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Relating climatological patterns to wetland conditions and wood duck production in the Southeastern Atlantic Coastal Plain

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Abstract Efforts to index annual population size and recruitment of the wood duck (*Aix sponsa*) on a geographic scale sufficiently large to be useful in managing this species have met with mixed results. A general relationship between climatic factors and wood duck production has been the most economical and promising approach, particularly in the Southeast, though further refinement or understanding of factors mediating the relationship has been lacking. Development of climate-based models that predict wetland hydrologic conditions during the wood duck breeding season can be a useful step to index recruitment and may provide useful insights into population dynamics. In this study, I illustrate the concept's potential by developing a robust deterministic model of wetland water conditions on the 78,000-ha Savannah River Site (SRS) in west-central South Carolina over a 13-year period (1984–1996). During 6 years (1982–1987) when more than 90% of all hatched ducklings were marked before leaving nest boxes on the SRS, production of female ducklings was related positively to estimated female recruitment into the population the following year (combined breeding and nonbreeding yearling population segments; $r_S=0.90$, $P=0.015$), indicating that duckling production was a reasonable proxy for recruitment. The return of females initially marked as ducklings suggested that deferred yearling breeding was highest in dry years that were preceded by wetter years, thereby contributing to lower productivity in such years. Annual wetland condition indices were related to 15 years of duckling production from SRS nest boxes. Productivity of wood ducks was positively associated with wetland hydrologic conditions. In wet years, an average of 9.8 ± 0.7 (SE) ducklings was produced by each female in the breeding population, but only 8.6 ± 0.5 (SE) ducklings/female were produced in dry years. Greater productivity in wet years was attributed in part to longer breeding seasons, which allowed more females in the population to produce second broods, and to reduced predation rates. Additional insights gained through application of the method are discussed.

Key words *Aix sponsa*, Carolina bay, climate, hydrologic condition, South Carolina, Southeastern Atlantic Coastal Plain, wetland, wood duck

Among the difficult challenges for managers of continental waterfowl populations has been the development of techniques to monitor the annual status of wood duck (*Aix sponsa*) populations (Bellrose and Holm 1994). Wood ducks rank among the top 4 duck species harvested in the United States (Martin and Padding 1999), but are difficult to census because they generally occupy a greater diversity of habitats than other waterfowl. Attempts to develop adequate indices of production for this

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species have not been considered successful (e.g., Hein and Haugen 1966, Brakhage 1990, Moser and Graber 1990). Moser and Graber (1990), for example, attempted to index wood duck production in Indiana and Missouri by using stream brood surveys. When brood survey data were compared to independent production indices (e.g., age-ratio estimates from the United States Fish and Wildlife Service's Parts Collection Survey) they found little potential for accurately predicting wood duck production. Using nest-box programs to monitor wood duck populations is more promising (Hepp et al. 1987, Zicus and Hennes 1987, Brakhage 1990, but see Brakhage and Eggeman 1998), but the manpower and costs required to operate large-scale nest-box programs can be prohibitive. Despite these shortcomings, the fragmented nature of wood duck populations (Bellrose and Holm 1994) and strong female-biased philopatry to natal (Hepp et al. 1989) and nesting (Hepp et al. 1987, Hepp and Kennamer 1992) areas suggest the potential for successful management of the species at the subpopulation level. Bowers and Martin (1975) demonstrated differences among population units in harvest characteristics and survival, further supporting the possibility for special regulation on a regional basis. Trost (1990) found a negative relationship between survival and band-recovery rates (an index to harvest rates), suggesting an additive effect of hunting to overall mortality and thus the need to exercise caution when regulating harvest of this species.

One promising approach to index wood duck production or recruitment has been use of climatological data (Moser and Graber 1990, Kelley 1997). In Missouri, annual precipitation totals ($May_{(yr\ i-1)}$–$April_{(yr\ i)}$) correlated positively with age ratios in the harvest (Moser and Graber 1990). Furthermore, as part of the Wood Duck Population Monitoring Initiative (Kelley 1997), predictive models based on precipitation and temperature data were generated for multiple levels of geographic scale, ranging from the entire eastern United States to various subpopulations. The model accounting for the most variation (75%) in fall population age ratios was for North Carolina and South Carolina combined.

Development of climate-based models that predict wetland hydrologic conditions during the breeding season should be considered as a potentially useful step toward refining estimates of annual production and recruitment for wood duck subpopulations, particularly those in the southern portion of the Atlantic Flyway. One advantage gained by this approach is the possible identification of factors mediating relationships between climate and wood duck recruitment. In this study, I first used precipitation and evaporation data from a National Weather Service station to develop a deterministic model of wetland hydrologic conditions on the 78,000-ha Savannah River Site (SRS) in west-central South Carolina over a 13-year period. I then related breeding characteristics and productivity of a wood duck population using nest boxes on the SRS to annual indices of wetland conditions on the SRS.

Study area

The SRS, a facility of the United States Department of Energy, lies in the Upper Coastal Plain Physiographic Province and occupies portions of Aiken,

A field technician inspects the contents of a wood duck nest box at Upper Three Runs Creek, a natural blackwater stream on the Savannah River Site, during a dry year. In wet years, nest boxes at the height shown here would be inundated periodically.

An aerial view of a Carolina bay on the Savannah River Site shows open-water, herbaceous-marsh, and scrub-shrub habitats that typify many bays. Photo by David E. Scott.

Barnwell, and Allendale counties in west-central South Carolina (White and Gaines 2000). About 30 km of the southwestern boundary of the SRS is formed by the Savannah River and its associated 3,800-ha swamp forest. Savannah River flow rates are regulated primarily through a series of 3 United States Army Corps of Engineers reservoirs upstream from the SRS, the nearest of which (Lake J. Strom Thurmond) is approximately 56 km (105 river km) from the SRS. Major community types of the SRS include old fields, sandhills, upland hardwood and pine forests, bottomland hardwood and swamp forests, and freshwater streams, ponds, and wetlands, including nearly 200 Carolina bays (Schalles et al. 1989, Workman and McLeod 1990). Carolina bays are isolated elliptical depression wetlands (50 m–8 km in length) that function much like the northern prairie potholes. Hydrologic regimes of Carolina bays are controlled largely by precipitation and evapotranspiration, although interactions with the water table also can be important (Lide et al. 1995). Vegetative communities within Carolina bays include open water aquatic macrophytes, herbaceous marsh, and wetland shrubs and trees. Many Carolina bays lack fish assemblages because of their periodic drying, and so diversity of invertebrates is often high (Taylor et al. 1999). Estimates place the number of Carolina bays at between 10,000 and 20,000 in the Southeast, but they are found in greatest densities in the Carolinas (Richardson and Gibbons 1993).

The general climate of the SRS is classified as humid subtropical, with oceanic influences (Hunter 1990). Winter weather is relatively short and mild, dominated by large continental air masses that bring rainfall of relatively low intensity but long duration, often lasting entire days. Summers are long and dominated by warm, moist, unstable air masses originating from the Gulf of Mexico. Precipitation primarily occurs during isolated afternoon and evening thunderstorms, and hurricanes during late summer or fall also may contribute substantially to total annual precipitation. Summer weather is cyclically affected by the western extension of the semi-permanent subtropical Atlantic anticyclone pressure system (i.e., the "Bermuda high"; Hunter 1990). When the Bermuda high shifts westward of its average position, the area generally experiences extremely dry conditions, while extreme wet conditions persist when the pressure system is located east of its average position (Stahle and Cleaveland 1992). On a scale of 3 to 5 years, occurrences of the El Niño-Southern Oscillation (ENSO) in the tropical Pacific have been shown to result in above-normal precipitation in the southeastern United States (Ropelewski and Halpert 1986).

Methods

From 1984 through 1996, surface water levels (nearest 0.5 cm) were monitored approximately weekly during the wood duck breeding season (February–June) at 9 wetland sites on the SRS as duck boxes at those sites and elsewhere (approx. 130 total nest boxes) were checked for nesting activity. Six of the 9 study sites are considered to be Carolina bays, ranging in size from <0.2 ha to 11.2 ha. Two other palustrine wetlands (Sites A and U), though not considered true Carolina bays, are hydrologically and floristically similar to Carolina bays found on the SRS. The smallest wetland study sites are considered seasonal wetlands that tend to dry in most years by mid-to-late summer and may remain dry over a period of one or more years during prolonged drought conditions. Other, larger wetland sites are semi-permanent and rarely dry completely, and then only briefly. Water level also was monitored at Upper Three Runs Creek (Site Q), which is one of 5 primary streams draining the SRS and is considered representative of undisturbed blackwater streams of the Upper Coastal Plain (Workman and McLeod 1990). Upper Three Runs Creek, a fifth-order stream at its confluence with the Savannah River, is a United States Geological Survey National Hydrologic Benchmark stream and is noted for having the greatest aquatic insect species richness of any stream in the Western Hemisphere (Voelz and McArthur 2000).

While checking nest boxes, I estimated dates of nest initiation and counted and individually labeled eggs. I captured and banded females, and determined nest fates. During 1982–1987, 2,945 of 3,232 (91%) ducklings leaving nest boxes were web-tagged with serially labeled #1 monel fish-fingerling tags and the annual marking effort was relatively constant (range: 88–95%). In 1988–1996, allantoic membranes (one/duckling) remaining in nests following duckling exodus were counted to provide hatched duckling numbers. Additional methodological details are given in Hepp et al. (1989) and Hepp and Kennamer (1992, 1993). Size of the breeding female population using nest boxes on the SRS was estimated annually (1982–1995) from capture–recapture data using the Jolly–Seber (J–S) capture–recapture model for open populations (Hepp et al. 1987, Kennamer and Hepp 2000). Each year, most successfully nesting females were captured and identified, thus J–S capture probabilities during the study were relatively high (1983–1994: $\bar{x}$=0.895, range= 0.789–1.00; Kennamer and Hepp 2000:Table 1).

Generalization of wetland hydrologic conditions

In certain months of the breeding season in some years, particularly June, there were fewer occasions when water levels were measured, usually coinciding with declines in number of new nest starts toward the end of breeding. Conversely, during peak months of breeding activity (i.e., March, April), water levels were monitored more frequently. To ultimately give equal weighting to wetland hydrologic conditions in all months of the breeding season, I first averaged the available water levels for

Table 1. Hydrologic condition ranks[a] for wetlands of the Savannah River Site, South Carolina, containing wood duck nest boxes, 1984–1996.

	Wetland study sites										
Year	A	B	C	D	E	N	Q	T	U	Rank-sums[b]	
1984	12	9	10	7	11	8	10.5	11	10	88.5	Wet[c]
1985	4	6	5	6	3	6	4	3	3	40.0	Dry
1986	2	1	1	4	3	3	1	4	4	23.0	Dry
1987	11	10	9	5	10	10	6	8	9	78.0	Normal
1988	1	2	3	1	3	1	2	1	2	16.0	Dry
1989	6	5	2	2	3	2	3	2	1	26.0	Dry
1990	5	3	4	3	3	4	9	5	5	41.0	Dry
1991	13	11	12	9	12	13	10.5	12	13	105.5	Wet
1992	8	8	8	12	8	9	5	9	12	79.0	Wet
1993	10	13	13	13	13	12	12	13	11	110.0	Wet
1994	7	7	6	11	7	7	7	7	7.5	66.5	Normal
1995	9	12	11	10	9	11	8	10	6	86.0	Wet
1996	3	4	7	8	6	5	13	6	7.5	59.5	Normal

[a] Years were ranked from least-to-greatest mean wetland water level within each wetland study site; ranks were divided equally among ties.

[b] Ranks were summed across wetland study sites to produce a generalized hydrologic condition of Savannah River Site wetlands each year.

[c] The range of rank-sums was divided into thirds yielding the categorical divisions of wetland hydrologic conditions: Dry (range: 16.0–47.4, $\bar{x}$ = 29.2), Normal (range: 47.5–78.5, $\bar{x}$ = 68.0), Wet (range: 78.6–110, $\bar{x}$ = 93.8).

In wet years, more yearling nesting and second broods by wood duck females contributed to greater population productivity.

each wetland by month (i.e., February–June) within 1984 through 1996. I then averaged monthly means within years for each wetland, considering this average as representing the overall hydrologic condition of the wetland during the breeding season of a given year.

Within each study site, I ranked years from least-to-greatest average wetland water levels; when average wetland water levels were the same for 2 or more years (i.e., ties encountered during the ranking process), the ranks were divided equally among ties. Ranks then were summed across study sites for each year to produce a value that generalized the hydrologic condition of wetlands on the SRS in that year (range: 16.0–110.0, Table 1).

Climatological data

I obtained climatological data from a National Weather Service cooperative station (i.e., Blackville 3 West, Barnwell County, South Carolina, USA) located approximately 20 km east of the SRS (nearest station providing necessary data). Climatological data included total monthly precipitation (nearest 0.01 inch) and total monthly evaporation (nearest 0.01 inch) from October 1982 through June 1996 (i.e., 165 months). For most months (n = 121), total evaporation was necessarily estimated because of missing data from some number of days during a given month. If number of missing data days in a month was from one to 7 (n = 110 months), the National Weather Service provided an adjusted figure for total evaporation. In this case, the total recorded evaporation amount was divided by number of recorded days, then multiplied by number of days in the month. When evaporation data were not available for >7 days during a given month, the National Weather Service provided no entry for total evaporation for that month (n = 11 months). In this case, I used a total evaporation estimate that was the average of non-missing evaporation totals of the appropriate month in the remaining years. I was justified in using this method because monthly evaporation totals in the data followed a well-defined sinusoidal pattern, with levels of evaporation increasing through spring and summer and declining through fall and winter. I converted all precipitation and evaporation data to metric units (cm) for analyses.

Modeling wetland conditions with climatological data

I determined various sequential accumulations of monthly rainfall and monthly evaporation with the restriction that no data from months later than June of the current year could be used to predict the current year's wetland conditions. Such a restriction assured that in future implementations of the methodology, sufficient time would be available to produce indices of wood duck production or recruitment before harvest regulations are established for the upcoming hunting season. Thus, climatological data from $\text{July}_{(\text{yr } i-1)}$ through $\text{June}_{(\text{yr } i)}$ were the source data to construct variables to associate with wetland hydrologic conditions during the breeding period of wood ducks.

I conducted stepwise regressions (PROC STEPWISE, SAS Institute 1989) with wetland hydrologic condition (i.e., rank-sums; Table 1) as the dependent variable. I limited model construction to only 4 climatological metrics as independent variables in a successful model: 1) cumulative precipitation over some interval (see below), 2) cumulative evaporation over some interval (see below), 3) cumulative precipitation minus cumulative evaporation (Water $\text{Balance}_{(\text{yr } i)}$), and 4) the previous year's water balance. I did not consider interactive effects of the climatological metrics in the modeling effort. A series of various sequential accumulations of precipitation and evaporation data within the $\text{July}_{(\text{yr } i-1)}$ through $\text{June}_{(\text{yr } i)}$ period were constructed and subjected to stepwise regression procedures to determine the intervals that produced a model with the greatest precision (r^2). I verified parsimony in model construction by using Mallows' C_p criterion (Mallows 1973), where values of C_p approaching, but less than, total number of model parameters indicate unbiased parameter estimates and model parsimony.

Wetland conditions and wood duck reproductive characteristics

Efforts to associate climatic variables and wood duck recruitment to use in harvest management strategies typically have used recruitment information from the fall period so that results would relate directly to the season of interest. Because I lacked estimates of fall SRS wood duck recruitment, I instead used measures of duckling production. Such a substitution assumes that neonate production is a good index to recruitment at some later point in time, but few studies have demonstrated the relationship for local breeding populations of birds (Weatherhead and Dufour 2000). Hepp et al. (1989) found that on the SRS, the rate of yearling recruitment into the breeding wood duck population averaged 5.2%, with no detection of yearly differences, and that hatch date did not affect the probability of being recruited. Thus, a strong relationship was suggested between duckling production and recruitment for wood ducks on the SRS. To confirm that speculation, I used data from 6 breeding seasons on the SRS when 2,945 day-old ducklings were marked individually before leaving the nest and looked at the return of females to breed in years subsequent to their marking. Duckling sexes were known in 2 years, and I assumed a 50:50 duckling sex ratio in 4 other years (Hepp et al. 1989). Using information in Hepp et al. (1989:Table 1) and Kennamer and Hepp (2000:Table 2), I estimated the annual number of female recruits at one year of age for the period 1983–1988. Although most female wood ducks breed as yearlings, some may defer breeding until their second or later year of life (Heusmann 1975, Kennamer and Hepp 2000). As a result, some individuals, while alive as yearlings or older birds, did not survive to initiate breeding in succeeding years and were never captured or identified during nest box checks. I therefore adjusted annual known numbers of yearling female recruits for unencountered recruit losses based on age-specific return rates as Heusmann (1975) did. I first adjusted return rates to account for annual variation in capture probabilities, thus producing survival rate estimates. Estimated survival averaged 0.712±0.058 and 0.767±0.051 for females between years 1 and 2, and between years 2 and 3, respectively. Only one web-tagged female was encountered for the first time beyond the third year of life; in calculations of unencountered recruit losses beyond the third year (for the 1987 female duckling cohort) I therefore simply used the same estimated survival rate as that for between years 2 and 3 (0.668, 1987 duckling cohort). I examined the relationship between annual numbers of marked female ducklings and estimated adult female recruits the following year using Spearman's Rank Correlation (r_S, PROC CORR, SAS Institute 1989).

To examine whether annual SRS-wide indices of wetland conditions related to wood duck reproductive characteristics (e.g., ducklings/successful nest and ducklings/female), I first divided the range of rank-sums into thirds (Table 1), yielding a categorical division of wetland conditions: dry (range = 16.0–47.4, $\bar{x}$ = 29.2), normal (range = 47.5–78.5, $\bar{x}$ = 68.0), wet (range = 78.6–110.0, $\bar{x}$ = 93.8). Means ($\bar{x}$) and standard errors (SE) of wood duck production and other breeding season characteristics are presented relative to these classifications of wetland hydrologic conditions. I also related wetland condition indices to ducklings produced/breeding female with Spearman's Rank Correlation (r_S, PROC CORR, SAS Institute 1989).

Wood duck reproductive characteristics were available for 1982 and 1983 in addition to 1984 through 1996, but water level data were not collected in those first 2 years. Using climatological data from the appropriate time periods, I indexed wetland conditions for those 2 additional years using Equation 1 (see Results). The J-S parameter estimate of female population size was nonestimable in 1996, the last year of the study, and thus was not available to determine ducklings produced/breeding female in that year. For all tests, levels of significance were accepted at $\alpha \leq 0.05$.

Results

Modeling wetland conditions with climatological data

Within the July–June range of climatological data available for constructing precipitation and evaporation accumulations and water balances, I found that precipitation totals from $\text{October}_{(\text{yr } i-1)}$ through $\text{May}_{(\text{yr } i)}$ and evaporation totals from $\text{February}_{(\text{yr } i)}$ through $\text{June}_{(\text{yr } i)}$ maximized the explanatory power of the stepwise regression model described below.

The most precise deterministic model ($r^2 = 0.89$, $P \leq 0.001$) included an annual water balance that related closely (partial $r^2 = 0.74$, $P \leq 0.001$) to wetland hydrologic conditions on the SRS from February through June. Inclusion of the previous year's

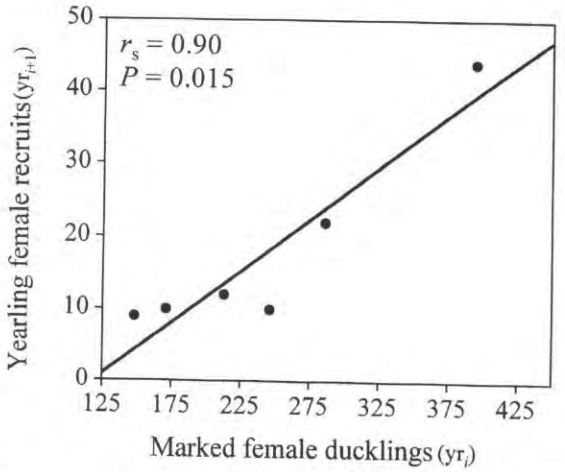

Figure 1. Estimated numbers of yearling female wood ducks (breeding and nonbreeding) recruited into the Savannah River Site, South Carolina, population in $year_{(i+1)}$ relative to size of female duckling cohorts marked in $year_{(i)}$, for years 1982–1987.

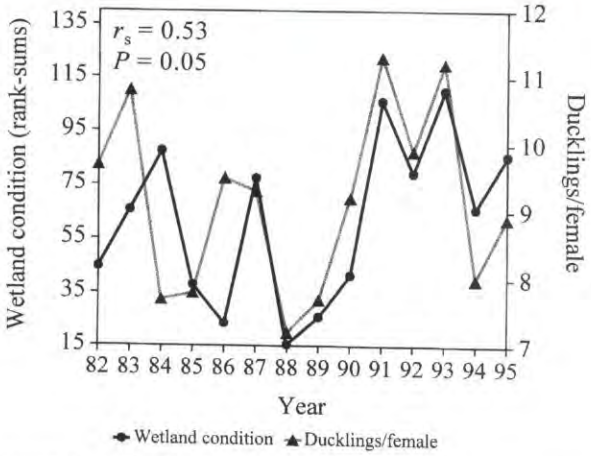

Figure 2. Wetland hydrologic condition indices (rank-sums, see Table 1) and wood duck ducklings produced per breeding female in the population using nest boxes on the Savannah River Site, South Carolina, 1982–1995.

water balance provided additional information that improved predictability of the model (partial $r^2 = 0.15$, $P = 0.004$). The precipitation and evaporation accumulation variables, by themselves, made no additional explanatory contributions and did not meet the default $P \leq 0.10$ significance level to enter the model. The 3-parameter model (including the intercept term) also was the most parsimonious model ($C_p = 2.05$). The equation describing wetland hydrologic conditions (WHC; i.e., rank-sums of Table 1) on the SRS during the wood duck breeding season was:

$$\text{WHC} = 61.25 + 1.21(\text{Water Balance}_{(\text{yr } i)}) + 0.51(\text{Water Balance}_{(\text{yr } i-1)}). \quad (1)$$

Standard errors of the parameter estimates were 3.21, 0.136, and 0.138 for the intercept term, Water $\text{Balance}_{(\text{yr } i)}$, and Water $\text{Balance}_{(\text{yr } i-1)}$, respectively.

Wetland conditions and wood duck reproductive characteristics

Estimated numbers of female wood ducks that were recruited into the population (breeding and nonbreeding) in $year_{(i+1)}$ were very correlated with size of the female duckling cohort marked in $year_{(i)}$ ($r_S = 0.90$, $P = 0.015$, Figure 1), indicating that annual duckling production was a reasonable proxy for recruitment that was not known in all years. When estimating one-year-old female recruits, I adjusted known breeding yearling females from web-tag returns to include web-tagged females not known to have nested as yearlings and unencountered recruit losses that presumably occurred between the first and third years of life (i.e., deferred yearling breeders). Estimated percentages of yearlings that deferred breeding ranged from 0% to 66.7% annually ($\bar{x} = 25.3 \pm 11.9\%$) and was greatest when dry wetland conditions prevailed (i.e., 1985: 66.7% and 1988: 56.8%), thus contributing to reduced productivity of the population in dry years.

In all years, regardless of wetland hydrologic conditions, production averaged just over 11 ducklings/successful nest (Table 2). In wet years, however, the average number of ducklings produced/female in the population tended to be higher than in dry years (9.8 vs. 8.6, Table 2) and was related to generally longer breeding seasons in wetter years when more females in the population were able to produce second broods (Table 2). Furthermore, nest predation rates tended to be lower in wet and normal years than in dry years (Table 2). Per-female duckling production was positively correlated ($r_S = 0.53$, $P = 0.05$, Figure 2) with indices of wetland hydrologic condition (rank-sums).

Discussion

Modeling wetland conditions with climatological data

Previous attempts at climate-based modeling of wood duck populations have relied on relating climatic variables directly to indices of wood duck production such as age ratios in the fall harvest

Table 2. Wood duck breeding season characteristic averages (SE) for years when wetlands were dry (n = 6 yrs), normal (n = 4 yrs), and wet (n = 5 yrs) on the Savannah River Site, 1982–1996.

	Wetland conditions		
Breeding characteristic	Dry	Normal	Wet
Ducklings/successful nest[a]	11.3 (0.35)	11.4 (0.24)	11.4 (0.35)
Ducklings/female[b]	8.6 (0.47)	9.3 (0.84)	9.8 (0.67)
Second broods (%)[c]	4.7 (2.99)	10.0 (2.98)	11.6 (2.99)
Season length (days)[d]	120 (11.0)	129 (6.76)	138 (6.95)
Predation (%)[e]	23.5 (3.20)	17.6 (4.94)	16.6 (5.27)

[a] Ratio of total ducklings hatched each year to total successful nests each year.

[b] Ratio of total ducklings hatched each year to the Jolly–Seber estimated female population size each year. Female population size was non-estimable in 1996, a normal year, so sample size in the normal wetland category for ducklings/female was 3 years rather than 4 years as for the other breeding characteristics.

[c] Percentage of all successful nests each year that were known second broods.

[d] Annual period from the start of the first nest to the start of the last nest.

[e] Percentage of nest starts each year that ended in predation.

(Moser and Graber 1990, Kelley 1997). Such age ratios generally are determined from parts (e.g., wing, rectrices) surveys conducted during special early season harvests, prior to potentially confounding migratory movements, and are adjusted for differential harvest vulnerabilities among the age and sex classes. While conditions within wetlands and their associated food resources have long been recognized to be of prime importance to breeding waterfowl (e.g., Johnsgard 1956), including the wood duck (Drobney and Fredrickson 1979), simply relating climatic variables to such production indices may not adequately address that underlying assumption, thus making it difficult to sort out other potential mediating influences on recruitment. An alternative approach to predict annual production of wood ducks would be first to optimally account for variation in the hydrologic condition of wetlands in the areas of interest and then relate wetland condition indices to known wood duck production or indices such as the fall population age ratios. In this study, the successful relating of climatic and wetland hydrologic conditions at the scale of the SRS (78,000 ha) suggests a degree of regional robustness and provides encouragement that development of similar strong relationships may be possible for larger regions, such as the states of South Carolina and North Carolina and possibly the entire southern portion of the Atlantic Flyway.

Most water level data used in this study were collected from lentic palustrine wetlands (primarily Carolina bays). However, producing generalizations of wetland hydrologic conditions over a relatively large geographic area using palustrine and riparian habitat types is important for 2 reasons. First, lentic palustrine wetlands such as Carolina bays are very sensitive to precipitation and evapotranspiration (Lide et al. 1995), so their use enhances the likelihood for successful development of climate-based wetland condition models. Furthermore, the high-density occurrence of Carolina bay wetlands in the Southeastern Atlantic Coastal Plain, particularly in the Carolinas, suggests that these wetlands probably provide extensive breeding habitats for wood ducks. As such, the relatively high level of success achieved in the climate-based wood duck recruitment modeling by Kelley (1997) for North and South Carolina combined may be attributable to the importance of these unique Southeastern wetlands to breeding wood ducks. Second, forested riparian habitats are thought to be the most important habitats for wood ducks in the southeastern United States (Bellrose and Holm 1994), so the need to assess conditions in that habitat type is essential. It is particularly notable that annual variation in hydrologic conditions at Upper Three Runs Creek (Site Q), the only forested riparian habitat included in the study, was comparable to that found in the other wetlands (Table 1). This finding may be ascribed to evapotranspiration patterns in addition to those of rainfall being recognized as critical determinants of flood pulse patterns in unregulated Southeastern river systems (Benke et al. 2000). Thus, while larger rivers like the Savannah may have altered flow regimes because of anthropogenic intervention, largely unregulated tributaries such as Upper Three Runs Creek may still function naturally to varying degrees.

In the model relating climatic and wetland hydrologic conditions, not only was the climatological water balance from the months immediately preceding and during the current breeding season important to predict wetland conditions, but there also was a significant residual effect of climatic factors from the preceding year. From the coefficients in Equation 1, the ratio of the contribution of the current season's water balance to the preceding season's water balance was 2.37:1. Earlier efforts to index annual population size or recruitment of

wood ducks with climatological data did not consider the possible influence of more than a single season's climate conditions (Moser and Graber 1990, Kelley 1997). By first modeling wetland hydrologic conditions with climatological data as in this study, it was more intuitive to incorporate any potential importance of the preceding year's climatic conditions.

Wetland conditions and wood duck reproductive characteristics

Age at the time of first reproduction in waterfowl typically varies by only about one to 2 years, with larger-bodied geese and swans generally requiring longer to initiate breeding than smaller species (Rohwer 1992). Coulson (1984) suggested that some common eiders (*Somateria mollissima*) skipped breeding in years when survival potential was poor to maximize reproductive output over the entire life span. Individual birds likely use this same reproductive strategy when choosing age at which to initiate breeding (Wittenberger 1979, McNamara and Houston 1996). For female wood ducks, age at first reproduction generally varies from the first to third years (Heusmann 1975, Bellrose and Holm 1994, Kennamer and Hepp 2000). Estimated percentages of yearling females on the SRS that deferred breeding annually were variable, ranging from 0% to 66.7%. The highest levels of deferred yearling breeding coincided with 2 years (1985 and 1988) having dry wetland conditions, which is consistent with the notion that postponement of first reproduction in poor years may convey survival benefits (and thus increased future reproductive potential) to some individuals. In drought years, tendencies also were shown for younger prairie-nesting ducks (Afton 1984, Serie et al. 1992) and arctic-nesting geese (Davies and Cooke 1983) to defer breeding. However, in 1986, the second driest among all years of this study, no yearling females deferred breeding. The common characteristic of the 2 drought years with high levels of deferred breeding was that wetland conditions in the preceding (i.e., hatch) year for both yearling cohorts were wetter than in the year when a decision about breeding was ultimately made. In contrast, the 1986 yearling cohort originally had hatched in a year that also was dry. In other words, there essentially was no change in wetland conditions between hatching and yearling years for the 1986 female cohort. These findings suggest that inexperience may contribute to diminished foraging efficiency of young females when substantial changes in wetland conditions occur during the first year of life and that some birds in poor physiological condition risk too much by attempting to breed. Regardless of the underlying mechanisms or decision-making process, there is little doubt of the implications of widely varying rates of deferred yearling breeding to overall wood duck productivity, but the small number of years when data were available precluded more extensive modeling of wetland conditions as related to this complex issue.

Results indicated that annual duckling production was a reasonable substitute for recruitment estimates when examining population productivity relative to wetland conditions. Increased wood duck productivity in wetter years was not related to higher duckling production in individual nests, but instead was related to more ducklings being produced by individual females that attempted breeding. An increased ability for females in the population to produce second broods in wet years was in part responsible for that outcome. Production of second broods by wood ducks is positively related to length of the breeding season (Kennamer and Hepp 1987, 2000). Generally, mild winters with abundant rainfall contribute to an early onset of wood duck nesting, whereas drought conditions reduce late-season nesting (R. A. Kennamer, Savannah River Ecology Laboratory, unpublished data; Vrtiska and Frederick 1993). On the SRS, typically less than 5% of all successful nests were second nests when the period of nest initiations was less than about 110 days. Conversely, when periods of nest initiation were 145 days or longer, as much as 19% of all successful nests were second nests. This relationship also is reported from a broad geographic area, where breeding season length and incidence of second broods decreased with increasing latitude (Moorman and Baldassarre 1988). Equally important as second broods, breeding seasons extended by favorable wetland conditions also may increase the opportunity for renesting following first nest failure. Thus, the southern portion of the wood duck breeding range, where second brood production and renesting efforts can contribute substantially to overall productivity, is a geographic region perhaps well-suited to success of such a modeling effort as described here.

As nest success increases, number of ducklings produced/female in the population also increases, so long as average number of ducklings produced/successful nest remains relatively constant

as in this study. Thus, variation in predation rates relative to annual wetland hydrologic conditions becomes an important consideration in addition to second brood potential. Dry conditions on the SRS allowed certain predators greater access to nest sites, so predation rates tended to be higher in dry years than in wetter years. Drought conditions in the prairie potholes also are known to result in higher predation rates among ground-nesting waterfowl (e.g., Rogers 1964, Afton 1984). Primary predators of wood duck nests on the SRS included rat snakes (*Elaphe obsoleta*), raccoons (*Procyon lotor*), and woodpeckers (*Melanerpes erythrocephalus*; *Colaptes auratus*; R. A. Kennamer, Savannah River Ecology Laboratory, unpublished data). Though these results were from nest boxes rather than natural cavities, similar predation rate patterns relative to wetland hydrologic conditions may be expected to occur in wood duck populations nesting in natural cavities, albeit absolute levels of predation generally would be higher in natural cavities (Bellrose and Holm 1994).

Although indices of wetland water conditions correlated reasonably well with duckling production/female, 2 of the 14 years (i.e., 1984 and 1986; Figure 2) had duckling production that was inconsistent with the respective wetland conditions. Correlation between wetland water conditions and duckling production improved substantially when I removed those 2 years ($r_S = 0.74$, $P = 0.006$). In 1984, a wet year, 2 conditions likely contributed to less than expected duckling production. First, 1984 was the peak year of a 4-year period (1982–1985) when woodpecker predation was relatively common, and such aerial predators or cavity competitors would not be expected to be impeded by high water levels. This finding suggests that wood duck recruitment models may be improved by incorporating sub-models of competitive cavity-nesting bird abundance. Second, 1984 was a shorter than expected breeding season. Although termination of breeding was timed typically for a wet year, onset of the breeding season in 1984 was among the latest over the 15-year study period. There was no apparent local winter temperature effect that could explain the delayed start of the 1984 nesting season. In 1986, higher than expected duckling production was associated with an abnormally long breeding season despite local drought conditions, and widespread occurrence of second broods (>18% of all successful nests) apparently contributed to increased per-female duckling production. Also, by 1986 the woodpecker predation noted in earlier years had become much less common.

Management implications

Central to our ability to effectively manage waterfowl resources, including the wood duck, is an accumulated knowledge of resource population dynamics, together with the etiology of natural- and human-induced responses. In a new era of adaptive resource management (Walters 1986, Johnson et al. 1996, United States Fish and Wildlife Service 2000) and with predictions of future changing environments shaped by human impacts and global climate shifts (Intergovernmental Panel on Climate Change [IPCC] 1990, Peters and Lovejoy 1992, Larson 1995, Sorenson et al. 1998, Naiman and Turner 2000), we are compelled to gain such knowledge more expeditiously than ever before. Methods to evaluate the responses of resource populations to changing environments and human exploitation provide managers with invaluable tools to gauge their successes and buffer resources from overuse. In the case of the wood duck, examinations of harvest trends have suggested that southern subpopulations currently may have greater potential to be exploited (Johnson et al. 1986, Serie and Chasko 1990, but see Heusmann 1990, Minser et al. 1990). However, without adequate methods to index recruitment, productivity, or population levels—all potentially useful components of an assessment of altered harvest strategies—managers will be reluctant to allow more liberal or special-season harvests. This study illustrates that wetland hydrologic conditions during the wood duck breeding season can be predicted very well from climatological data, that a relationship is demonstrable between wetland conditions and wood duck productivity, and that a greater understanding of wood duck population dynamics can be gained by using such an approach. The methodology presented here is particularly relevant to the Southeastern Atlantic Coastal Plain, and if expanded to such a regional scale, it could provide information to resource managers that is not currently available for wood duck populations.

Fully implementing this methodology would require historical hydrologic data from numerous wetlands or watersheds within the region of interest along with the necessary climatological data from associated weather stations. However, a simpler

initial testing of the method may be possible for the Southeastern Atlantic Coastal Plain, assuming that climatic patterns and their effects on SRS wetlands are indicative of the larger region. Using precipitation and evaporation totals from the months identified here, water balances could be constructed for a series of weather stations considered representative of the region. Indices of wetland hydrologic conditions in the vicinity of each participating weather station could then be determined as in Equation 1 by simply using 2.37 and 1.00 (i.e., from the ratio of Equation 1 coefficients) as coefficients for water balances in the current and preceding year, respectively, and disregarding the Equation 1 intercept. Wetland hydrologic condition indices averaged across the region (perhaps weighted or standardized by station to account for overall interstation variability patterns in annual accumulations) then could be related to wood duck fall recruitment estimates derived from early season harvest data and parts-collection information such as those available for North Carolina and South Carolina (Kelley 1997) or Florida (Brakhage and Eggeman 1998). Inclusion of some relevant regional temperature factor(s) with the wetland condition index might further improve the relationship.

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