990	0.891	314,146	331,152	102,817,000	9,359,584	1.239	11.860	53.958
1991	0.774	281,483	323,926	103,300,000	9,344,582	1.019	10.771	61.524
1992	0.892	277,831	330,076	103,783,000	9,329,580	0.004	9.426	55.034
1993	0.876	290,584	406,832	104,267,000	9,314,631	0.001	12.061	57.182
1994	0.784	298,511	353,780	104,750,000	9,300,461	0.003	12.710	53.328
1995	1.117	312,567	414,911	105,233,000	9,286,291	0.000	7.881	55.167
1996	1.157	303,709	365,202	105,717,000	9,272,740	0.001	13.127	54.634

^a \hat{A}_t = estimated fall age ratio (young per adult in fall population); $N_t^{(0)}$ = breeding population of black ducks (indexed by MWI count in previous January); $M_t^{(0)}$ = breeding population of mallards (indexed by MWI count in previous January); $HAB_t^{(0)1}$ = ha of forest area in eastern Canada; $HAB_t^{(0)2}$ = ha of forested wetlands in northeastern U.S.; $HAB_t^{(0)3}$ = index to beaver abundance in eastern Canada; $PPT_t^{(0)}$ = weighted average March–May precipitation (in), $TMP_t^{(0)}$ = minimum mean monthly May–July temperatures ($^{\circ}$ F), for U.S. Atlantic coastal states Maryland and north.

Appendix 2. Area, age- and sex-specific hunting kill rates American black ducks, 1961–1993.

Area ^a	Year	Adult male		Adult female		Young male		Young female	
		\hat{K}	SE	\hat{K}	SE	\hat{K}	SE	\hat{K}	SE
2	1961	0.1724	0.0284	0.1724	0.0284	0.3252	0.0265	0.3252	0.0265
2	1962	0.2030	0.0232	0.2030	0.0232	0.3598	0.0281	0.3598	0.0281
2	1963	0.2203	0.0234	0.2203	0.0234	0.3351	0.0305	0.3351	0.0305
2	1964	0.1891	0.0187	0.1891	0.0187	0.3238	0.0251	0.3238	0.0251
2	1965	0.1795	0.0165	0.1795	0.0165	0.3355	0.0199	0.3355	0.0199
2	1966	0.1981	0.0171	0.1981	0.0171	0.3822	0.0213	0.3822	0.0213
2	1967	0.2151	0.0182	0.2151	0.0182	0.3306	0.0195	0.3306	0.0195
2	1968	0.1968	0.0161	0.1968	0.0161	0.3209	0.0190	0.3209	0.0190
2	1969	0.1755	0.0152	0.1755	0.0152	0.3901	0.0252	0.3901	0.0252
2	1970	0.2094	0.0174	0.2094	0.0174	0.2797	0.0212	0.2797	0.0212
2	1971	0.1887	0.0165	0.1887	0.0165	0.3372	0.0229	0.3372	0.0229
2	1972	0.1821	0.0165	0.1821	0.0165	0.2988	0.0258	0.2988	0.0258
2	1973	0.1689	0.0186	0.1689	0.0186	0.2839	0.0284	0.2839	0.0284
2	1974	0.1843	0.0224	0.1843	0.0224	0.3891	0.0539	0.3891	0.0539
2	1975	0.1704	0.0223	0.1704	0.0223	0.3471	0.0447	0.3471	0.0447
2	1976	0.1729	0.0237	0.1729	0.0237	0.2790	0.0335	0.2790	0.0335
2	1977	0.1476	0.0228	0.1476	0.0228	0.2530	0.0323	0.2530	0.0323
2	1978	0.1911	0.0245	0.1911	0.0245	0.2404	0.0342	0.2404	0.0342
2	1979	0.1508	0.0206	0.1508	0.0206	0.2593	0.0320	0.2593	0.0320
2	1980	0.1918	0.0255	0.1918	0.0255	0.2775	0.0372	0.2775	0.0372
2	1981	0.1866	0.0249	0.1866	0.0249	0.3387	0.0447	0.3387	0.0447
2	1982	0.1343	0.0214	0.1343	0.0214	0.2761	0.0393	0.2761	0.0393
2	1983	0.1567	0.0237	0.1567	0.0237	0.3095	0.0341	0.3095	0.0341
2	1984	0.0950	0.0162	0.0950	0.0162	0.1678	0.0252	0.1678	0.0252
2	1985	0.1136	0.0194	0.1136	0.0194	0.2222	0.0324	0.2222	0.0324
2	1986	0.0907	0.0158	0.0907	0.0158	0.1790	0.0278	0.1790	0.0278
2	1987	0.0973	0.0170	0.0973	0.0170	0.1863	0.0254	0.1863	0.0254
2	1988	0.1031	0.0158	0.1031	0.0158	0.2059	0.0262	0.2059	0.0262

(Continued)

^a Banding reference area (Fig. 1a); area 1 excluded because of insufficient data.

Appendix 2 (continued). Area, age- and sex-specific hunting kill rates American black ducks, 1961–1993.

Area ^a	Year	Adult male		Adult female		Young male		Young female	
		\hat{K}	SE	\hat{K}	SE	\hat{K}	SE	\hat{K}	SE
2	1989	0.1026	0.0167	0.1026	0.0167	0.2318	0.0297	0.2318	0.0297
2	1990	0.0952	0.0145	0.0952	0.0145	0.1541	0.0187	0.1541	0.0187
2	1991	0.0906	0.0133	0.0906	0.0133	0.1705	0.0186	0.1705	0.0186
2	1992	0.0891	0.0132	0.0891	0.0132	0.1781	0.0215	0.1781	0.0215
2	1993	0.0896	0.0138	0.0896	0.0138	0.1783	0.0202	0.1783	0.0202
2	1994	0.0649	0.0136	0.0649	0.0136	0.1137	0.0182	0.1137	0.0182
3	1961	0.2464	0.0336	0.2464	0.0336	0.3776	0.0252	0.3776	0.0252
3	1962	0.2319	0.0232	0.2319	0.0232	0.2967	0.0260	0.2967	0.0260
3	1963	0.2381	0.0217	0.2381	0.0217	0.3858	0.0249	0.3858	0.0249
3	1964	0.1686	0.0171	0.1686	0.0171	0.3548	0.0231	0.3548	0.0231
3	1965	0.1863	0.0170	0.1863	0.0170	0.3286	0.0206	0.3286	0.0206
3	1966	0.1820	0.0168	0.1820	0.0168	0.3715	0.0198	0.3715	0.0198
3	1967	0.1851	0.0176	0.1851	0.0176	0.3173	0.0205	0.3173	0.0205
3	1968	0.2238	0.0192	0.2238	0.0192	0.3059	0.0211	0.3059	0.0211
3	1969	0.1854	0.0169	0.1854	0.0169	0.3632	0.0263	0.3632	0.0263
3	1970	0.1830	0.0175	0.1830	0.0175	0.3207	0.0195	0.3207	0.0195
3	1971	0.1489	0.0140	0.1489	0.0140	0.2585	0.0212	0.2585	0.0212
3	1972	0.1412	0.0147	0.1412	0.0147	0.2310	0.0263	0.2310	0.0263
3	1973	0.1589	0.0188	0.1589	0.0188	0.3364	0.0293	0.3364	0.0293
3	1974	0.1764	0.0223	0.1764	0.0223	0.2869	0.0301	0.2869	0.0301
3	1975	0.1432	0.0187	0.1432	0.0187	0.2922	0.0292	0.2922	0.0292
3	1976	0.1738	0.0228	0.1738	0.0228	0.3416	0.0282	0.3416	0.0282
3	1977	0.1125	0.0180	0.1125	0.0180	0.2130	0.0224	0.2130	0.0224
3	1978	0.1705	0.0217	0.1705	0.0217	0.3120	0.0283	0.3120	0.0283
3	1979	0.1179	0.0188	0.1179	0.0188	0.3529	0.0401	0.3529	0.0401
3	1980	0.1976	0.0267	0.1976	0.0267	0.3508	0.0330	0.3508	0.0330
3	1981	0.1323	0.0219	0.1323	0.0219	0.3304	0.0374	0.3304	0.0374
3	1982	0.1243	0.0211	0.1243	0.0211	0.2469	0.0317	0.2469	0.0317
3	1983	0.1014	0.0183	0.1014	0.0183	0.2391	0.0376	0.2391	0.0376
3	1984	0.0875	0.0173	0.0875	0.0173	0.2759	0.0385	0.2759	0.0385
3	1985	0.1003	0.0200	0.1003	0.0200	0.2048	0.0387	0.2048	0.0387
3	1986	0.1007	0.0199	0.1007	0.0199	0.1544	0.0337	0.1544	0.0337
3	1987	0.1236	0.0245	0.1236	0.0245	0.1849	0.0321	0.1849	0.0321
3	1988	0.0748	0.0165	0.0748	0.0165	0.1764	0.0264	0.1764	0.0264
3	1989	0.0795	0.0152	0.0795	0.0152	0.1094	0.0209	0.1094	0.0209
3	1990	0.0755	0.0127	0.0755	0.0127	0.0915	0.0181	0.0915	0.0181
3	1991	0.0656	0.0111	0.0656	0.0111	0.1800	0.0273	0.1800	0.0273
3	1992	0.0586	0.0109	0.0586	0.0109	0.1061	0.0264	0.1061	0.0264
3	1993	0.0568	0.0108	0.0568	0.0108	0.1156	0.0236	0.1156	0.0236
3	1994	0.0588	0.0131	0.0588	0.0131	0.1096	0.0198	0.1096	0.0198
4	1961	0.1121	0.0352	0.1121	0.0352	0.3043	0.0258	0.3043	0.0258
4	1962	0.1878	0.0247	0.1878	0.0247	0.3101	0.0209	0.3101	0.0209
4	1963	0.2095	0.0209	0.2095	0.0209	0.2992	0.0183	0.2992	0.0183
4	1964	0.1539	0.0162	0.1539	0.0162	0.3127	0.0205	0.3127	0.0205
4	1965	0.1532	0.0154	0.1532	0.0154	0.3567	0.0212	0.3567	0.0212
4	1966	0.1469	0.0150	0.1469	0.0150	0.3453	0.0199	0.3453	0.0199
4	1967	0.1804	0.0181	0.1804	0.0181	0.3382	0.0198	0.3382	0.0198
4	1968	0.1792	0.0152	0.1792	0.0152	0.3243	0.0187	0.3243	0.0187
4	1969	0.1494	0.0130	0.1494	0.0130	0.3553	0.0217	0.3553	0.0217
4	1970	0.1741	0.0148	0.1741	0.0148	0.3899	0.0214	0.3899	0.0214
4	1971	0.1277	0.0124	0.1277	0.0124	0.2834	0.0181	0.2834	0.0181
4	1972	0.1305	0.0133	0.1305	0.0133	0.2401	0.0194	0.2401	0.0194
4	1973	0.1222	0.0144	0.1222	0.0144	0.2145	0.0194	0.2145	0.0194
4	1974	0.1566	0.0169	0.1566	0.0169	0.2987	0.0237	0.2987	0.0237

(Continued)

^a Banding reference area (Fig. 1a); area 1 excluded because of insufficient data.

Appendix 2 (continued). Area, age- and sex-specific hunting kill rates American black ducks, 1961–1993.

Area ^a	Year	Adult male		Adult female		Young male		Young female	
		\hat{K}	SE	\hat{K}	SE	\hat{K}	SE	\hat{K}	SE
4	1975	0.1740	0.0188	0.1740	0.0188	0.2727	0.0221	0.2727	0.0221
4	1976	0.1383	0.0185	0.1383	0.0185	0.3056	0.0251	0.3056	0.0251
4	1977	0.0784	0.0135	0.0784	0.0135	0.1958	0.0201	0.1958	0.0201
4	1978	0.1151	0.0164	0.1151	0.0164	0.2800	0.0254	0.2800	0.0254
4	1979	0.1019	0.0157	0.1019	0.0157	0.2751	0.0233	0.2751	0.0233
4	1980	0.1852	0.0248	0.1852	0.0248	0.3389	0.0275	0.3389	0.0275
4	1981	0.0888	0.0156	0.0888	0.0156	0.2289	0.0251	0.2289	0.0251
4	1982	0.1019	0.0158	0.1019	0.0158	0.2992	0.0191	0.2992	0.0191
4	1983	0.1095	0.0140	0.1095	0.0140	0.2332	0.0158	0.2332	0.0158
4	1984	0.0845	0.0116	0.0845	0.0116	0.2696	0.0204	0.2696	0.0204
4	1985	0.1105	0.0138	0.1105	0.0138	0.3102	0.0185	0.3102	0.0185
4	1986	0.1229	0.0139	0.1229	0.0139	0.2972	0.0205	0.2972	0.0205
4	1987	0.1002	0.0148	0.1002	0.0148	0.3123	0.0197	0.3123	0.0197
4	1988	0.1332	0.0163	0.1332	0.0163	0.2718	0.0194	0.2718	0.0194
4	1989	0.0998	0.0150	0.0998	0.0150	0.2415	0.0274	0.2415	0.0274
4	1990	0.1075	0.0146	0.1075	0.0146	0.2093	0.0247	0.2093	0.0247
4	1991	0.0983	0.0141	0.0983	0.0141	0.2532	0.0245	0.2532	0.0245
4	1992	0.0809	0.0135	0.0809	0.0135	0.1931	0.0273	0.1931	0.0273
4	1993	0.0669	0.0120	0.0669	0.0120	0.2815	0.0262	0.2815	0.0262
4	1994	0.0636	0.0142	0.0636	0.0142	0.1999	0.0316	0.1999	0.0316
5	1961	0.1868	0.0641	0.1868	0.0641	0.3552	0.0482	0.3552	0.0482
5	1962	0.1292	0.0297	0.1292	0.0297	0.3132	0.0627	0.3132	0.0627
5	1963	0.2318	0.0352	0.2318	0.0352	0.2862	0.0322	0.2862	0.0322
5	1964	0.1272	0.0199	0.1272	0.0199	0.2496	0.0316	0.2496	0.0316
5	1965	0.1722	0.0228	0.1722	0.0228	0.3248	0.0271	0.3248	0.0271
5	1966	0.1020	0.0142	0.1020	0.0142	0.2711	0.0215	0.2711	0.0215
5	1967	0.1387	0.0173	0.1387	0.0173	0.2745	0.0206	0.2745	0.0206
5	1968	0.1123	0.0134	0.1123	0.0134	0.2411	0.0174	0.2411	0.0174
5	1969	0.1132	0.0124	0.1132	0.0124	0.3166	0.0173	0.3166	0.0173
5	1970	0.1377	0.0138	0.1377	0.0138	0.3124	0.0168	0.3124	0.0168
5	1971	0.1150	0.0115	0.1150	0.0115	0.3186	0.0165	0.3186	0.0165
5	1972	0.1177	0.0120	0.1177	0.0120	0.3103	0.0188	0.3103	0.0188
5	1973	0.1092	0.0128	0.1092	0.0128	0.3064	0.0156	0.3064	0.0156
5	1974	0.1277	0.0142	0.1277	0.0142	0.2697	0.0176	0.2697	0.0176
5	1975	0.1100	0.0133	0.1100	0.0133	0.2559	0.0177	0.2559	0.0177
5	1976	0.1083	0.0145	0.1083	0.0145	0.2970	0.0205	0.2970	0.0205
5	1977	0.0701	0.0110	0.0701	0.0110	0.2334	0.0175	0.2334	0.0175
5	1978	0.1107	0.0147	0.1107	0.0147	0.3052	0.0192	0.3052	0.0192
5	1979	0.0896	0.0121	0.0896	0.0121	0.2427	0.0181	0.2427	0.0181
5	1980	0.1657	0.0202	0.1657	0.0202	0.3373	0.0189	0.3373	0.0189
5	1981	0.0780	0.0113	0.0780	0.0113	0.2442	0.0174	0.2442	0.0174
5	1982	0.1045	0.0128	0.1045	0.0128	0.2454	0.0166	0.2454	0.0166
5	1983	0.1086	0.0110	0.1086	0.0110	0.2421	0.0151	0.2421	0.0151
5	1984	0.0876	0.0099	0.0876	0.0099	0.2469	0.0149	0.2469	0.0149
5	1985	0.0965	0.0112	0.0965	0.0112	0.2337	0.0165	0.2337	0.0165
5	1986	0.0778	0.0092	0.0778	0.0092	0.2171	0.0175	0.2171	0.0175
5	1987	0.0806	0.0117	0.0806	0.0117	0.1918	0.0187	0.1918	0.0187
5	1988	0.0675	0.0102	0.0675	0.0102	0.1925	0.0195	0.1925	0.0195
5	1989	0.0636	0.0103	0.0636	0.0103	0.1741	0.0158	0.1741	0.0158
5	1990	0.0741	0.0104	0.0741	0.0104	0.1995	0.0187	0.1995	0.0187
5	1991	0.0726	0.0094	0.0726	0.0094	0.1669	0.0117	0.1669	0.0117
5	1992	0.0661	0.0092	0.0661	0.0092	0.1795	0.0151	0.1795	0.0151
5	1993	0.0618	0.0092	0.0618	0.0092	0.1786	0.0133	0.1786	0.0133
5	1994	0.0420	0.0084	0.0420	0.0084	0.1473	0.0123	0.1473	0.0123

^a Banding reference area (Fig. 1a); area 1 excluded because of insufficient data.

Appendix 3. Age- and sex-specific nonhunting survival for American black ducks, 1961–1993.

Year (<i>t</i>)	Adult male		Adult female		Young male		Young female	
	$\hat{\theta}_t$ ^a	SE	$\hat{\theta}_t$	SE	$\hat{\theta}_t$	SE	$\hat{\theta}_t$	SE
1961	0.811	0.100	0.508	0.085	0.609	0.065	0.636	0.074
1962	0.697	0.082	0.594	0.072	0.545	0.056	0.595	0.064
1963	0.884	0.101	1.000	0.120	0.722	0.070	0.641	0.077
1964	0.753	0.080	0.498	0.065	0.711	0.066	0.534	0.062
1965	0.833	0.088	0.633	0.078	1.000	0.088	0.513	0.058
1966	0.542	0.061	0.526	0.064	0.731	0.064	0.588	0.059
1967	0.680	0.071	0.673	0.078	0.567	0.046	0.641	0.060
1968	0.935	0.090	0.756	0.085	0.738	0.062	0.751	0.072
1969	0.695	0.070	0.501	0.057	0.615	0.057	0.510	0.053
1970	0.767	0.078	0.780	0.086	0.660	0.058	0.623	0.063
1971	0.751	0.078	0.648	0.077	0.729	0.066	0.642	0.070
1972	0.648	0.076	0.597	0.083	0.621	0.068	0.602	0.079
1973	0.618	0.078	0.497	0.075	0.513	0.054	0.545	0.067
1974	0.979	0.126	0.757	0.114	0.615	0.075	0.564	0.082
1975	0.881	0.129	0.684	0.114	0.670	0.092	0.628	0.096
1976	0.618	0.102	0.567	0.110	0.597	0.084	0.562	0.098
1977	0.612	0.092	0.529	0.098	0.617	0.071	0.516	0.076
1978	0.948	0.136	0.554	0.100	0.641	0.087	0.595	0.091
1979	0.514	0.076	0.647	0.111	0.555	0.070	0.522	0.079
1980	0.990	0.158	0.670	0.128	0.729	0.105	0.728	0.118
1981	0.608	0.100	0.592	0.111	0.669	0.091	0.692	0.109
1982	0.710	0.102	0.564	0.097	0.790	0.090	0.649	0.089
1983	0.702	0.098	0.778	0.130	0.740	0.091	0.683	0.101
1984	0.617	0.088	0.464	0.082	0.597	0.076	0.519	0.081
1985	0.733	0.104	0.590	0.103	0.663	0.083	0.696	0.102
1986	0.629	0.098	0.497	0.093	0.651	0.098	0.664	0.111
1987	0.655	0.109	0.611	0.119	0.645	0.087	0.517	0.089
1988	0.898	0.149	0.651	0.129	0.800	0.121	0.758	0.135
1989	0.506	0.084	0.439	0.089	0.534	0.074	0.527	0.095
1990	0.867	0.122	0.537	0.098	0.731	0.102	0.609	0.102
1991	0.677	0.109	0.607	0.111	0.635	0.094	0.501	0.086
1992	0.751	0.137	0.762	0.150	0.872	0.152	0.512	0.113
1993	0.705	0.171	0.633	0.167	1.000	0.229	0.688	0.186

^a Estimated non hunting survival rates year *t* to *t* + 1.

Appendix 4. Predictor variables^a used in development of survival models for American black ducks.

Year (<i>t</i>)	$N_t^{(2)}$	$M_t^{(2)}$	$HAB_t^{(2)}$	$TMP_t^{(2)}$
1961	448,200	1,394,500	267,022	24.75
1962	466,400	2,066,200	265,167	22.01
1963	584,400	2,909,300	263,312	22.40
1964	488,600	2,053,400	261,457	24.07
1965	457,000	2,761,000	259,603	25.88
1966	494,900	2,778,800	257,748	27.96
1967	472,100	1,673,900	255,893	23.25
1968	479,800	1,714,200	254,038	23.62
1969	422,300	2,967,900	252,183	19.92
1970	393,900	3,069,300	250,328	21.07
1971	413,700	1,969,300	248,473	27.47
1972	429,600	2,325,243	248,322	27.32
1973	325,500	1,672,955	248,170	28.07
1974	355,000	2,269,111	248,019	28.23
1975	434,300	2,994,342	247,867	21.87
1976	362,500	1,624,471	247,716	16.91
1977	360,800	1,781,055	247,564	22.34
1978	314,600	1,590,188	247,413	24.91
1979	281,500	1,664,000	247,261	27.23
1980	330,500	2,023,475	247,243	18.62
1981	309,600	1,907,125	247,224	20.98
1982	293,800	1,241,937	247,206	29.14
1983	287,800	1,063,733	247,187	21.46
1984	278,900	1,531,100	247,168	25.57
1985	322,500	1,658,644	247,150	23.65
1986	272,000	1,386,133	247,131	25.53
1987	335,900	2,054,565	247,112	25.35
1988	310,000	2,034,174	247,094	26.47
1989	314,146	1,910,739	247,075	22.42
1990	281,483	2,128,088	247,056	27.62
1991	277,831	1,203,041	247,038	26.44
1992	290,584	1,340,050	247,019	27.42
1993	298,511	1,490,777	247,001	20.77

^a $N_t^{(2)}$ = the estimate of black duck abundance from the MWI for the U.S., Atlantic and Mississippi Flyway totals, in January of year *t* + 1 (i.e., in the biological year corresponding to the estimates of θ_t); $M_t^{(2)}$ = the estimate of mallard abundance from the MWI for the U.S., Atlantic and Mississippi Flyway totals, in January of year *t* + 1; $HAB_t^{(2)}$ = total ha of coastal wetland habitat along the Atlantic coast of the U.S. in year *t*; $TMP_t^{(2)}$ = weighted mean December and January temperatures for the U.S. Atlantic coastal states Maryland and north.