Biological Report 7
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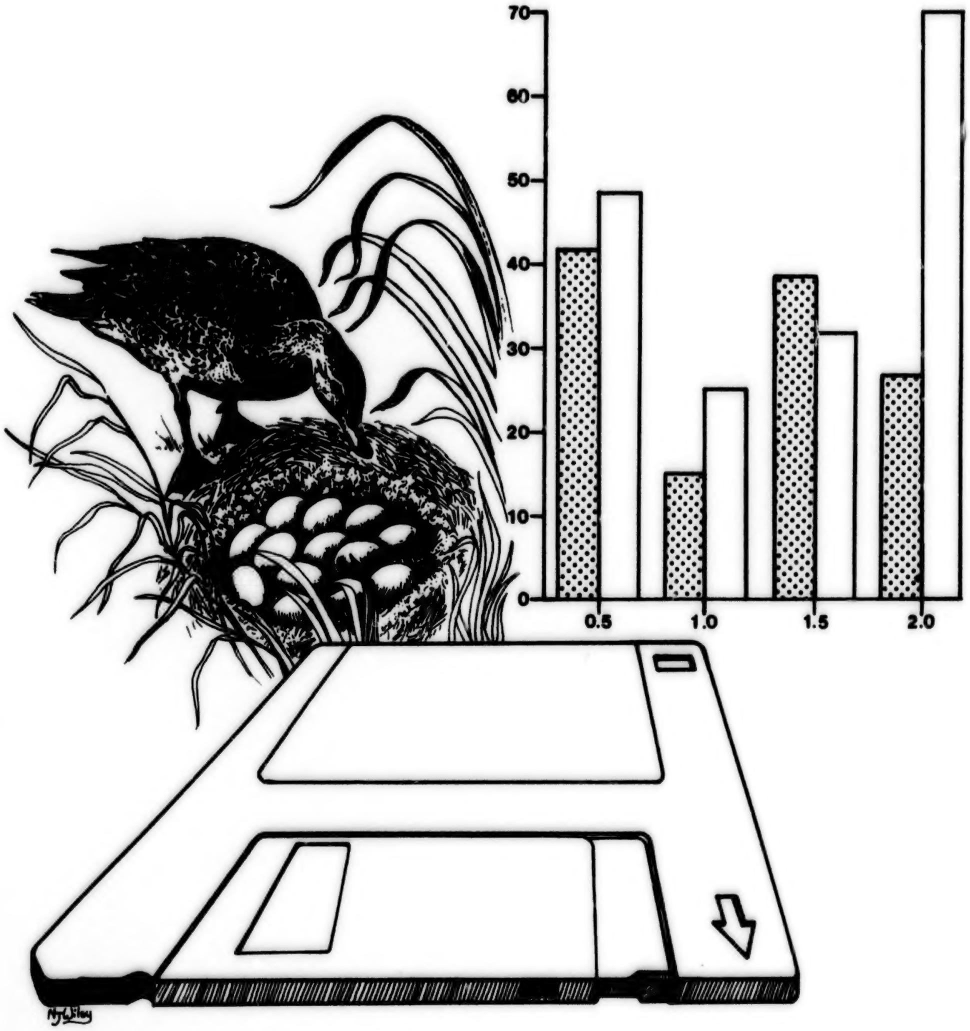

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By

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Abstract. We adapted a stochastic computer model to simulate productivity of the northern pintail (*Anas acuta*). Researchers at the Northern Prairie Wildlife Research Center of the U.S. Fish and Wildlife Service originally developed the model to simulate productivity of the mallard (*A. platyrhynchos*). We obtained data and descriptive information on the breeding biology of pintails from a literature review and from discussions with waterfowl biologists. All biological parameters in the productivity component of the mallard model (e.g., initial body weights, weight loss during laying and incubation, incubation time, clutch size, nest site selection characteristics) were compared with data on pintails and adjusted accordingly. The function in the mallard model that predicts nest initiation in response to pond conditions adequately mimicked pintail behavior and did not require adjustment.

Recruitment rate was most sensitive to variations in parameters that control nest success, seasonal duckling survival rate, and yearling and adult body weight. We simulated upland and wetland habitat conditions in central North Dakota and compared simulation results with observed data. Simulated numbers were not significantly different from observed numbers of successful nests during wet, average, and dry wetland

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conditions. The simulated effect of predator barrier fencing in a study area in central North Dakota increased recruitment rate by an average of 18.4%. This modeling synthesized existing knowledge on the breeding biology of the northern pintail, identified necessary research, and furnished a useful tool for the examination and comparison of various management options.

Key words: Northern pintail, *Anas acuta*, productivity model, mallard, *Anas platyrhynchos*, breeding ecology, population modeling, waterfowl management, simulation, recruitment.

Waterfowl ecologists have become concerned about substantial declines in numbers of several species of dabbling ducks, most notably during 1979 to 1991 (U.S. Fish and Wildlife Service 1985; U.S. Fish and Wildlife Service and Canadian Wildlife Service 1991). Although the causes of these long-term declines are not fully understood, losses of wetland and upland habitat in the prairie breeding grounds (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1991) and associated effects of predation on nesting hens and nests (Sargeant et al. 1984) are clearly important influences on waterfowl populations (Cowardin and Johnson 1979; Duebbert and Lokemoen 1980). As managers worked to understand the interactions of habitat losses, the effects of predation, and duck productivity, they recognized the utility of simulation models. Models have been used to compare potential management options and at the same time to gain insight into the dynamics of waterfowl and habitat interactions.

Since the mid-1970's, researchers at the Northern Prairie Wildlife Research Center of the U.S. Fish and Wildlife Service developed a computer modeling system that simulates the productivity of mallards (*Anas platyrhynchos*), a species for which data are relatively complete. This modeling system includes four components: (1) habitat and nest data bases, (2) a pair-wetland regression model, (3) a stochastic model of the productivity of the mallard, and (4) various routines for the input and summarization of data (Cowardin et al. 1988). The present version of the modeling system or "mallard model" (Johnson et al. 1987) is used to compare potential management of mallards at local and regional scales in the prairie pothole region of the United States (Cowardin et al. 1983, 1988). The mallard model is useful for examination and comparison of various management options and as an aid in decision making (Cowardin et al. 1988). In addition to providing benefits for management, the mallard model synthesizes information about the breeding biology of mallards and identifies aspects that have yet to be researched comprehensively (Johnson et al. 1987).

The mallard model is an important breakthrough; modeling systems with similar capabilities are needed for other species of ducks with declining populations. However, necessary biological information for integrating all the components of this modeling system is often incomplete and difficult to acquire for most species.

The mallard model is based exclusively on information on the biology of mallards. But, the model incorporates important variables about the breeding dynamics of any species of dabbling duck, such as daily survival of hens, initiation of nests, selection of nest sites, survival of clutches until hatching, and survival of broods until fledging. We recognized that the basic structure of the mallard model could be used as a framework for modeling other species of dabbling ducks. For species with similar life histories, some components of the mallard model need little or no modification, whereas the main component that models productivity requires major changes. We hypothesized that the mallard model could be adapted to another species if the productivity component is properly modified.

The northern pintail (*Anas acuta*) is of particular concern to waterfowl ecologists and managers because pintail populations have suffered the most noticeable decline of any duck. In 1991, the breeding population was at a record low of >50% below the 1955–88 average (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1991). Because of concern about survival of the species and benefits from modeling for mallards, the U.S. Fish and Wildlife Service recognized the value of developing and testing a model for northern pintails. Biologists of the Prairie Pothole Joint Venture of the North American Waterfowl Management Plan also identified a need to evaluate responses by populations of northern pintails and other species to habitat management, but, because of a lack of certain biological information and models to integrate this information, reliable estimates of production are restricted to mallards (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1992). Researchers at Ducks Unlimited Canada who attempted to evaluate alternative management of prairie habitat in Alberta (Alberta Forestry, Lands, and Wildlife et al. 1989) applied the mallard model but were limited by the unavailability of a northern pintail model (R. T. Clay, Ducks Unlimited Canada, Winnipeg, personal communication).

In response to the need for a modeling system for the northern pintail, we adapted the productivity component of the mallard model to northern pintails. We modified only the productivity component and did not address differences in settling rates and homing between the species. Our specific objectives were to (1) compare the similarities and differences in breeding biology of northern pintails and mallards and identify aspects of northern pintails with inadequate data, (2) modify the productivity component of the mallard model as necessary for northern pintails, (3) conduct sensitivity analysis of the northern pintail productivity component, and (4) test the northern pintail model with available field data or expert opinion on the species breeding biology.

Methods

Literature Review and Modeling Approach

We searched four computerized literature sources (*Wildlife Review*, U.S. Fish and Wildlife Service; BIOSIS Data Base; Reinecke and Delnicki [1992]; Julie Moore & Associates Wildlife Database), reviewed data bases on file at the Northern Prairie Wildlife Research Center, and identified unpublished sources of information on the northern pintail in discussions with waterfowl biologists. We used data from these sources to modify the model.

We carefully reviewed other models of waterfowl populations and compared their general framework with the mallard model. The models of Walters et al. (1974), Johnson and Sargeant (1977), and Cowardin and Johnson (1979) are noteworthy earlier models that influenced the development of the mallard model. Frederick et al. (1987) simulated refuging populations of geese, including selection of feeding habitat, in some detail. Koford et al. (1992) recently included elements of the productivity model in the development of a stochastic model of the entire life cycle of midcontinent mallards. A series of habitat suitability models for northern pintails was developed by Suchy and Anderson (1987).

Values that are used in the northern pintail productivity model can be classified as parameters or variables. Parameters are fixed throughout an execution of the program and are usually characteristics of the species (e.g., number of days of incubation). Parameters also include the estimated statistical parameters of regression equations. Variables are not constant throughout an application and are usually characteristics of the habitat or wetland condition (e.g., vegetation measurements). Most often variables such as the latter are viewed as input to the model. We were consistent in our use of these terms throughout. We compared each variable and parameter in the productivity component of the mallard model with available data for northern pintails and modified them as needed. Generally accepted published sources usually provided sufficient evidence for changing a parameter (i.e., consider incubation time). We also applied the model to independent data and evaluated the results in terms of the robustness of the extant structure of the model. This interactive process, whereby models are improved and biological understanding enhanced, is described as a bootstrapping process (Starfield and Bleloch 1986) or a spiral approach to modeling (Innis 1979).

The principal computer source code for the model is written in FORTRAN. Two data files are used for a typical application of the mallard productivity model. One file contains information about daily wetland conditions, the number and age distribution of birds settling in an area, duration of arrival period, and upland habitat characteristics. The other file includes the survival rate of ducklings, brood survival rate, and hen survival rates. In addition to these values from external files, the productivity component has several parameters representing scaling factors, regression coefficients, and a variety of maximum, average, and minimum biological values embedded in the FORTRAN source code.

To simplify modification of these parameters, we created a third file named INPUT.PIN (Appendix A) for the northern pintail model. We then placed parameters from the FORTRAN source code of the mallard model into the INPUT.PIN file and substituted corresponding variable names in the FORTRAN source code of the northern pintail model.

Specific Modifications of the Model Structure

Nest Initiation in Response to Wetland Condition

In the mallard model, wetland condition, date, body weight, and remaining egg-laying potential influence the probability of a hen initiating a nest on a particular day (Johnson et al. 1987). We analyzed frequencies of nest initiation by northern pintails relative to wetland condition to determine whether they were similar to mallards'. We compared observed estimates of northern pintail and mallard nest initiations per pair in response to wetland condition with the same approach for each species. Our goal was to determine whether we could retain the nest initiation function of the mallard model for the northern pintail model.

Data for this analysis were collected by U.S. Fish and Wildlife Service personnel during annual surveys at the Woodworth study area, Stutsman County, North Dakota, during 1965–81 (Northern Prairie Wildlife Research Center files; Higgins et al. 1992). We stratified data by year for the following parameters: percentages of wetlands containing water in mid-May and mid-June, pooled data for nest success of upland-nesting duck species, and total acres searched for nests. Throughout this paper, "successful nest" refers to a nest in which at least one egg hatches and "nest success" refers to the proportion of a sample of nests in which clutches survive from initiation through hatching. In addition, we obtained the following data for both northern pintails and mallards: estimated number of pairs in the breeding population, number of found nests, and number of successful nests. Of the years with available data, we selected 10 that were similar in total searched area. Two of these years were omitted because they contained at least one value that we considered extreme and unrealistic. This reduced the sample size to 8 years. Although the cause of these extreme values was unknown, the omitted years had either very high or very low percentages of wetland basins with water.

As an index to nesting intensity, we calculated the number of nest initiations per pair for each year from equations 1 through 4. To account for differences in the area searched each year, we scaled area values by dividing each by the maximum searched area during any year:

$$C_i = B_i / B' \qquad (1)$$

where

C_i = the scaled searched area for year *i*,

B_i = the searched area, and

B' = the maximum searched area among the years in the sample.

We estimated the number of successful nests by each species at the Woodworth study area by dividing the observed number of successful nests by the scaled searched area:

$$\hat{Y}_i = Y_i / C_i \qquad (2)$$

where

$\hat{Y}_i$ = the estimated number of successful nests and

Y_i = the number of successful nests found during the surveys.

Because of low sample sizes of nests found at the Woodworth study area, we estimated numbers of initiated nests by dividing estimated numbers of successful nests by the pooled year-specific nest success of all upland-nesting ducks (Miller and Johnson 1978):

$$\hat{G}_i = \hat{Y}_i / \hat{S}_i \qquad (3)$$

where

$\hat{G}_i$ = the estimated number of initiated nests and

$\hat{S}_i$ = nest success of all upland-nesting duck species combined.

We calculated the estimated number of nest initiations per pair by dividing the estimated number of initiated nests by the number of pairs in the breeding population:

$$\hat{H}_i = \hat{G}_i / \hat{O}_i \qquad (4)$$

where

$\hat{H}_i$ = the estimated nest initiations per pair and

$\hat{O}_i$ = the number of pairs.

We used linear regression analysis to test relations between H_i and three measures of wetland conditions. These were percentages of wetlands containing water in mid-May, mid-June, and the average of May and June. Slopes of the regression lines for northern pintails and mallards were compared with analysis of covariance (Fig. 1).

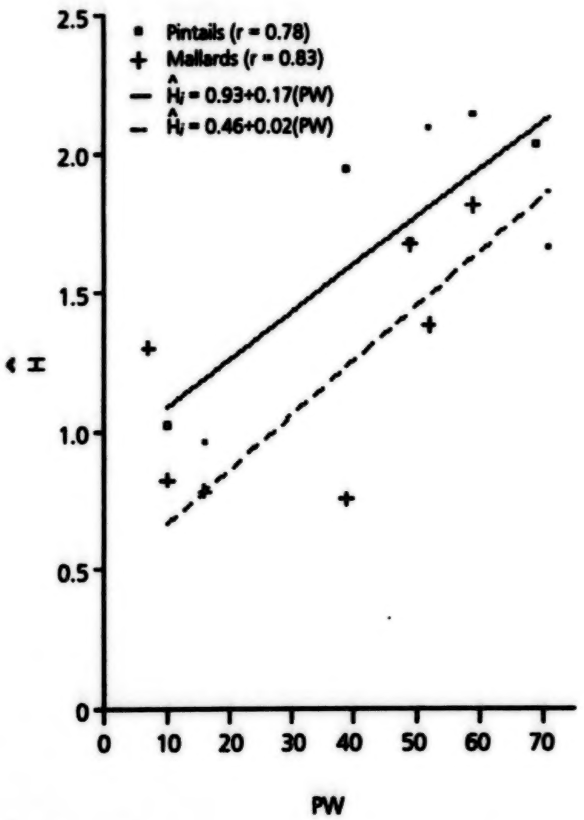

Fig. 1. Relation between estimated nest initiations per pair ($\hat{H}_i$) of northern pintails and mallards (*Anas platyrhynchos*) and percentage of wetlands containing water in mid-June (PW) at the Woodworth study area, Stutsman County, North Dakota, 1966–81.

Nest Site Selection

The productivity component of the mallard model determines nest site selection by calculating attractiveness values for various habitats based on numerical indexes of vegetative cover height and density. The index was obtained with a modified version of a method developed by Robel et al. (1970) termed "visual obstruction measurement" or "VOM." Visual obstruction measurements usually range from 0 dm for short and sparse cover to 4 dm for tall and dense cover.

We used data from three study areas in North Dakota to analyze the attractiveness of cover to northern pintails: the Woodworth study area in Stutsman County, the Koenig study area in McLean County, and the Central Grasslands Research Station in Stutsman and Kidder counties. We included data from seven nesting seasons at the Woodworth study area (1975–81), from four nesting seasons at the Koenig study area (1978–81), and from two nesting seasons at the Central Grasslands Research Station (1985–86) in the analysis. For each year and study area, we compiled two sets of VOMs: (1) VOMs from along field transects in available nesting habitat and (2) VOMs from active nest sites of northern pintails and mallards. We used only VOMs that were observed before plant growth affected measurements of the vegetation.

We used a series of steps to relate VOMs observed in available nesting habitat with VOMs observed at nest sites selected by northern pintails and mallards. For each study area and year, we grouped the percentages of VOMs in available habitat and the percentages of VOMs at nest sites according to four vegetative height (decimeter) classes:

Class 0.5— $0 < \text{VOM} \le 0.5$
Class 1.0— $0.5 < \text{VOM} \le 1.0$
Class 1.5— $1.0 < \text{VOM} \le 1.5$
Class 2.0— $1.5 < \text{VOM}$

Then, for each vegetative height class, we divided the percentage of VOMs from nest sites by the percentage of VOMs from available nesting habitat (Fig. 2) and used the ratio as a measure of nest site selection. In this example, the respective ratios of the four vegetative height classes 0.5–2.0 were 0.2, 0.6, 2.5, and 10.0 dm.

This procedure resulted in 52 observations for each species. We performed weighted regression analyses with a General Linear Model procedure (SAS Institute, Inc. 1987) to test relations between the ratios and class levels. Each ratio was weighted by the reciprocal of its approximate variance (Var[ratio]), which was estimated by:

$$\text{Var(ratio)} = \frac{(1-w_i)}{w_i} \times \frac{(\text{total of field VOMs}) + (\text{total of nest VOMs})}{(\text{total of nest VOMs})^2} \tag{5}$$

where

$$w_i = \frac{(\text{count of field VOMs}) + (\text{count of nest VOMs})}{(\text{total of field VOMs}) + (\text{total of nest VOMs})} \tag{6}$$

We compared simple regression, polynomial regression, and simple regression with VOM class designated as the classification variable to examine piecewise linear relations for best fit of the data.

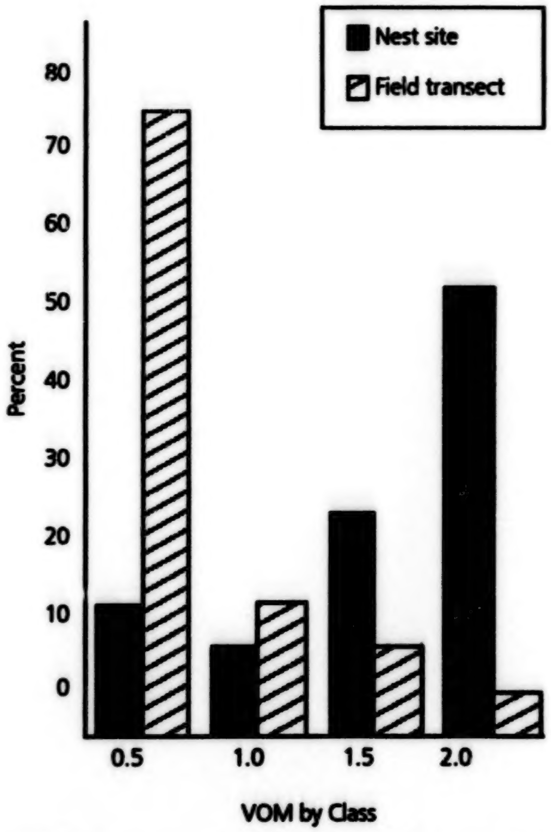

Fig. 2. Percentage of northern pintail (*Anas acuta*) nest site visual obstruction measurements (VOMs) and percentage of field transect VOMs by vegetative height class in the Koenig study area, McLean County, North Dakota, 1981.

Table 1. *Levels of parameters and variables in the sensitivity analysis of the northern pintail (*Anas acuta*) productivity model.*

Parameter or variable name and levels	Value	Change from control (%)
Cropland to grassland ratio[a]		
Control	50:50	
High	100:0	+100
Low	0:100	−100
Semipermanent basins with water (%)		
Standard[b]	65.0	
High	87.0	+34
Low	34.7	−47
Yearling (and adult) body weights (g)		
Standard	800 (900)	
High	860 (960)	+6.9
Low	740 (840)	−6.9
Nest success (p)[c]		
Standard	0.135	
High	0.633	−80[d]
Low	0.039	+80
Seasonal duckling survival rate for successful broods (p)[c]		
Standard	0.540	
High	0.810	+50
Low	0.270	−50
Brood survival rate (p)[c]		
Standard	0.740	
High	0.920	+25
Low	0.550	−25

[a] For the cropland to grassland ratio the control was a plot with a 1:1 ratio rather than the standard 1:0.57 ratio.

[b] Standard values that represent favorable waterfowl habitat in central North Dakota.

[c] Proportion = p.

[d] To vary nest success, daily nest mortality rates were adjusted by ±80% in each habitat.

Sensitivity Analysis

We conducted sensitivity analysis to determine the influence of parameters and variables on simulated results; variation imposed on selected parameters entered into the model (input) was restricted to biologically realistic limits similar to those used by Johnson et al. (1987). We varied six parameters or variables, one at a time, above and below their respective standard values (Table 1). For each parameter or variable, we used values that represented means and ranges for good waterfowl habitat in central North Dakota similar to those used by Johnson et al. (1987).

We simulated cropland to grassland ratios because they represent the two most common habitats in the prairie pothole region. Values of wetland condition in the sensitivity analysis represented the percent of semipermanent wetlands containing water. We altered the mean body weights of yearling and adult birds upon arrival by ±60 g and adjusted daily mortality rates of nests by ±80% in each habitat to alter nest success. We altered the rates for seasonal duckling survival of successful broods by ±50% and brood survival by ±25% (Table 1).

We used simulated recruitment rate, defined as the number of females added to the fall population per female in the breeding population (Johnson et al. 1987), to assess the sensitivity of the model to changes in input variables and parameters. The model was considered sensitive to changes in a variable or parameter if the percent change in recruitment rate was greater than the percent change in the variable or parameter. Each test used the average of three simulations of 1,000 northern pintails, making the effective sample size 3.

Table 2. *Habitat characteristics with which nesting of northern pintails at the Woodworth study area, Stutsman County, North Dakota, was simulated.*

Habitat type	Relative availability (%)	Visual obstruction measurement ranges (dm)[a]	Daily clutch mortality rates[a]
Cropland (fall-plow grain)	0.030	0.01–25.0	0.044–0.999
Planted cover	0.240	15.0–40.0	0.049
Planted cover (burned)	0.030	1.01–25.0	0.065–0.999
Grassland (nongrazed)	0.400	8.0–13.0	0.047
Grassland (burned)	0.060	0.01–13.0	0.047–0.999
Other	0.030	17.0–22.0	0.068
Wetland (temporary)	0.003(74)[b]	12.0–17.0	0.070
Wetland (seasonal)	0.061(49)	12.0–17.0	0.070
Wetland (semipermanent)	0.091(28)	12.0–17.0	0.070
Wetland (permanent)	0.035(0)	12.0–17.0	0.070

[a] Values change in response to phenological events or catastrophic events such as burning or plowing.

[b] Percentage of habitat available for nesting if <100 is placed in parentheses.

Interactions Among Factors

We evaluated interactions among parameters and variables with a full factorial analysis of variance. The six parameters and variables were employed at two levels (Table 1). We executed each of the 64 (2^6) simulations with initial cohorts of 1,000 northern pintails. To compare the amount of variability of each main effect, two-way interactions and three-way interactions, we ranked them in descending order of their respective F-ratios with 1 df.

Model Testing and Application

Testing

To test the validity of the model's ability to simulate productivity of northern pintails, we simulated nesting at the Woodworth study area. We specified actual habitat conditions at the Woodworth study area in the principal habitat file of the model. We obtained data for this file from the Woodworth study area files, Northern Prairie Wildlife Research Center files, and Higgins et al. (1992) and through interviews with the Woodworth study area site manager (M. Callow, Squaw Creek National Wildlife Refuge, personal communication; Table 2). We executed simulations with dry, average, and wet wetland conditions. We used three to four replications of each simulation because it is typical to have only a few years of data with which to make comparisons of field data. We scaled results to the average estimated number of northern pintail pairs at the Woodworth study area during each of the wetland conditions. Simulated numbers of nest initiations and successful nests were compared with field data from the Woodworth study area during 1970–78 and 1981. Averages of each wetland condition were compared with t-test procedures.

Predator Barrier Fence Application

To examine the utility of the model in predicting effects of management on northern pintail recruitment, we simulated the use of predator barrier fencing at the Woodworth study area. We simulated fencing at about 81 ha (200 acres) of planted cover to achieve nest success of about 55% inside the fence. We executed three simulations with dry, wet, and average wetland conditions and scaled results to 30 pairs, the average number of annually (1965–81) observed northern pintail pairs at the Woodworth study area (Higgins et al. 1992).

Results

Literature Review and Modeling Approach

We modified 11 parameters for the northern pintail model (Table 3). The primary source of data on the breeding biology of the northern pintail was Bellrose (1976). Because we found no appropriate data to modify weight loss of hens from laying and incubating eggs, we scaled the values for northern pintails with the same daily rates as the corresponding parameters in the mallard productivity model.

Table 3. *Definitions, values, and sources of estimates of parameters modified in the productivity model for northern pintails.*

Parameter	Definition	Input value	Source
H	Hatch time of clutch (days)	31	Bellrose (1976)
INCTIME	Incubation of clutch (days)	23	Bellrose (1976)
WTBAR(1)	Average weight of arriving yearling female pintails (grams)	800	Bellrose (1976)
WTBAR(2)	Average weight of arriving adult female pintails (grams)	900	Bellrose (1976)
CLUA	Intercept in regression equation to calculate clutch size with average equal to 7.75 eggs	15.43	Bellrose (1976)
CLUB	Slope in regression equation to calculate clutch size	0.063	Johnson et al. (1987)
ROBELA	Slope in regression equation to calculate nest site selection attractiveness based on VOMs of available habitats	0.97	Calculated
ROBELB	Intercept (see ROBELA)	0.28	Calculated
ROBLMIN	Intercept (see ROBELA)	2.23	Calculated
LOSSLAY	Weight lost per day during laying (grams)	7.5	Scaled from Johnson et al. (1987)
LOSSINC	Weight lost per day during incubation (grams)	1.5	Scaled from Johnson et al. (1987)

Specific Modifications of the Model Structure

Nest Initiations in Response to Wetland Conditions

Estimated nest initiations (H_i) increased with percentages of wetlands containing water ($P < 0.05$; Table 4). Because the correlation was highest during mid-June, we used this relation in subsequent comparisons. Neither the slope ($F = 0.107$; 1, 11 df; $P = 0.749$) nor the intercept ($F = 2.07$; 1, 11 df; $P = 0.178$) of the regressions for northern pintails and mallards were different, and therefore we used the nest initiation function from the mallard model in the northern pintail model.

Nest Site Selection

Vegetation obstruction measurements were lower in habitats with northern pintail nest sites than in habitats with mallard nest sites, and northern pintails were not as strongly attracted as mallards to habitats with high VOMs (Fig. 3). Simple linear regression ($F = 6.76$, 1 df, $P = 0.01$) provided the best fit for the data on northern pintails. The regression equations predicting attractiveness (A) of available habitats for nesting by northern pintails (Fig. 4) are as follows:

if VOM ≤ 2.0 dm, then A = 0.28 + 0.97(VOM)

if VOM > 2.0 dm, then A = 2.23

Attractiveness of habitats with VOMs > 2.0 was determined arbitrarily because small sample sizes of observed data precluded quantitative analysis (Fig. 4). Simple regression with VOM classes as

Table 4. *Correlation coefficients (r^2) of regressions of estimated nest initiations per pair ($\hat{H}_i$) on percentages of all wetlands containing water in mid-May, mid-June, and average of May and June for northern pintails and mallards* (Anas platyrhynchos) *nesting in the Woodworth study area, North Dakota, 1966–81.*

	Mid-May			Mid-June			Average		
Species	r^2	N[a]	P[b]	r^2	N	P	r^2	N	P
Pintail	0.55	8	0.04	0.61	7	0.04	0.64	7	0.03
Mallard	0.30	7	0.20	0.69	6	0.04	0.49	6	0.12

[a] Number of years in the regression.

[b] Probability of a greater r^2.

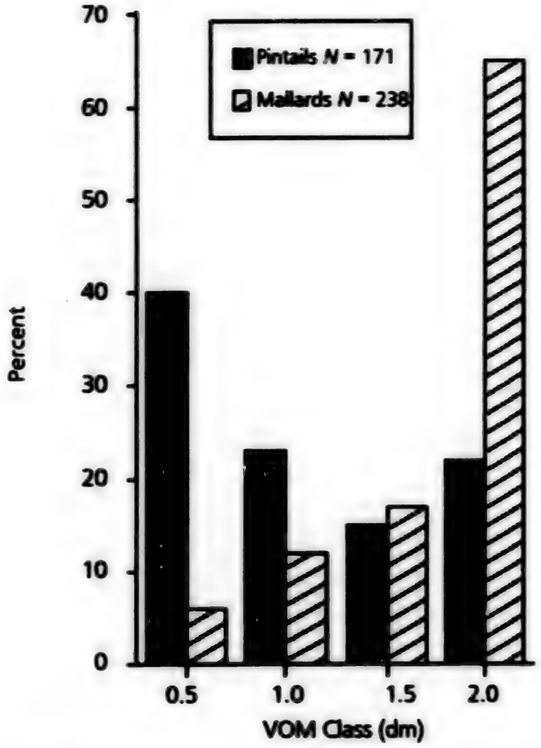

Fig. 3. Percentage of northern pintail and mallard nests in each visual obstruction measurement (VOM) class in the Woodworth study area, Koenig study area, and Central Grasslands Research Station, Stutsman and Kidder counties, North Dakota, 1975–86.

classification variables provided the best fit for data on mallards ($F = 17.2$, 3 df, $P = 0.0001$; Fig. 4).

Sensitivity Analysis

Simulated recruitment rates were most sensitive to nest success and yearling and adult body weight (Table 5). Decreasing nest success caused recruitment rate to decrease by −64%; increasing nest success caused recruitment rate to increase by 207%. Increasing the yearling and adult body weights increased recruitment by 18%, and reducing the body weights decreased recruitment by 15%. Varying the cropland to grassland ratio, wetland condition, seasonal duckling survival rate, and brood survival rate produced small changes in recruitment rate.

Interaction Among Factors

All main effects and two-way interactions in the factorial analysis of variance of sensitivity on recruitment were significant. Nest success, seasonal duckling survival rate, and the two-way interaction between them ranked the most significant (Table 6). Nest success and seasonal duckling survival rate were involved in all significant two-way and three-way interactions (Table 6).

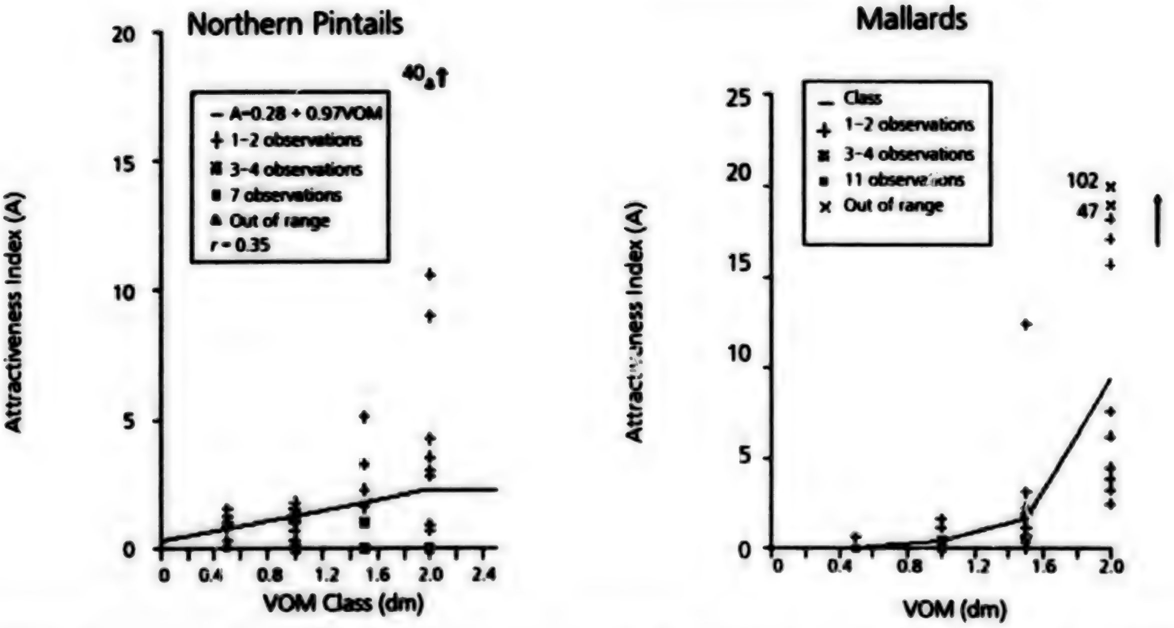

Fig. 4. Regression of the nest site attractiveness index (A) of northern pintails and mallards on visual obstruction measurements (VOMs) in the Woodworth study area, Koenig study area, and Central Grasslands Research Station, North Dakota, 1975–86.

Table 5. *Changes in simulated recruitment rate from varying parameters and variables in the northern pintail productivity model.*

Parameter or variable and percent change from control (%)[a]	Recruitment rate		
	Average[b]	SE	Change (%)
Control	0.439	0.004	
Cropland to grassland ratio			
1:1 control[c]	0.478	0.050	
1:0	0.399	0.021	−16.5
0:1	0.508	0.024	+6.2
Wetland condition			
+34	0.484	0.039	+10.2
−47	0.251	0.011	−42.8
Yearling and adult body weight			
+6.9	0.519	0.027	+18.2
−6.9	0.374	0.024	−14.8
Nest success[d]			
−80	1.347	0.016	+206.8
+80	0.159	0.010	−63.8
Seasonal duckling survival rate for successful broods			
+50	0.647	0.011	+47.4
−50	0.251	0.012	−42.8
Brood survival rate			
+25	0.553	0.027	+26.0
−25	0.337	0.010	−23.2

[a] Controls were standard values that represent favorable waterfowl habitat in central North Dakota.

[b] $N = 4$ simulations.

[c] For cropland to grassland ratio the control ratio of 1:1 was used rather than the standard control ratio of 1:0.57.

[d] To vary nest success, daily clutch mortality rates were adjusted by ±80% in each habitat.

Model Testing and Application

Simulated values of numbers of successful nests were not different from observed values at the Woodworth study area during wet ($t = 1.0$, 4 df, $P = 0.35$), average ($t = 0.1$, 6 df, $P = 0.94$), and dry ($t = -0.2$, 4 df, $P = 0.88$) wetland conditions (Table 7). Simulated numbers of nest initiations were different from observed numbers during the wet ($t = 5.9$, 4 df, $P = 0.004$) and average ($t = 3.9$,

Table 6. *Main effects, two-way interactions, and three-way interactions (P = 0.0001) from a factorial analysis of variance of the sensitivity of recruitment rate in the northern pintail productivity model, ranked according to F value.*

Parameter or variable	*F* value[a]
Nest success	100,000
Seasonal duckling survival rate	61,367
Nest success × seasonal duckling survival rate	40,510
Brood survival rate	14,693
Wetland condition	10,032
Nest success × brood survival rate	9,846
Yearling and adult body weight	7,039
Wetland condition × nest success	5,323
Yearling and adult body weight × nest success	3,753
Wetland condition × seasonal duckling survival rate	3,156
Seasonal duckling survival rate × brood survival rate	3,102
Yearling and adult body weight × seasonal duckling survival rate	2,139
Nest success × seasonal duckling survival rate × brood survival rate	2,047
Wetland condition × nest success × seasonal duckling survival rate	1,732
Yearling and adult body weight × nest success × seasonal duckling survival rate	1,141
Cropland to grassland ratio	1,011

[a] 1 df.

Table 7. *Comparison between simulated and observed northern pintail productivity in the Woodworth study area, North Dakota, 1970–78 and 1981.*

Source	Wetland conditions	Comparisons N	Average pairs	Average nest initiations	Average successful nests
Observed	Wet	3	36.0	20.3	9.3
Simulated	Wet	3	36.0	72.3[a]	12.3
Observed	Average	4	34.2	20.8	10.2
Simulated	Average	4	34.2	64.2[a]	10.5
Observed	Dry	3	17.0	11.7	4.0
Simulated	Dry	3	17.0	18.3	3.6

[a] Significantly different from observed data ($P < 0.01$).

Table 8. *Effect of simulated predator barrier fencing on northern pintail recruitment rates under wet, average, and dry wetland conditions at the Woodworth study area, North Dakota.*

Wetland conditions	Recruitment rate		
	Average[a]	SE	Change (%)
Wet	0.701	0.022	+18.2
Average	0.624	0.036	+21.6
Dry	0.365	0.006	+15.5

[a] N = 4 simulations.

6 df, $P = 0.006$) wetland conditions, but simulated and observed values were not different during dry wetland conditions ($t = 1.7$, 4 df, $P = 0.16$; Table 7). The simulated effect of installing predator barrier fencing increased the recruitment rate of northern pintails during the three wetland conditions by an average of 18.4% (range = 16–22%; Table 8).

Discussion

Literature Review and Modeling Approach

We determined that the breeding ecologies of northern pintails and mallards are sufficiently similar to permit the use of the mallard productivity model as a basis for a model of northern pintail productivity. Ecological factors controlling nesting attempts, egg laying, incubation, nest success, and hen and brood survival of the two species are similar. For example, we could not detect differences between mallards and northern pintails in nest initiations in response to wetland condition. Consequently, we did not change that model function to adequately model productivity. However, we confirmed that nest site selection between the two species was different. Unlike mallards, northern pintails nested more often in shorter, sparser cover than in taller, ranker cover. The model functions had to be modified accordingly.

We identified several aspects of the breeding ecology of the northern pintail for which data are unavailable. For example, because northern pintail hens generally weigh less than mallard hens and may carry less body fat (Krapu 1979), we suspect the potential for renesting to be less in northern pintails than in mallards (Duncan 1987b), but available data are inconclusive. Data on nest success by northern pintails are needed by habitat class, region, and year (Cowardin et al. 1985, 1988; Lokemoen et al. 1990). More information is needed about brood survival (of both individual ducklings and entire broods; Duncan 1983; Duebbert and Frank 1984; Duncan 1986, 1987a) and on survival of hens during the breeding season. Because of the lack of data on these factors, we were forced to use the parameter values from the mallard model for northern pintails.

Specific Modifications of the Model Structure

Anecdotal observations and speculation reinforced the view that northern pintails are nomadic before settling on nesting grounds. For example, northern pintails use the least predictable wetland habitats and are notable opportunists when habitat conditions are unstable from one year to the next (Johnson and Grier 1988). Northern pintails presumably settle on breeding grounds in direct response to wetland condition and available nesting habitat (Hochbaum and Bossenmaier 1972). Derrickson (1977) found that during the laying and incubation periods, northern pintails are much more mobile than other species of surface-feeding ducks. Quantitative information on this aspect of the northern pintail's breeding ecology is not yet available.

We emphasize that we did not alter the function in the component of the mallard model that determines the settling rate of pairs as a function of semipermanent wetlands. That function is not a part of the stochastic productivity component per se (Cowardin et al. 1988). Settling rates more highly correlate with pond conditions in northern pintails than in other dabblers, and northern pintails exhibit the lowest association with permanent ponds (Johnson and Grier 1988). Much improvement is needed in the modeling of northern pintail settling rates in relation to wetland habitat conditions. Until such work is accomplished, users of the model who wish to simulate northern pintail productivity should base the nest initiation function on the assumption that after northern pintails settle in a nesting area, they remain and attempt to nest and raise a brood to fledging.

Selection of a nest site by females is a complex of behaviors that is poorly understood (Jessen et al. 1964; Johnson et al. 1987). The regression equation that we used to calculate attractiveness of nesting habitats as a function of vegetation obstruction measurements agrees with the tendency of northern pintails to nest in relatively sparse cover (Bellrose 1976; Holm 1984; Duebbert et al. 1986; Duebbert and Kantrud 1987). Northern pintails select open areas with lower vegetation obstruction measurements at their nest sites than do any other species of dabbling ducks (Krapu 1977). The regression equation that we estimated for mallards agrees with mallards' preference for nest sites with tall and dense cover over sites with low or sparse cover (Kirsch et al. 1978; Klett et al. 1988). We speculate that the inclination of northern pintails to nest in a wide variety of habitats with sparse cover is related to their opportunistic behavior toward ephemeral wetlands (Calverley and Boag 1977). We suggest that northern pintails are more discriminating about local wetland conditions, which might be related to food supply and nutrition (Krapu 1974, 1979; Krapu and Swanson 1975, 1977), than about nest sites.

Sensitivity Analysis

Identification of Influential Parameters

We used sensitivity analysis to determine which parameters and variables had the greatest influence on simulations. In general, identification of these parameters helps to suggest future field research to obtain accurate and precise estimates of sensitive parameters (Steinhorst et al. 1978; Frederick et al. 1987). Examination of parameters to which the model is or is not sensitive identifies a particular element of the real system that is important or, if the corresponding ecosystem parameter is previously known to be one to which the system is sensitive, it furnishes a validation of the model. Sensitivity analyses also help us to understand the modeled system and to revise and update a model in light of new information.

Specifically, the productivity component of the northern pintail model was sensitive to the same parameters and variables, varied individually and in interaction, as the model for the mallard. Nest success, yearling and adult body weight, and seasonal duckling and brood survival rates had the greatest influence on simulated results during sensitivity analysis. This similarity is a function of both the common model structure and similarity in the breeding ecologies of the two species.

Changes in simulated recruitment rates from decreasing and increasing nest success were highly nonlinear. An increase in nest success by >60% resulted in an increase of 207% in recruitment. Nest success of northern pintails at this level has been reported in even sparsely vegetated habitats (Duncan 1987b), perhaps, because nesting density is often low. Predators do not develop an efficient search response when prey density is low. Northern pintails may be especially vulnerable to intensified use of the landscape, including grazing or disturbance by tillage that decrease nest success. Habitat fragmentation concentrates nesting ducks and predators into smaller patches of habitat.

Body weight was another parameter small changes of which produced large changes in recruitment rate. Increases in yearling and adult body weights of 6.9% increased recruitment by over 2 times that amount (18%). We suggest that enhancement and protection of ephemeral and temporary wetlands, preferred by migrating and nesting northern pintails as feeding habitat, would substantially improve recruitment.

Survival rates of ducklings and broods are profound influences on recruitment. However, sensitivity analysis showed that changes in recruitment were nearly equivalent to the changes we modeled. We therefore predict that changes in ecological conditions affecting these parameters result in similar changes in recruitment in nature.

Model Testing and Application

Data that could be used to validate the northern pintail model were sparse, consequently, we were limited in the comparisons we could make. We would have preferred to have independent observations of population levels and important internal variables, such as nesting habitat preferences, for comparison with simulations (Frederick et al. 1987). But, we could compare simulations with only limited observed data to determine whether the model performed in a consistent and acceptable manner (Starfield and Bleloch 1986).

The northern pintail productivity model realistically simulated reasonable numbers of successful nests by breeding northern pintails in central North Dakota. However, simulated nest initiations were significantly greater than observed values during two of the three wetland conditions. We speculate that the simulated values may be closer to the unknown actual number of initiations than to the reported observed values. For example, the number of nest initiations observed in a field study is probably always below the number of actual initiations because nest searching techniques are imperfect (Miller and Johnson 1978). Nests are easily missed in dense habitat and nests destroyed or abandoned early in nesting are never found. Because there is no "nest-search" sampling in the model, nests are never "missed." We do not know the true nesting density in the field, but the modeling result suggests that biologists should be as cautious in interpretation of field data as in the interpretation of simulations (Starfield and Bleloch 1986).

We presented an example of how the northern pintail model could be useful for examining the effects of potential management. As expected, simulations indicated that predator barrier fences benefit northern pintails. However, the model does not help to address all related aspects of management. It does not reveal all possible problems of predator barrier fencing, such as the absence of safe exits for ducklings, lack of homing to fenced areas by northern pintails, or consequences of predators penetrating a fence. Managers still have to use their knowledge of the breeding ecology of northern pintails and the subtleties of proposed management to interpret predictions of the model.

Implications for Management and Research

The mallard and northern pintail productivity models can aid wildlife managers in choosing management options that increase productivity by these species and can aid biologists in directing future research. The mallard model has been used to compare management options for site-specific and regional applications (Johnson et al. 1987; Cowardin et al. 1988). The northern pintail model should be equally useful. Experimenting with the model is like asking questions about the similarity between intuitively predicted and actual productivity. For example, our simulated predator barrier fencing illustrated how the model can quantify the magnitude of an expected effect of management. The result forces us to see that other complexities in the system not under a manager's control tend to alter a consistent benefit. And it forces the biologist to look at the details that influence the results (Appendix B).

Interest in examining the effects of different land-use practices on attracting breeding hens and improving recruitment is high among waterfowl managers. For evaluations of simulated effects of land-use practices, managers must be aware that benefits from independent management are not additive (Cowardin et al. 1988). For example, if recruits per hectare of cover from several different land uses are added, productivity is overestimated because no adjustment is made for competition among the land-use practices.

Furthermore, we did not alter the functions in the mallard model that determine the settling rate of pairs. The ecology and biology of the northern pintail suggest recruitment is very sensitive to modifications in that part of the modeling system. The northern pintail model, like the mallard model, is best suited for evaluating availability and modifications of habitat for northern pintails in specific areas. An improved model that incorporates empirically derived functions on settling and facilitates evaluation of recruitment at the landscape level is needed.

Starfield and Bleloch (1986) commented that, "The purpose of building models is not to mimic nature but to enable one to think usefully about a problem." Although the northern pintail and mallard models may be considered predictive models, it is important not to focus on the truth or reality of the models but to consider their strengths and weaknesses and to be aware of the range of conditions over which they are useful (Caswell 1976). Modeling and field validation are continully interacting processes (Mankin et al. 1975), and we urge biologists to gather new and pertinent data on the ecology of northern pintails that can be used to improve the current model.

As many modelers have recognized, "field biologists are often suitably suspicious of computer models but have unlimited faith in what they have measured" (Starfield and Bleloch 1986:88). We argue that often this great reliance on imperfect field data stifled biologists' ability to think novelly about ecological systems. Through this modeling, we synthesized knowledge about the breeding biology of the northern pintail, identified necessary research, and developed a useful tool for examining and comparing alternative management of habitat. Biologists and modelers should continue to work together to design further research and management of northern pintails.

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Appendix A. Default Values in the Input File INPUT.PIN

Value	Variable or parameter	Description
31.0	H	Hatch time in days
-5.0	INSTAGE	Scaling factor
23.0	INCTIME	Incubation time in days
2560.0	FOURSQMI	Four square mile acreage
675.0	MINWTN	Minimum weight in grams
3.0	INA	Scaling factor
800.0	WTBAR(1)	Average weight of immature arrivals (grams)
900.0	WTBAR(2)	Average weight of adult arrivals (grams)
60.0	WTSTD(1)	SD average weights of immatures
60.0	WTSTD(2)	SD average weights of adults
450.0	MINWTELP	Minimum weight used in egg-laying potential function
15.0	SCALE	Scaling factor
15.43	CLUA	Regression coefficient for clutch function
0.0331	CLUB	Regression coefficient for clutch function
0.89	CLUDEL	Scaling factor
4.0	NESTLESS	Days before renesting is possible
0.97	ROBELA	Regression coefficient Nest Site Selection (NSS) function
0.28	ROBELB	Regression coefficient NSS function
2.23	ROBLMIN	Regression coefficient NSS function
0.50	SUCCBRK	Scaling factor
0.25	SUCSCALE	Scaling factor
1125.0	MAXWT	Maximum weight (grams) used in weight function
7.5	LOSSLAY	Weight (grams) lost per day during egg laying
1.5	LOSSINC	Weight (grams) lost per day during incubation
0.587	ASRAF	Annual survival rate of adult females
0.555	ASRIF	Annual survival rate of immature females
0.719	SSRAF	Summer survival rate of adult females

Appendix B. Northern Pintail Productivity Model Sample Input and Output

Input parameters and variables for the pintail productivity model [Facsimile of computer screen with entered data.]

```
 Title.......:  STANDARD.BENCH
 Habitat File:  \MM\HAB\STANDARD.HAB
 Random Number Generator Seed: 84489

------------------INPUT PARAMETERS-----------------

 Seasonal brood survival rate=  0.7400
 Seasonal duckling survival rate= 0.5400
 Daily hen mortality rate= 0.0010
 Hen mortality rate given nest is destroyed= 0.0600

 This run uses 1000 birds
 of which 400 are young (sy) and 600 are adult (asy)

 The actual breeding population is 1000 pairs.

 This run does not use homing.

 Water conditions are:
  Day
12345678910111213141516171819202122232425262728293031
Mar                8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8
Apr
777777777 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7
May
777777777 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7
Jun
666666666 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6
Jul
666666666 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6 6
Aug
555555555 5 5 5 5 5 5 5 5 5 5 5 5

There are 17 habitats on map STANDARD CENTRAL
1.  CROPLANDFALLPLGR Availability=   0.229600
 Robel Changes: 125 0.01 159 5.00 18325.00 22025.00 22125.00
 Dmr changes: 114.0651 115.9999 116.2500 125.1000 164.0630
2.  CROPLANDFALLPLRO Availability=   0.066800
 Robel Changes: 170 0.01 22417.50 24022.50 24122.50 24222.50
 Dmr changes: 160.0651 161.9999 162.2500 170.1000 195.9999
3.  CROPLANDSTUBLGRN Availability=   0.077000
 Robel Changes: 110 3.00 111 0.01 140 0.01 163 5.00 18625.00
```

```
 Dmr changes: 110.0651 111.9999 112.2500 140.1000 164.0630
4.  CROPLANDSTUBROCR Availability=   0.022400
 Robel Changes: 100 2.50 111 0.01 170 0.01 24022.50 24122.50
 Dmr changes: 110.0651 111.9999 112.2500 170.1000 194.9999
5.  CROPLANDSUMRFALO Availability=   0.091600
 Robel Changes: 60 1.50 152 3.50 153 0.01 168 0.01 220 0.01
 Dmr changes: 152.0651 153.9999 168.2500 178.2500 179.0651
6.  GRASLAND         Availability=   0.245700
 Robel Changes: 121 8.00 14513.00 22013.00 22113.00 22213.00
 Dmr changes: 121.0535 122.0535 123.0535 124.0535 124.0535
7.  GRASLANDWILDLIFE Availability=   0.032600
 Robel Changes: 121 8.00 14513.00 22013.00 22113.00 22213.00
 Dmr changes: 121.0470 122.0470 123.0470 124.0470 124.0470
8.  HAYLAND          Availability=   0.030000
 Robel Changes: 110 8.00 17135.00 172 5.00 20120.00 202 5.00
 Dmr changes: 100.0651 145.0260 171.9000 172.1590 178.0400
9.  OTHER            Availability=   0.013300
 Robel Changes: 6017.00 14522.00 22022.00 22122.00 22222.00
 Dmr changes: 60.0680 220.0680 221.0680 222.0680 223.0680
10. PLNTCOVR         Availability=   0.019900
 Robel Changes: 10515.00 15040.00 16040.00 17040.00 18040.00
 Dmr changes: 60.0490 100.0490 110.0490 120.0490 130.0490
11. R OF WAY         Availability=   0.012100
 Robel Changes: 105 9.00 15220.00 18120.00 182 5.00 222 5.00
 Dmr changes: 105.0600 182.5000 183.0600 223.0600 224.0600
12. SCRBLAND         Availability=   0.000700
 Robel Changes: 6017.00 14522.00 22022.00 22122.00 22222.00
 Dmr changes: 60.0680 220.0680 221.0680 222.0680 223.0680
13. TEMP.WETLAND     Availability=   0.003600
 Robel Changes: 6012.00 14517.00 22017.00 22117.00 22217.00
 Dmr changes: 60.0700 220.0700 221.0700 222.0700 223.0700
14. SEAS.WETLAND     Availability=   0.025500
 Robel Changes: 6012.00 14517.00 22017.00 22117.00 22217.00
 Dmr changes: 60.0700 220.0700 221.0700 222.0700 223.0700
15. SEMI.WETLAND     Availability=   0.019100
 Robel Changes: 6012.00 14517.00 22017.00 22117.00 22217.00
 Dmr changes: 60.0700 220.0700 221.0700 222.0700 223.0700
16. PERM.WETLAND     Availability=   0.002100
 Robel Changes: 6012.00 14517.00 22017.00 22117.00 22217.00
 Dmr changes: 60.0700 220.0700 221.0700 222.0700 223.0700
17. WOODLAND         Availability=   0.011800
 Robel Changes: 6017.00 14522.00 22022.00 22122.00 22222.00
 Dmr changes: 60.0680 220.0680 221.0680 222.0680 223.0680
 Birds enter the area beginning on day    91
  and ending on day   131

Output from pintail productivity model
----------------MODEL RESULTS---------------------

 Nests per hen =      1.9740
 Hatch rate =      0.1348
 Hen success rate =      0.2660
 Estimated hen success rate(Cowardin and Johnson 1979)=0.2850
 Average clutch size=      7.9474
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 Summer mortality rate of hens (182 days ending 30 Sept.)=0.2669
 Recruitment rate = 0.4345 (Female recruits / Hens in spring)

 Age ratio of females in the fall=  0.5927
 Age ratio of males in fall      =  0.5213
 Age ratio in the fall           =  0.5547 (Recruits / Breeders in the fall)
 Proportional population change index = 0.9339

 In the nesting population, 400 of 1000 hens are yearlings.

Habitat Nest w/  Initiated Nest    Total Percent Density
        hatched
#       Clutches Nests    Success  Recru.  Recruits  Index
1.      13        206     0.0631    34       3.9125   0.3505
2.       2         46     0.0435     8       0.9206   0.2690
3.       4         88     0.0455    10       1.1507   0.4464
4.       0         12     0.0000     0       0.0000   0.2093
5.       5        116     0.0431    19       2.1864   0.4947
6.      13        770     0.1727   441      50.748    1.2242
7.      26        104     0.2500    87      10.0115   1.2462
8.      18        119     0.1513    59       6.7894   1.5495
9.       2         73     0.0274     8       0.9206   2.1440
10.     27         96     0.2812    93      10.702    1.8844
11.      4         44     0.0909    12       1.3809   1.4205
12.      0          6     0.0000     0       0.0000   3.3482
13.      1         11     0.0909     2       0.2301   1.1936
14.     12        135     0.0889    40       4.6030   2.0680
15.      9         67     0.1343    27       3.1070   1.3703
16.      0          8     0.0000     0       0.0000   1.4881
17.     10         73     0.1370    29       3.3372   2.4166
        ___      ____             ___
Total  266       1974             869
```

A list of current *Biological Reports* follows.

1. The Ecology of Humboldt Bay, California: An Estuarine Profile, by Roger A. Barnhart, Milton J. Boyd, and John E. Pequegnat. 1992. 121 pp.
2. Fenvalerate Hazards to Fish, Wildlife, and Invertebrates: A Synoptic Review, by Ronald Eisler. 1992. 43 pp.
3. An Evaluation of Regression Methods to Estimate Nutritional Condition of Canvasbacks and Other Water Birds, by Donald W. Sparling, Jeb A. Barzen, James R. Lovvorn, and Jerome R. Serie. 1992. 11 pp.
4. Diflubenzuron Hazards to Fish, Wildlife, and Invertebrates: A Synoptic Review, by Ronald Eisler. 1992. 36 pp.
5. Vole Management in Fruit Orchards, by Mark E. Tobin and Milo E. Richmond. 1993. 18 pp.
6. Ecology of Band-tailed Pigeons in Oregon, by Robert L. Jarvis and Michael F. Passmore. 1992. 38 pp.

TAKE PRIDE

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U.S. DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

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END

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