Demographics of Wood Ducks in Florida

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Abstract: During 1987–1996, 9,598 wood ducks (*Aix sponsa*) were banded, and 358 bands were recovered and reported during the hunting season. Males survived at an estimated annual ration of 0.585 (SE = 0.028) and females at 0.406 (SE = 0.040). Analysis of capture-recapture data from box-nesting female wood ducks resulted in a mean survival rate estimate of 0.490 (SE = 0.012), which was higher than that estimated for females from preseason banding (P = 0.045). Band recovery rates averaged 0.021 (SE = 0.002) for males and 0.018 (SE = 0.002) for females, suggesting that harvest rates were relatively low. The preseason age-ratio (an estimate of recruitment) during 1989–1996 averaged 1.18 (SE = 0.18) young per adult, which is comparable to other reported estimates for wood ducks. We found no evidence that the Florida population of female wood ducks either declined or increased over the study period.

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The wood duck is the most abundant of the 3 species of ducks that regularly breed in Florida (Bellrose 1980). Wood ducks rank third in Florida's duck harvest (U.S. Fish and Wildl. Serv., Off. Migratory Bird Manage. 1980–1997), which includes a special September duck season to provide additional hunting opportunity. In the eastern United States, wood ducks consistently have ranked among the top 3 duck species harvested (U.S. Fish and Wildl. Serv., Off. Migratory Bird Manage. 1980–1997). However, unlike other abundant and heavily harvested species of ducks, waterfowl managers have no reliable indicator of population size or trends for wood ducks (Brakhage 1990). Consequently, managers have relied on estimates of survival and recovery rates obtained from band-recovery data to assess population status for this species and make harvest management decisions (e.g., Bowers and Martin 1975, Johnson et al. 1986).

In 1987, the Florida Game and Fresh Water Fish Commission (FGFWFC) began developing a statewide program for monitoring Florida's breeding wood duck population. Our objective in this paper is to report on several aspects of that effort; specifically, survival, band-recovery rates, recruitment, and population growth rates.

We acknowledge the assistance of many FGFWFC employees and volunteers who contributed to the statewide wood duck population monitoring project. Numerous private landowners allowed access to their property and helped with duck trapping. F. Johnson (U.S. Fish and Wildlife Service—Office of Migratory Bird Management [USFWS-OMBM]) contributed in many ways to this work and deserves special credit. We appreciate the help with design and data access and analyses from U.S. Geological Survey—Biological Resources Division (USGS-BRD) staff, particularly J. Hines, J. Nichols, and B. H. Powell. We especially thank the hunters who reported bands. R. Bielefeld, R. Malecki, C. Moore, and T. O'Meara provided helpful reviews of the manuscript.

Methods

Survival and Recovery Rates

We used recoveries from preseason banding efforts to estimate average annual survival and recovery rates for resident wood ducks. FGFWFC and USFWS staff annually affixed USFWS leg bands to wood ducks in Florida during June-September (before the hunting season), 1987–1996. Bait-trapping and night-lighting were the primary capture techniques, and birds were released immediately after banding. To estimate recovery and survival rates, we used banding and recovery data (USGS-BRD's Bird Banding Laboratory [BBL]) from normal, wild birds banded preseason, 1987–1996, and recovered during the September–February hunting seasons. Wood ducks were classified to sex and age as locals (pre-fledgling), hatch-year (fledged young), or after-hatch-year ($\geq$1 year old) at the time of banding. Recovery rate was the probability that a banded bird alive during the banding period was shot or found dead the next hunting season and its band reported to BBL. We assumed band-reporting rates were constant over years and used recovery rates as an index to harvest (retrieved kill) rates. Survival rate was defined as the probability that a banded bird alive at the midpoint of the banding period survived 1 year. For each sex, data from birds banded as local and hatch-year were combined because direct recovery rates were similar (males: $\chi^2 = 0.225$, df = 1, $P = 0.635$; females: $\chi^2 = 1.873$, df = 1, $P = 0.171$). Direct recovery rate was the number of direct band recoveries divided by the number of bandings. A direct recovery was a band that was recovered and reported in the same year that the band was placed on the bird. Variances of direct recovery rates were calculated using the formula for variance of a a proportion (Tacha et al. 1982).

We estimated recovery and survival rates for males and females with models developed by Brownie et al. (1985), using programs BROWNIE and ESTIMATE. BROWNIE models survival and recovery rates for 2 age classes, and ESTIMATE models these rates for combined age classes. We selected the most appropriate model for a given data set by examining chi-square goodness-of-fit tests and likelihood ratio tests, which compare a general model against a more specific model (Brownie et al. 1985:8). We used $\alpha = 0.10$ for assessing goodness-of-fit, with the null hypothesis that the model fits, and α = 0.05 for likelihood ratio tests, with the null hypothesis that the simpler model is more appropriate. We compared survival and recovery rates using program CONTRAST (Sauer and Hines 1989), which calculates a chi-square statistic to test null hypotheses that rates are equal. We assumed estimates were independent and covariances were zero.

We used Band Analysis System (Ver. 1.5), developed by the National Biological Service, to summarize banding and recovery data. A map of banding locations was produced with MapViewer (Golden Software, Inc.) using output from this program.

We also estimated survival rates for adult female wood ducks using capture-recapture methods. We used data from 550 nest boxes monitored at least once during the nesting season (21 Jan–31 Aug) in each of 8 years (1989–1996) (Fig. 1). Unmarked females captured in these boxes were fitted with USFWS leg bands. Captured birds were immediately returned to their nests. Captures of previously and newly banded female wood ducks in nest boxes provided the data used in this analysis.

We used program JOLLY to compute Jolly-Seber (JS) estimates of survival rate and associated standard errors (SEs) for females in our nest box sample. We used SEs provided by program JOLLY unless we detected a significant lack of fit for a model. In

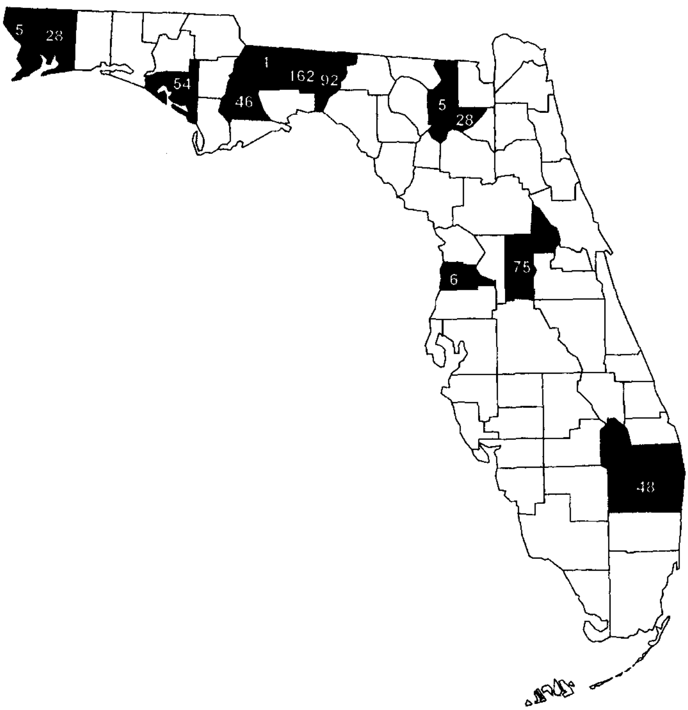

Figure 1. Distribution by county of nest boxes (*N*=550) used for capture-recapture estimate of adult female wood duck survival in Florida, 1989–1996.

this case, we adjusted SEs by a variance inflation factor, as recommended by Lebreton et al. (1992:84). Program JOLLY also estimates population size of females nesting in boxes, number of new hens recruited each year, and the probability that a hen alive and in the population will be captured. The program uses the JS capture-recapture model for open-populations (Jolly 1965, Seber 1965, 1982:196–255). JOLLY tests the fit of models with time-specific survival rates and capture probabilities (Model A), constant survival rate and time-specific survival rates and capture probabilities (Model B), and constant survival rate and constant capture probability (Model D). Program output includes goodness-of-fit statistics for each model and results of likelihood ratio tests between models. We used $\alpha = 0.10$ for assessing goodness-of-fit, with the null hypothesis that the model fits, and $\alpha = 0.05$ for likelihood ratio tests, with the null hypothesis that the simpler model is more appropriate. Survival rates from this approach are probability estimates that an individual survived and returned to the sampled area. Female wood ducks are highly philopatric to nesting areas (Grice and Rogers 1965, Hepp et al. 1987). Consequently, we assumed that probability of returning to the sampled area was 1 and survival rates represented only the probability that the individual survived. Therefore, we compared these survival rate estimates to estimates resulting from analysis of preseason banding data, as independent estimates of average annual survival rates for adult female wood ducks breeding in Florida.

Preseason Age Ratios

We collected wings from wood ducks killed by hunters during Florida's September duck seasons, 1989–1996, to estimate age-sex composition of the harvest. Wings came from hunters solicited through a mail questionnaire, notices, press releases, and casual contacts, and from hunters encountered at check stations and public boat ramps. Methods for wing-collection efforts and analyses to estimate age-sex composition of the harvest were described in detail by Eggeman and Brakhage (1996). We assumed that wood ducks killed during the September season were birds that had spent the previous breeding season in Florida (Brakhage and Eggeman 1998).

We estimated annual preseason age ratios using the estimated age ratio of the harvest and an estimate of differential vulnerability to hunting of young and adult wood ducks. The annual differential vulnerability estimate was the ratio of young to adult direct recovery rates, and the variance of this ratio was calculated as the variance of a quotient of 2 estimates (Hansen et al. 1953:514). We then calculated a weighted mean of the annual differential vulnerability estimates (each weighted by 1/variance) so that the more reliable annual estimates had more influence on the estimated mean. The weighted mean was used as the estimate for differential vulnerability, and we considered it to be constant across years. To estimate annual preseason age ratios, we divided each year's age ratio of the September season harvest by the differential vulnerability estimate. The variance was calculated as the variance of a quotient of 2 estimates (harvest age ratio/differential vulnerability) (Hansen et al. 1953:514). We also calculated preseason age ratios for females alone and estimated differential vulnerability based on direct recovery rates for females. Estimates of average preseason age ratios were simple means of annual estimates.

Population Growth Rate

We estimated the finite rate of population increase, λ (Caughley 1977:52) for female wood ducks in Florida as $\hat{\lambda} = \hat{S} + \hat{R}\hat{S}'$, where $\hat{S}$ = estimated adult survival rate, $\hat{S}'$ = estimated young survival rate, and $\hat{R}$ = estimated preseason age ratio (a measure of recruitment). This relationship follows from the model projecting population size: $N_{t+1} = SN_t + RS'N_t$, assuming no net immigration/emigration, and λ defined as N_{t+1}/N_t (Caughley 1977:52). A $\hat{\lambda} = 1$ indicates a stable population. Var ($\hat{\lambda}$) was estimated using formulas for variance of a product of 2 estimates ($\hat{R}\hat{S}'$) (Hansen et al. 1953), then that variance was summed with var ($\hat{S}$) to estimate the variance of the sum of 2 estimates (assuming covariance = 0). In the case where $\hat{S} = \hat{S}'$, $\hat{\lambda} = \hat{S}(1 + \hat{R})$, and var ($\hat{\lambda}$) was estimated as the variance of a product of 2 estimates (Hansen et al. 1953). We estimated alternative values for $\hat{\lambda}$ using values for $\hat{S}$ from the preseason band-recovery analysis and from the JS model.

Results

Survival

During 1987–1996, 358 recoveries of 9,598 banded wood ducks (Table 1) allowed us to estimate age- and sex-specific survival rates (Table 2). Of the recoveries, 100 were adult males, 135 were young males, 57 were adult females, and 66 were young females. Program BROWNIE Model H02 (constant survival with year-specific recovery rates) provided adequate fit to the band-recovery data for males and females (males: χ^2 goodness-of-fit = 26.30, df = 30, P = 0.660; females: χ^2 goodness-of-fit = 12.19, df = 8, P = 0.143). For males, results from program BROWNIE provided insufficient evidence to reject the assumption that recovery and survival rates were similar between adults and young (Model H0 vs. H1: χ^2 = 23.70, df = 19, P = 0.208). Results from Model 2 of program ESTIMATE (χ^2 goodness-of-fit = 30.08, df = 27, P = 0.311) suggest that recovery rates for combined age classes were year-

Table 1. Numbers of wood ducks banded in Florida, during the preseason period (Jun-Sep) 1987–1996.

	Females		Males		
Year	Adult	Young	Adult	Young	Total
87	259	247	400	371	1,277
88	317	156	346	209	1,028
89	293	89	285	91	758
90	302	129	381	190	1,002
91	131	140	133	218	622
92	269	247	257	367	1,140
93	306	488	279	453	1,526
94	197	109	221	170	697
95	239	185	211	226	861
96	174	143	145	225	687
Total	2,487	1,933	2,658	2,520	9,598

Table 2. Estimates of annual recovery rate and constant survival of preseason-banded wood ducks in Florida, 1987–1996.

	Annual recovery rate				Survival rate		
Age-sex	$\bar{x}$	SE	CV	Range	Estimate	SE	CV
Program BROWNIE, Model H02							
Females							
Adult	0.014	0.002	0.143	0.004 – 0.027	0.445	0.051	0.115
Young	0.024	0.004	0.167	0.013 – 0.039	0.501	0.136	0.271
Males							
Adult	0.016	0.002	0.125	0.004 – 0.023	0.606	0.035	0.058
Young	0.026	0.003	0.115	0.010 – 0.044	0.838	0.136	0.162
Program ESTIMATE, Model 2							
Females	0.018	0.002	0.111	0.005–0.028	0.406	0.040	0.098
Males	0.021	0.002	0.095	0.009–0.028	0.585	0.028	0.048

specific and survival rates were constant. For females, results from program BROWNIE again provided insufficient evidence to reject the assumption that recovery and survival rates were similar between adults and young (Model H0 vs. H1: $\chi^2 = 21.24$, df = 19, $P = 0.323$). We again selected Model 2 from program ESTIMATE (χ^2 goodness of fit = 7.90, df = 11, $P = 0.722$). Because program ESTIMATE Model 2 provided the most parsimonious model for both males and females, we used its estimates (Table 2) for all comparisons with previously published estimates and for population-growth modeling.

All 3 of the program JOLLY models provided adequate fit ($P > 0.10$) to capture-recapture data ($N = 1{,}442$) of box-nesting females (Table 3). Tests between models led us to select Model D (χ^2 goodness-of-fit = 23.93, df = 22, $P = 0.351$). Average survival rate was estimated at 0.490 (SE = 0.012, CV = 0.025), and average capture probability was high (0.808, SE = 0.019). The estimated breeding population in these boxes ranged from 249 (SE = 8.70) in 1990 to 432 (SE = 12.54) in 1995. Annual estimates of recruitment of new females in this population averaged 215 (SE = 9.05).

Recruitment

Estimated annual harvest age ratios of all wood ducks killed during the September seasons during 1989–1996 ranged from 0.92 to 3.16 and, for females, from 1.26 to 3.11 (Table 4). We estimated differential vulnerability at 1.34 (SE = 0.12) for all birds and 1.38 (SE = 0.18) for females. Florida's preseason age ratio for wood ducks during 1989–1996 averaged 1.18 (SE = 0.18) young per adult. Florida's preseason age ratio for females during 1989–1996 averaged 1.30 (SE = 0.16).

Population Growth Rate

With $\hat{R}$ estimated at 1.30 (preseason age ratio) and $\hat{S}$ and $\hat{S}'$ estimated at 0.406 (preseason band recovery analysis, Table 2), we estimated the finite rate of population growth ($\hat{\lambda}$) at 0.94 (SE = 0.12). We found no evidence to reject the null hypothesis of

Table 3. Capture-recapture data for 1,442 box-nesting female wood ducks in Florida.

	Year returns were last caught	Capture year							
		89	90	91	92	93	94	95	96
	1989		61	4	0	0	0	0	0
	1990			74	8	0	0	0	0
	1991				114	6	4	0	0
	1992					125	11	1	0
	1993						118	16	1
	1994							130	11
	1995								136
Previously banded birds returning		0	61	78	122	131	133	147	148
New birds banded		156	142	179	208	182	178	204	193
Total caught		156	203	257	330	313	311	351	341
Total released		156	203	256	330	311	310	348	337

$\hat{\lambda}=1$ (Z = 0.701, P = 0.484). We also calculated $\hat{\lambda}$ using the JS estimate for adult females ($\hat{S}$) and the preseason banding estimate ($\hat{S}'$) for young females. Consequently, with $\hat{S}$ estimated at 0.490 and $\hat{S}'$ estimated at 0.406, $\hat{\lambda}$ = 1.02 (SE = 0.08), which also was not different from 1 (Z = 0.226, P = 0.820).

Discussion

The southeastern subpopulation of wood ducks occurs in the states of Georgia and Florida (Kelley 1997). Our survival rate estimate for males in Florida (0.585, SE = 0.028) was similar to that reported for the southeastern subpopulation of adult male wood ducks for 1977–1994 (0.636, SE = 0.019, χ^2 = 2.27, df = 1, P = 0.132) but lower than that reported for southeastern young male wood ducks (0.870, SE = 0.104, χ^2 = 7.00, df = 1, P = 0.008). No difference was detected in the survival rate estimate for female wood ducks in Florida (0.406, SE = 0.040) versus southeastern adult females (0.468, SE = 0.047, χ^2 = 1.009, df = 1, P = 0.315) or young females

Table 4. Estimated age ratios (young per adult) of harvests from Florida's special September duck season and estimated preseason age ratios of wood ducks in Florida, 1989–1996.

	Harvest age ratio (SE)		Preseason age ratio (SE)	
Year	all	females	all	females
1989	1.70 (0.61	2.15 (0.74)	1.27 (0.47)	1.56 (0.56)
1990	3.16 (0.85)	3.11 (0.75)	2.36 (0.66)	2.24 (0.58)
1991	0.92 (0.20)	1.29 (0.27)	0.69 (0.16)	0.93 (0.22)
1992	1.38 (0.31)	1.27 (0.28)	1.02 (0.25)	0.92 (0.22)
1993	1.32 (0.34)	1.26 (0.33)	0.99 (0.27)	0.91 (0.25)
1994	1.54 (0.42)	1.80 (0.47)	1.14 (0.32)	1.30 (0.36)
1995	1.41 (0.43)	2.00 (0.58)	1.05 (0.33)	1.44 (0.44)
1996	1.25 (0.29)	1.53 (0.34)	0.93 (0.23)	1.10 (0.27)

(0.546, SE = 0.084, χ^2 = 2.26, df = 1, *P* = 0.132). During 1988–1995, Florida bandings made up 72% of the total for the southeastern subpopulation; therefore, it is not surprising that survival estimates from wood ducks banded in Florida were similar to those of the southeastern subpopulation (Kelley 1997). Precision of the survival rate estimate for southeastern young females was poorer (CV = 0.15) than that of the other estimates, reducing power to detect a difference.

Females are of particular management interest because they are the truly resident segment of the population, exhibiting strong philopatry to natal and nesting areas. Males pair with females in wintering areas where populations are mixed. The propensity for males to follow females to the females' natal areas to breed (Kirby 1990) suggests that females best represent the resident segment of the population. Distribution of recoveries of Florida-banded birds supports this idea (Brakage and Eggeman 1998).

Among North American ducks, females typically survive at lower rates than males (Johnson et al. 1992), likely a result of risks associated with nesting and brood rearing (Johnson and Sargeant 1977, Sargeant et al. 1984, Sargeant and Raveling 1992). The estimated survival rate for female wood ducks in Florida is generally lower than other survival rate estimates reported for adult female wood ducks (Bowers and Martin 1975, Johnson et al. 1986, Nichols and Johnson 1990, LeMaster and Trost 1994, Kelley 1997). A long nesting season (178–223 days) and increased opportunity for hatching and raising 2 broods during a single nesting season (Brakhage and Eggeman 1998) may be responsible for the difference. LeMaster and Trost (1994) estimated a mean summer survival rate of 0.580 (SE = 0.060) for southern adult female wood ducks, compared to 0.855 (SE = 0.045) for northern adult females. The authors suggested that the difference may be a result of higher depredation in southern areas during the summer.

The average annual female survival rate estimated from preseason banding (0.406) was lower than the JS estimate (0.490, χ^2 = 4.00, df = 1, *P* = 0.045). Precision of these estimates was relatively high, contributing to good power to detect the difference. We considered 2 explanations for this discrepancy. First, we suspected that the survival probability of box nesting females may not be representative of the entire population of female wood ducks, but rather the portion of the population that nests in boxes. Most nest boxes had predator protection, potentially reducing female mortality during nesting. Our capture probability for the capture-recapture study was high, improving precision of JS estimates and reducing bias if assumptions were violated (Carouthers 1973).

A second possible explanation for this discrepancy is that nightlighting, our primary capture technique during preseason banding, reduced survival. Of the capture techniques employed, nightlighting seems potentially the most stressful for the birds. We conducted separate band-recovery analyses for birds caught by nightlighting versus birds caught by all other methods (primarily bait-trapping). For males and females, nightlighted and non-nightlighted, evidence suggested constant recovery and survival rates, with no difference between age classes (Model 3, program ESTIMATE). We detected no differences in survival rates between capture techniques for males (χ^2 = 0.297, df = 1, P = 0.58) or females (χ^2 = 0.668, df = 1, P = 0.41). Male survival rates averaged 0.578 (SE = 0.034) for nightlighted birds and 0.599 (SE = 0.021) for non-nightlighted birds. Average recovery rate for nightlighted males was 0.021 (SE = 0.002) and for non-nightlighted males was 0.021 (SE = 0.003) (χ^2 = 0.023, df = 1, P = 0.868). Although it was not a significant difference, the survival rate estimate for nightlighted females (0.378, SE = 0.049) was substantially lower than for non-nightlighted females (0.445, SE = 0.066). Power to detect this difference likely was low because the banded sample was divided between capture techniques and precision declined. The estimate for nightlighted females was lower than the estimate from the JS estimate (χ^2 = 4.93 df = 1, P = 0.026), but the survival rate estimate for non-nightlighted females was not different from the JS estimate (χ^2 = 0.450, df = 1, P = 0.502).

If nightlighted females survive at a lower rate than females captured by other methods, then there is potential for bias in the preseason banding estimate because a large proportion (66%) of the sample was captured by nightlighting. Average recovery rate for nightlighted females was 0.019 (SE = 0.002) and 0.015 (SE = 0.003) for non-nightlighted females (χ^2 = 1.23, df = 1, P = 0.27). Capture locations differed between capture techniques, and geographic vatiation may be the source of variation observed between capture techniques, rather than techniques themselves. Also, supplemental feeding associated with bait trapping may improve the survival of bait-trapped females, which had recently experienced the energetic costs of reproduction.

Survival appears to be more closely related to hunting pressure for wood ducks than for other duck species (see review in Nichols and Johnson 1990). Trost (1990) found a significant negative relationship between survival rates and recovery rates (an index to harvest rates) for wood ducks throughout North America. The average recovery rate for male wood ducks in Florida (Table 2) was lower than that reported for the southeastern subpopulation of adult male wood ducks (0.028, SE = 0.002, χ^2 = 6.12, P = 0.013) and southeastern young male wood ducks (0.034, SE = 0.003, χ^2 = 13.00, P = 0.000), and also lower than for male wood ducks from more northern reference areas (Kelley 1997). Average recovery rates for female wood ducks in Florida (Table 2) is lower than that reported for southeastern adult females (0.028, SE = 0.003, χ^2 = 7.69, df = 1, P = 0.005), southeastern young females (0.026, SE = 0.003, χ^2 = 4.92, df = 1, P = 0.026), and generally lower than for more northern adult females (Kelley 1997).

This geographic pattern of lower recovery rates for southern birds usually is attributed to the reduced exposure and risk to hunting for southern wood ducks compared to northern birds (see Bowers and Martin 1975, Nichols and Johnson 1990). Florida's special September duck season provides for harvest opportunity for locally breeding wood ducks in addition to that of the regular duck season. The fact that Florida's recovery rates remain even lower than those of the southeastern wood duck population, which includes Georgia, suggests that hunting mortality for locally breeding wood ducks remains low (assuming spatially and temporally constant band reporting rates). Unfortunately, we can make no meaningful pre- and post-comparisons of survival or recovery rates to assess effects of Florida's September season, be-

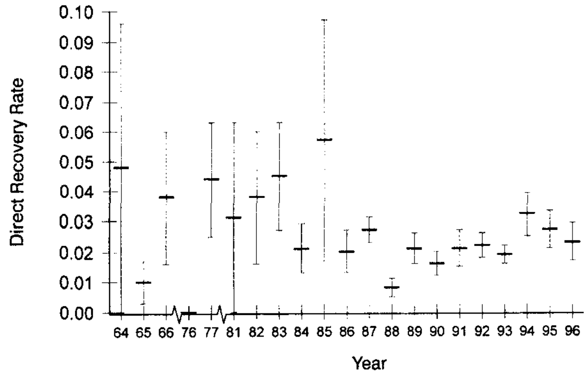

Figure 2. Direct recovery rates (± SE) of Florida-banded wood ducks.

cause banded sample sizes were too small before 1981 when the season began. Only 5 of the years during the period 1961–1980 had banded sample sizes >20, and only 2 years had sample sizes >100. However, annual estimates of direct recovery rates during years when banded sample sizes were >20 show no evidence of an increase after special September seasons began in 1981 (Fig. 2).

Nichols and Johnson (1990) reviewed available information on wood duck population dynamics and concluded that, among North American ducks, the wood duck ranks high in terms of reproductive rate. Characteristics accounting for this high rate include a large proportion of females nesting each year, large clutch size, high nesting success, persistent renesting, and second broods. Nesting data for Florida were typical in terms of these characteristics (Brakhage and Eggeman 1998). In Florida, and presumably at other southern latitudes, a long nesting season further contributes to these reproductive efforts. Florida's average preseason age ratio for wood ducks during 1989–1996 is comparable to other estimates for wood ducks (Nichols and Johnson 1990). Florida's preseason age ratio of females alone is similar to those reported for the southern Atlantic and Mississippi Flyways (Bellrose and Holm 1994:443).

Conclusions

Trost (1990) provided evidence that wood duck populations may be more susceptible than other duck species to effects of hunting. This is significant in our case because of added hunting pressure associated with the special September duck season. However, recovery rates suggest that harvest pressure remains low, and population growth rates suggest a stable population. Recent estimates of wood duck harvest per hunter-day during the September season remain similar (Brakhage and Eggeman 1998), suggesting that the population has not declined (assuming constant vulnerability of wood ducks to harvest). We found no evidence to suggest the September season in Florida was causing negative effects on wood duck populations. Further research on the relative importance of factors influencing mortality in adult female wood ducks in Florida would be of management value.

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