Studies in Avian Biology No. 21:39–49, 2000.

INTEGRATION OF RESEARCH WITH LONG-TERM MONITORING: BREEDING WOOD DUCKS ON THE SAVANNAH RIVER SITE

ROBERT A. KENNAMER AND GARY R. HEPP

Abstract. In 1981, long-term monitoring of the breeding of Wood Ducks (*Aix sponsa*) was initiated on the Savannah River Site by the Savannah River Ecology Laboratory in partial response to environmental legislative requirements surrounding the restart of a U.S. Department of Energy nuclear production reactor (L-Reactor). Although the reactor itself was operated only for two years, the study of Wood Ducks continues today, 15 years following its initiation, and has made significant contributions to our basic understanding of the population ecology of this unique species, and waterfowl in general.

Marking and recapturing individual females in nesting boxes were key aspects of the long-term study because it enabled us to produce annual population parameter estimates (e.g., population size, survival rate, recruitment), which are valued indicators of population stability. We were able to generate precise parameter estimates, though marking relatively small numbers of breeding females, because capture probabilities were high. Identifying field methods (e.g., long-term consistency in capture effort) that allowed precise parameter estimation was among the most important consequences of our work. The longevity of the monitoring effort was also important because it allowed us to examine the natural range of variation in reproductive characteristics of this species. We used retrospective analyses of the long-term data and initiated companion short-term studies to explore factors related to and responsible for the identified variation within the population.

Our work illustrates some of the beneficial aspects of ecological research derived from long-term monitoring efforts: they generate essential baseline data and provide a means of continually refining management practices, provide answers to important ecological questions that cannot be addressed easily by using experimental methods, and establish a foundation for formulating and testing new hypotheses. In this paper, we review the conditions that motivated the initiation of this study, the initial goals of the work, and the ecological knowledge that has been gained thus far from the commitment of SRS managers and researchers to long-term population monitoring.

Key Words: *Aix sponsa*; Anatidae; breeding ecology; long-term study; population ecology; Savannah River Site; South Carolina; Wood Duck.

In 1980, the U.S. Department of Energy (DOE) made a decision to restart a nuclear production reactor, L-Reactor, on the Savannah River Site (SRS) in west-central South Carolina because of increased demand for weapons-grade plutonium. The L-Reactor previously had been operated from 1953 until 1968 when it was placed on stand-by status. Since reactor operations required the discharge of circulated cooling water, the DOE intended to release L-Reactor thermal effluents directly into Steel Creek upon restart as it had done during earlier operations of that same reactor. Heightened public awareness of environmental issues during the 1970s, however, had resulted in the passage of extensive legislation related to environmental protection. The National Environmental Policy Act (NEPA) and the Federal Water Pollution Control Act (including the Clean Water Act of 1977) specified numerous areas such as water quality, wetlands protection, and habitat alteration that the DOE was required to evaluate before restarting the reactor (Smith et al. 1981). Furthermore, Executive Orders 11988 and 11990 specifically addressed alterations of wetland ecosystems for federal projects, while regulations such as 10 CFR 1022 and the Sikes Act (PL 93–425) placed controls over habitat and wildlife management issues on federal lands (Smith et al. 1981). Under the provisions of these legislative mandates, the DOE developed plans to prepare an Environmental Impact Statement for the project. The University of Georgia's Savannah River Ecology Laboratory received DOE funding to assist in the collection of environmental information for addressing the legislatively mandated questions.

Wood Ducks (*Aix sponsa*) occur naturally on no other continent and are uniquely adapted to living in forested wetlands where they nest in cavities of trees. Sportsmen, bird watchers, and researchers have long been attracted by this colorful waterfowl species. Wood Ducks, for example, comprise more than 10% of the annual waterfowl harvest in the United States, and in the Atlantic and Mississippi Flyways it is second only to the Mallard (*Anas platyrhynchos*) in numbers of birds shot annually (Hepp and Bellrose 1995).

Much of the popularity of Wood Ducks can be associated with their highly publicized population collapse and subsequent recovery during the early part of the 20th century. In the late 1800s, populations of Wood Ducks began to decline largely due to the market hunting profession, and by the early 1900s concern was expressed for the observed dramatic decrease (Bellrose 1990). In 1918, legal hunting of Wood Ducks was banned by the Migratory Bird Treaty Act, leading to a population upswing over the next 20 years (Bellrose 1990). Since the 1930s, thousands of nest boxes have been erected by the public and government agencies; these have further contributed to the success and expansion of locally breeding populations of this species.

As early as the mid-1930s, Wood Ducks commonly were found in swamps and lagoons along the Savannah River forming the border between South Carolina and Georgia (Murphy 1937). Wood Ducks were considered locally abundant in the vicinity of the SRS as a breeding species prior to the closure of the site to the public in 1952 (Murphy 1937). Fendley (1978) studied the ecology of Wood Ducks using nest boxes in the Steel Creek area on the SRS in the mid-1970s, following the 1968 shutdown of the L-Reactor, and provided baseline information from which new studies could be developed.

INITIATION OF THE LONG-TERM WOOD DUCK STUDY

Impacts resulting from earlier operations of the L-Reactor had altered habitats within the lower reaches of Steel Creek and the surrounding Savannah River Swamp System into which Steel Creek emptied, creating a large flooded herbaceous marsh (Steel Creek delta, >100 ha) with extensive standing dead timber (Sharitz et al. 1974, Smith et al. 1981). In addition to the thermally induced effects on the ecosystem, from 1960 to 1970 approximately 260 curies of the fission products collectively termed radiocesium (primarily ^{137}Cs, 30-yr half-life) were released inadvertently into Steel Creek (Marter 1970).

Earlier research of Fendley (1978) suggested that the impacted/recovering Steel Creek area had a higher carrying capacity for breeding Wood Ducks than either before or during the period of reactor effluent discharges. The proposed reactor restart therefore had the potential to substantially reduce local habitat for breeding Wood Ducks and other species of wintering migratory waterfowl.

The primary emphasis of the newly organized study was to assess Wood Duck reproduction within the Steel Creek ecosystem with a nest box monitoring program. Nest boxes also were established in several other SRS wetlands to serve as "control" habitats for comparative studies. Nest boxes (Fig. 1) were checked approximately weekly during the breeding season. We estimated dates of nest initiation, and counted and individually labeled eggs; females were captured, weighed, and banded, and nest fates were determined. In some years, we weighed newly hatched ducklings and then web-tagged the young with #1 monel fish-fingerling tags for future identification. Other methodological details are given in Hepp et al. (1989, 1990) and Hepp and Kennamer (1992, 1993).

IMPACT STUDIES OF THE NUCLEAR REACTOR RESTART

Results of nest box monitoring from the early 1980s confirmed that habitat alterations in lower Steel Creek associated with former thermal effluent discharges from L-Reactor were favorable to breeding Wood Ducks (Smith et al. 1981, 1982). The opening of the otherwise closed-canopy swamp allowed establishment of an extensive herbaceous/shrub marsh with species such as parrot-feather (*Myriophyllum brasiliense*), cut grass (*Leersia* spp.), knot grass (*Scirpus cyperinus*), smartweed (*Polygonum* spp.), buttonbush (*Cephalanthus occidentalis*), and black willow (*Salix nigra*; Sharitz et al. 1974, Smith et al. 1981). Wood Ducks probably were attracted to such an area because it provided the essential requirements for both nesting and brood-rearing; natural cavities produced by primary excavators were abundant in the dead standing timber, and the herbaceous/shrub marsh provided an abundance of food and cover for young Wood Ducks. Nest-box use by Wood Ducks in this habitat averaged 30–70% annually (Smith et al. 1982).

At Upper Three Runs Creek, a natural southeastern blackwater stream that also empties into the Savannah River, no habitat alterations from site activities ever had occurred. This river swamp forest was characterized generally by a closed canopy of bald cypress (*Taxodium distichum*) and tupelo gum (*Nyssa aquatica*) along the stream channel, with mixed bottomland hardwood species such as white ash (*Fraxinus americana*), red maple (*Acer rubrum*), water hickory (*Carya aquatica*), and water elm (*Planera aquatica*) found throughout the seasonally inundated floodplain (Smith et al. 1981, Workman and McLeod 1990). Such floodplain areas are considered the traditional habitat of Wood Ducks in the southeastern United States (Bellrose and Holm 1994). Nest box use by Wood Ducks in this undisturbed riparian habitat (10–20% annually), however, was consistently lower than that in disturbed sites (Smith et al. 1982).

Since ongoing environmental studies in 1981 and 1982 identified habitats in the Steel Creek corridor and delta as being favorable to breeding and wintering waterfowl, as well as to endangered Wood Storks (*Mycteria americana*) and threatened American Alligators (*Alligator mis-*

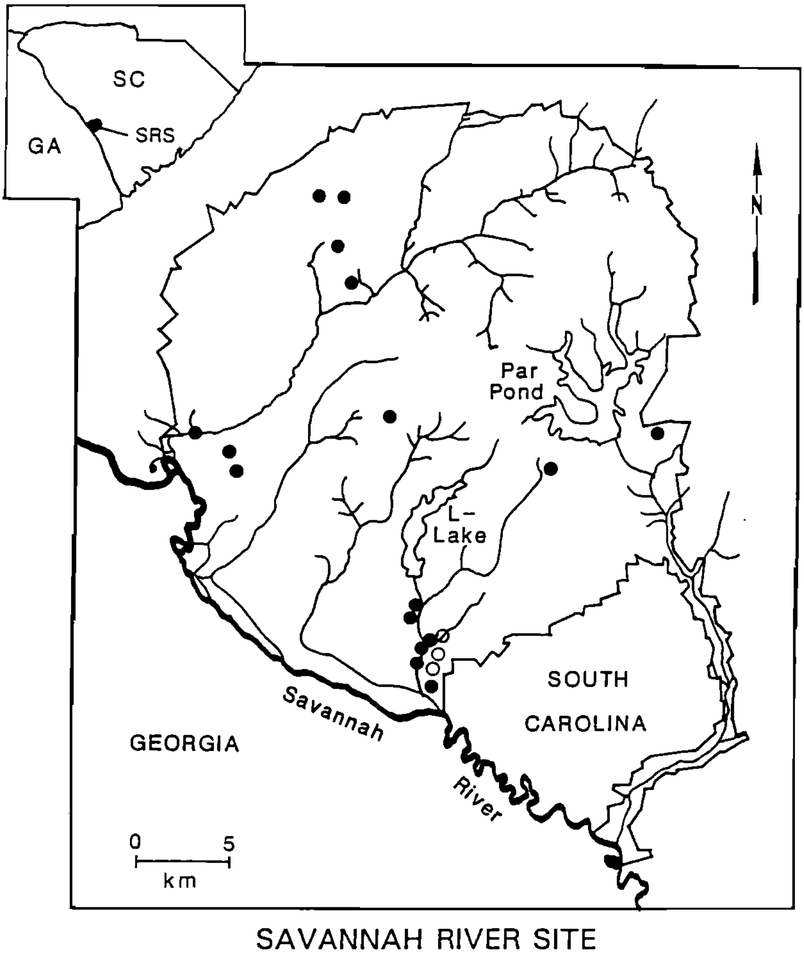

FIGURE 1. Distribution of Wood Duck nest box locations on the Savannah River Site, South Carolina. Locations (N = 16) designated by closed circles were available prior to 1984; additional locations (N = 3) designated by open circles were available beginning in 1984.

sissippiensis), further concerns focused on ecosystem impacts likely to result from restarting the reactor and their effects on these species. The consensus was that if reactor effluents were to be discharged directly into Steel Creek in a manner similar to earlier operations, the Steel Creek corridor and delta would revert to highly simplified communities typical of other SRS streams already receiving thermal effluents at that time (Smith et al. 1982). For any chosen course of action, the unavoidable increased water flows would alter the natural hydrology of the system and a process of mitigating the possible negative impacts would have to be implemented. Thus, in 1984, additional Wood Duck nest boxes were erected in wetlands adjacent to the Steel Creek floodplain (Fig. 1, open circles) that would not be affected by the proposed reactor restart (Smith et al. 1983). These "mitigation" boxes along with existing nest structures continued to be monitored for Wood Duck use in the long-term study.

Among the options considered for handling thermal reactor effluents was the DOE-preferred direct discharge of effluents into streams and the less-desirable construction of a cooling-water impoundment or cooling tower. However, the National Pollution Discharge Elimination System (NPDES) provisions of the Clean Water Act no longer allowed direct discharge of thermal waters, thus excluding the DOE's preferred option as a viable alternative (McCort et al. 1988). Therefore, in the fall of 1984, construction began on a 405-ha cooling impoundment (L-Lake; Fig. 1) within the Steel Creek drainage, upstream from the delta. L-Reactor was finally restarted on 31 October 1985, but was only in operation for about two years.

STUDIES USING THE LONG-TERM MONITORING DATA

ESTIMATION OF POPULATION PARAMETERS

The study of life-history characteristics is an important facet of ecology, particularly in studies of population regulation. Along with information on fecundity of individuals or groups of individuals, estimates of population parameters such as survival and recruitment are essential to examine fitness and to infer the stability of populations. In the case of game species such as the Wood Duck, population parameter estimates can be used by resource managers to assess effects of hunter harvest on populations.

Most female Wood Ducks that nested in boxes on the SRS each year were captured and marked with U.S. Fish and Wildlife Service leg bands. We used capture histories of individual females to estimate several population parameters for breeding females on the SRS (Hepp et al. 1987a). Annual survival rates of waterfowl, including Wood Ducks, had been determined previously through the development and use of models to analyze band-recovery data (e.g., Anderson 1975, Nichols et al. 1982, Conroy and Eberhardt 1983), but few studies had used capture-recapture models to estimate population parameters of breeding birds (Hepp et al. 1987a). We estimated annual survival, population size, and recruitment of breeding females using the Jolly-Seber (J-S) capture-recapture model for open populations (Table 1). Capture probabilities over the course of the study were generally high (Table 1), averaging 0.85 ± 0.02 (SE), and resulted in relatively precise parameter estimates. High capture probabilities were a consequence of consistent researcher commitment to capture nesting females among years, aided by weekly nest box checks.

FEMALE RECRUITMENT

To examine sources of variation in recruitment of female Wood Ducks, we marked over 2,900 day-old ducklings in six breeding seasons and tested whether hatch date and body mass at hatching influenced subsequent recruitment of females into the breeding population (Hepp et al. 1989). Most studies have reported an inverse relationship between survival probability and hatch date (Perrins 1965, Pierotti 1982, Cooke et al. 1984, Dow and Fredga 1984, Martin and Hannon 1987), and tests of the relationship between body mass and post-fledging survival in birds have produced varying results (Perrins 1980, Nur 1984, Newton and Moss 1986, Martin and Hannon 1987).

Most (73%) returning females were first found nesting as yearlings (Table 2). We found that females hatching late in the nesting season returned to breed at the same rate as early-hatched females. We attributed this result to the long breeding season of Wood Ducks in South Carolina (15-yr mean of 129 days for nest establishment) and suggested that hatching date may be relatively more important at more north-

TABLE 1. JOLLY-SEBER ESTIMATES OF POPULATION PARAMETERS FOR BREEDING WOOD DUCKS USING NEST BOXES ON THE SAVANNAH RIVER SITE, SOUTH CAROLINA[a]

	Population size		Survival rate		Recruitment		Capture probability	
Yr (t)	N_t	SE (N_t)	ϕ_t	SE (ϕ_t)	B_t	SE (B_t)	P_t	SE (P_t)
1979	–	–	0.41	0.11	–	–	–	–
1980	29.5	5.9	0.71	0.17	23.4	10.4	0.69	0.17
1981	44.4	11.8	0.62	0.12	10.0	6.7	0.44	0.14
1982	37.5	3.8	0.59	0.09	25.7	1.9	0.83	0.11
1983	48.0	0.0	0.52	0.09	36.6	5.1	1.00	0.00
1984	62.6	8.1	0.50	0.07	11.4	3.4	0.83	0.10
1985	42.1	2.9	0.68	0.08	34.3	2.3	0.84	0.08
1986	62.8	2.0	0.77	0.06	46.8	4.0	0.95	0.05
1987	95.3	5.0	0.64	0.07	48.2	6.4	0.89	0.06
1988	109.1	8.7	0.52	0.06	24.1	4.7	0.79	0.07
1989	80.6	4.9	0.62	0.07	47.3	4.9	0.84	0.07
1990	97.7	5.9	0.52	0.05	41.4	2.5	0.88	0.06
1991	92.0	0.0	0.61	0.05	55.7	3.2	1.00	0.00
1992	111.4	4.3	0.56	0.05	61.2	4.5	0.93	0.05
1993	123.2	5.5	0.58	0.05	38.7	4.3	0.91	0.05
1994	109.5	5.7	–	–	–	–	0.88	0.06
1995	–	–	–	–	–	–	–	–
Means	76.3	1.5	0.59	0.02	36.1	0.7	0.85	0.02

[a] Bias-adjusted estimates of Seber (1982) are presented. Goodness-of-fit (Pollock et al. 1985) $\chi^2 = 11.7$, 15 df, $P = 0.70$.

TABLE 2. AGES OF FEMALE WOOD DUCKS WHEN CAPTURED DURING FIRST NESTING ATTEMPTS[a]

Year of hatch	Female age (yr) 1	2	3	4	5	6	Total returns
1982	9	1	0	0	0	0	10
1983	6	0	0	0	0	0	6
1984	4	5	1	0	0	0	10
1985	7	0	0	0	0	0	7
1986	16	2	1	0	0	0	19
1987	16	7	4	0	1	0	28
Total	58 (73%)	15 (19%)	6 (8%)	0	1 (1%)	0	80

[a] Data from 2,945 web-tagged ducklings (males and females) hatched from 1982–1987, and with at least 8 years of potential recovery.

ern latitudes where shorter breeding seasons (e.g., 7-yr mean of 66 days for nest establishment in Massachusetts; Grice and Rogers 1965) may limit the ability of late-hatched young to mature sufficiently before fall migration. We also found that body mass at hatching had no effect on recruitment of Wood Duck neonates in 5 of 6 years, and suggested that duckling body mass may be linked to recruitment only in years when habitat conditions are poor and food for growing Wood Ducks is not readily available.

PHILOPATRY AND NEST-SITE FIDELITY

Many species of migratory birds exhibit a high degree of fidelity to natal areas and previous breeding sites (Greenwood and Harvey 1982). We used long-term data involving the capture and recapture of breeding females and day-old ducklings to study philopatry and nest-site fidelity of female Wood Ducks (Hepp et al. 1987a, 1989; Hepp and Kennamer 1992). Waterfowl exhibit female-biased philopatry (Rohwer and Anderson 1988), so analyses were limited to females. There were two objectives to these studies. First, we assessed the degree of philopatry and nest-site fidelity exhibited by Wood Ducks. Second, we evaluated sources of variation in nest-site fidelity and determined the benefits of returning to the same nest site in consecutive years.

Philopatry of adult female Wood Ducks initially was assessed indirectly by comparing the average annual survival rate estimated with the J-S capture-recapture model for open populations (see discussion above and Table 1) with survival estimated using band-recovery models (Hepp et al. 1987a). The J-S model estimates the proportion of females surviving and returning to the general study area, while band recovery models estimate only survival. We found no difference in these two survival estimates and concluded that surviving adult females on the SRS showed a high probability of returning to the study area (Hepp et al. 1987a).

Natal philopatry was examined by marking day-old ducklings with web-tags and recapturing the females as adults when they returned to nest in boxes (Hepp et al. 1989). Forty percent (27 of 67) of returning females nested on the wetland study site where they had hatched; returning females that did not nest on their natal wetland nested nearby ($N = 40$, $\bar{x} = 1.6 \pm 0.2$ [SE] km). Local density of breeding females (females/box) did not influence whether females nested on their natal wetland (Hepp et al. 1989).

Female ducks often return to use the same breeding site from one year to the next (Anderson et al. 1992). We tested several predictions concerning sources of variation in nest-site fidelity of Wood Ducks and the consequences of returning to the same nest site (Hepp and Kennamer 1992). Females that nested successfully used the same box to a greater extent (47.2%) in the next breeding season than those that were unsuccessful (10.8%). A positive association between nest success and nest-site fidelity also occurred within breeding seasons, between first and second nests. However, female age (yearling or adult) and population size did not influence nest-site fidelity.

Females returning to the same box nested earlier than females using different boxes, but did not have larger clutches (Table 3) or greater nest success. Females that nested unsuccessfully improved their nest success the following year by using a different nest box (Hepp and Kennamer 1992).

EFFECTS OF AGE AND EXPERIENCE ON REPRODUCTIVE PERFORMANCE

Parental age often has been shown to have an important effect on reproductive success in birds (Sæther 1990). Older individuals of many species nest earlier in the season, produce larger clutches, and have greater fledging success than younger conspecifics (Raveling 1981, Rockwell et al. 1983, Afton 1984, Reese and Kadlec 1985, Nol and Smith 1987, Harvey et al. 1988). However, most studies do not separate the effects of age from the potentially confounding effects of

TABLE 3. LEAST-SQUARES MEANS ± SE OF THE RELATIVE DATE OF NEST INITIATION AND CLUTCH SIZE OF FIRST NESTS (BY TYPE OF NEST SITE FIDELITY) FOR FEMALE WOOD DUCKS ON THE SAVANNAH RIVER SITE (SAMPLE SIZES IN PARENTHESES; HEPP AND KENNAMER 1992)

Nest fidelity type	Relative date of nest initiation[a]	Clutch size[b]
Same nest box	23.3 ± 2.3 (106) A[c]	12.3 ± 0.4 (33) A
Different nest box, same wetland	35.9 ± 2.3 (95) B	11.2 ± 0.4 (31) A
Different nest box and wetland	42.4 ± 3.2 (52) B	12.0 ± 0.5 (20) A

[a] Initiation date of nests was expressed as the number of days elapsed since initiation of the first nest each year.
[b] Nonparasitized nests.
[c] Least-squares means in columns followed by different upper case letters are significantly different ($P < 0.05$).

breeding experience. We used data from the long-term study to test whether reproductive success of Wood Ducks was age specific and to evaluate several explanations for age-specific variation (Hepp and Kennamer 1993).

Yearling females initiated nests 11–19 days later than older females. Heavy females, independent of age, nested earlier than light females. However, clutch size, mean egg mass, and number of ducklings were not affected by female age when body mass and nesting date were considered (Table 4). We also found no evidence that differential survival of yearling females explained age-related patterns of reproduction (Hepp and Kennamer 1993).

We separately tested the effects of breeding experience and age on nesting date and female body mass. Two year-old females that had nested as yearlings were heavier and initiated nests almost 4 weeks earlier than two-year-old females not known to have previous breeding experience (Table 5). Nesting date of inexperienced two-year-old females did not differ from that of yearlings, but body mass of the former group was greater (Table 5). These results suggest that prior breeding experience has a greater effect on nesting date than female age per se.

Overall, age had little effect on reproductive success of Wood Ducks. Breeding experience influenced timing of nesting, and females that nested early in the breeding season had several advantages over those that initiated nests later; early-nesting females produced larger clutches, hatched more young from successful nests, were at less risk from predators (primarily black ratsnakes, *Elaphe obsoleta*), and were more likely to initiate second nests (Hepp and Kennamer 1993).

SECOND BROODS

Most North American waterfowl do not nest successfully more than once each breeding season. Wood Ducks, however, are capable of having two broods in a single nesting season (e.g., Odom 1970, Fredrickson and Hansen 1983). On the SRS, females commonly produced two broods in a season, but frequency of double broods varied annually (0–19% of successful nests).

We found that frequency of double broods was related positively to length of the breeding season (Fig. 2). In general, mild winters with abundant rainfall contribute to an early nesting season onset, while drought conditions reduce late-season nesting. 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 is similar to that reported from a broad geographic area, where both breeding season

TABLE 4. ONE-WAY ANALYSIS OF COVARIANCE TESTING THE EFFECTS OF WOOD DUCK AGE (1-5 YRS) ON CLUTCH SIZE, MEAN EGG MASS, AND NUMBER OF DUCKLINGS PER NEST WITH NESTING DATE AND FEMALE BODY MASS AS COVARIATES (HEPP AND KENNAMER 1993)

	Clutch size			Mean egg mass			Ducklings per nest		
Independent variable	F	df	P	F	df	P	F	df	P
Age	1.05	4,91	NS	0.38	4,88	NS	0.56	4,65	NS
Nesting date[a]	43.17	1,91	***	7.08	1,88	**	12.25	1,65	***
Female body mass	4.09	1,91	*	45.14	1,88	***	4.09	1,65	*
R^2		0.36			0.50			0.34	

[a] Nesting date of first nests standardized ($x - \bar{x}$) to control for annual variation. NS > 0.05; * < 0.05; ** < 0.01; *** < 0.001.

TABLE 5. RESULTS OF T-TESTS EVALUATING EFFECTS OF FEMALE WOOD DUCK AGE AND EXPERIENCE ON REPRODUCTIVE PERFORMANCE CHARACTERISTICS, TIME OF NESTING (DEVIATION FROM POPULATION MEAN, IN DAYS) AND FEMALE BODY MASS (G) (FROM HEPP AND KENNAMER 1993)

	Nesting date[a]				Female body mass			
Comparison	$\bar{x}$	t	df	P	$\bar{x}$	t	df	P
Experienced adults	−12.8				591			
vs.		8.07	180	0.0001		2.12	316	0.03
Inexperienced adults	13.0				581			
Inexperienced adults	13.0				581			
vs.		0.09	204	0.93		4.82	200	0.0001
Yearlings	13.5				551			

[a] Time of nesting standardized ($x - \bar{x}$) to control for annual variation in nest initiation date.

length and incidence of second broods declined with increasing latitude (see Moorman and Baldassarre 1988).

We found no relationship between female age or early incubation body mass and the probability of producing a second brood (Kennamer and Hepp 1987). However, double-brooded females lost a smaller percentage of body mass (4.3%) during incubation of first nests than single-brooded females (9.4%). We suggested that greater weight loss by females during incubation reduced the chance of producing a second brood by increasing the time necessary to replenish nutrient reserves. Alternatively, weight loss exhibited by single-brooded females may have been sufficiently stressful to terminate reproductive activity (Bluhm et al. 1983).

CONCURRENT SHORT-TERM STUDIES

Long-term population monitoring provided the foundation for developing useful new field techniques, exploring natural sources of variation in the population, and developing and testing new hypotheses. Numerous short-term studies were initiated that served not only to complement our long-term study, but also to advance our understanding of Wood Duck population ecology and enhance the species' management potential.

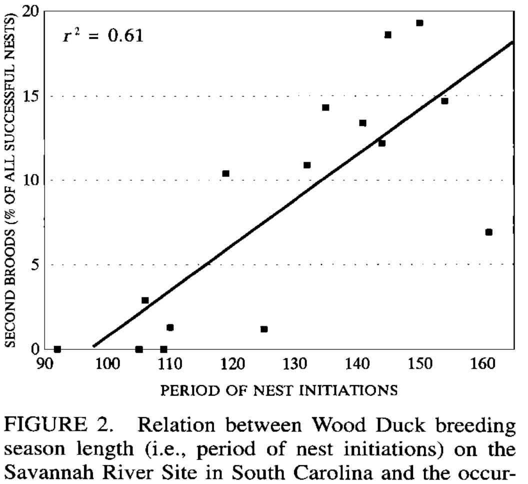

FIGURE 2. Relation between Wood Duck breeding season length (i.e., period of nest initiations) on the Savannah River Site in South Carolina and the occurrence of second broods, 1982–1996.

AGE DETERMINATION OF BREEDING FEMALES

Techniques for determining age are important for studying many aspects of population ecology. Knowledge of population age structure is useful for estimating annual production rates, and for determining age-specific differences in survival and reproduction. We developed a quantitative method using wing feather characteristics to distinguish yearling from adult female Wood Ducks during the breeding season (Harvey et al. 1989a). We used a sample of females that included adults (N = 39), yearlings (N = 31), and females of unknown age (N = 48) from which we pulled the tenth secondary (S10), first primary (P1), and the most proximal greater covert (MPGC). A total of 16 measurements was taken of these three feathers, and discriminant analysis procedures selected three variables that provided the greatest separation of the age groups. These variables included the length (mm) of S10 from the first dark barbs to the tip of the vane, mass (mg) of P1, and width (mm) of the MPGC. The discriminant model correctly classified >90% of known-age female Wood Ducks (Harvey et al. 1989a). This technique has allowed us to age unmarked females captured at nests, thereby increasing our sample of known-age females.

VARIATION IN EGG AND DUCKLING COMPONENTS

There has been great interest in how waterfowl acquire and use nutrients for reproduction (Alisauskas and Ankney 1992). Allocation of nutrients by breeding females can influence subsequent growth (e.g., O'Connor 1975) and survival (e.g., Ankney 1980) of offspring. We therefore examined within- and among-female

TABLE 6. VARIATION IN MASS AND COMPOSITION OF EGGS AMONG WOOD DUCK HENS (N = 87 EGGS FROM 29 FEMALES; HEPP ET AL. 1987B)

Variable	Among-female variance component (%)[a]	R^2 [b]
Fresh-egg mass	71.0	0.35**
Yolk		
Wet	53.0	0.18*
Dry	52.3	0.21*
Water	56.4	NS
Lipid (%)	68.9	NS
Lipid (g)	52.0	0.19*
Lean dry mass	55.9	0.20*
Albumen		
Wet	78.2	0.36**
Dry	74.5	0.31**
Water	78.1	0.34**
Shell		
Wet	73.1	0.25*
Dry	79.7	0.18*
kJ/egg	55.0	0.29**

[a] $P < 0.0001$ for all variables.
[b] Summarizes results of regression analyses to test effects of the body mass of female Wood Ducks on the mass and composition of eggs. Values used in the analyses were within-clutch means (N = 24).
NS = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

variation in the size and composition of eggs and investigated the relationship between egg mass and the structural size, body mass, and lipid reserves of ducklings (Hepp et al. 1987b).

Most variation (52–80%) in the size and composition of eggs was due to variation among females (Table 6). Composition of eggs did not vary with female age; however, mass and composition of eggs were related positively to body mass of females, and the relationship was strongest for albumen components. Heavy females produced heavier eggs with larger yolk, albumen and shell components than light females. In addition, female body mass was independent of female structural size (i.e., tarsus and wing length).

We suggested that early incubation body mass provides a good index to the "quality" of prebreeding females. Estimates of female lipid reserves before egg-laying, for example, were correlated positively ($r_s = 0.66$, $P = 0.001$) with body mass in early incubation. Heavy females with large lipid reserves may be more effective in gathering exogenous protein than light females, which could explain the stronger relationship between female mass and the protein-rich albumen component. These results are consistent with the idea that female Wood Ducks may delay egg production until they reach a threshold level of lipid reserves (Alisauskas and Ankney 1992).

For females producing two clutches in a single breeding season, egg mass and clutch size were greater in first nests than in second nests (Kennamer and Hepp 1987), indicating a lower commitment of nutrients to second clutches. We examined egg composition for two complete sets of first and second clutches (41 eggs). Total clutch lipids averaged 14.9 g less in second clutches than in first clutches; reduced lipid allocation to individual eggs of second clutches accounted for 14% of the total reduction in clutch lipids, while 86% of the total reduction in lipids was due to reduced clutch size in second clutches.

Relationships between egg size and the size and composition of the neonate indicated that components of day-old Wood Ducks increased in direct proportion to fresh-egg mass. While egg mass was a relatively good predictor of duckling mass, there was not a strong relationship between egg mass and lipid content of the neonate, suggesting that rate of lipid metabolism varied among developing embryos (Hepp et al. 1987b).

BODY MASS DYNAMICS AND REPRODUCTIVE COSTS TO INCUBATING FEMALES

Incubating birds must provide the proper thermal environment for embryonic development while maintaining their own physical condition. The ability of individuals to successfully balance these conflicting demands potentially could influence current and future reproductive success. Body mass of female waterfowl varies in an annual cycle and typically is lowest at the end of incubation. Interspecific differences in the proportion of body mass lost during incubation reflect different levels of metabolic reserves and varying incubation strategies (Afton and Paulus 1992). We documented changes in female body mass during incubation and examined sources of variation in these changes (Harvey et al. 1989b). We also tested whether body mass of incubating females was related to their reproductive success and survival (Hepp et al. 1990).

Incubating female Wood Ducks lost an average of 1.3 ± 0.1 (SE) g/day (31-day average incubation period; Bellrose and Holm 1994), which is among the lowest reported for waterfowl (Afton and Paulus 1992). Change in body mass was highly variable (range = +1.5 to −4.3 g/day) and was not related to clutch mass, nesting date, or female age; females that were heavier at the beginning of incubation lost body mass at a greater rate than light females. We suggested that heavy females possess greater post-laying lipid reserves to use during incubation than light females. These remaining lipids may provide incubating females with an important buffer, beyond which they must use endogenous protein or spend less time incubating and more time foraging to meet energy requirements.

Early incubation body mass of individual females was similar in consecutive years, but there was little consistency in rate of incubation body-mass change between years. Varying and unpredictable environmental conditions (e.g., food availability, wetland conditions) may affect the rate at which female mass changes during incubation (Harvey et al. 1989b).

Body mass at the start of incubation was not related to either hatching success or length of the incubation period (Hepp et al. 1990). In one of three years, females that were heavy at the end of incubation survived better to the next breeding season than those that were light. Reduced survival of light females in the one year coincided with greater loss of body mass in that year, indicating that incubation can be an important reproductive cost to females in some years. We found no evidence that incubation costs affected reproduction in the next breeding season (Hepp et al 1990).

Intrabrood Developmental Asynchrony

Waterfowl commonly begin incubation before they finish laying eggs (Afton and Paulus 1992), thus creating developmental asynchrony within clutches. However, precocial broodmates must be prepared to leave the nest together shortly after hatching, generally ≤24 hr. Embryos apparently are able to synchronize time of hatch by adjusting developmental rates (Vince 1964, 1968).

We examined levels of developmental asynchrony in Wood Duck clutches and found that at the end of laying, embryo development ranged from 0–5 days ($\bar{x}$ = 2.2 days; Kennamer et al. 1990). Large clutches showed greater levels of developmental asynchrony than small clutches, and in one of two years, clutches with more than 3 days of developmental asynchrony had reduced hatching success.

Arnold et al. (1987) showed that viability of duck eggs declines with time, and they proposed that females begin incubation before clutches are complete to maintain high hatching success. Flint et al. (1994) suggested that variation in egg composition within clutches may permit synchronized hatch. We therefore investigated the relationship of laying sequence to the size and composition of Wood Duck eggs (Kennamer et al. 1997).

We found that patterns of Wood Duck egg size and composition were related to laying sequence; egg size increased during the first half of laying and decreased thereafter (Fig. 3, top). Furthermore, egg-laying sequence effects were

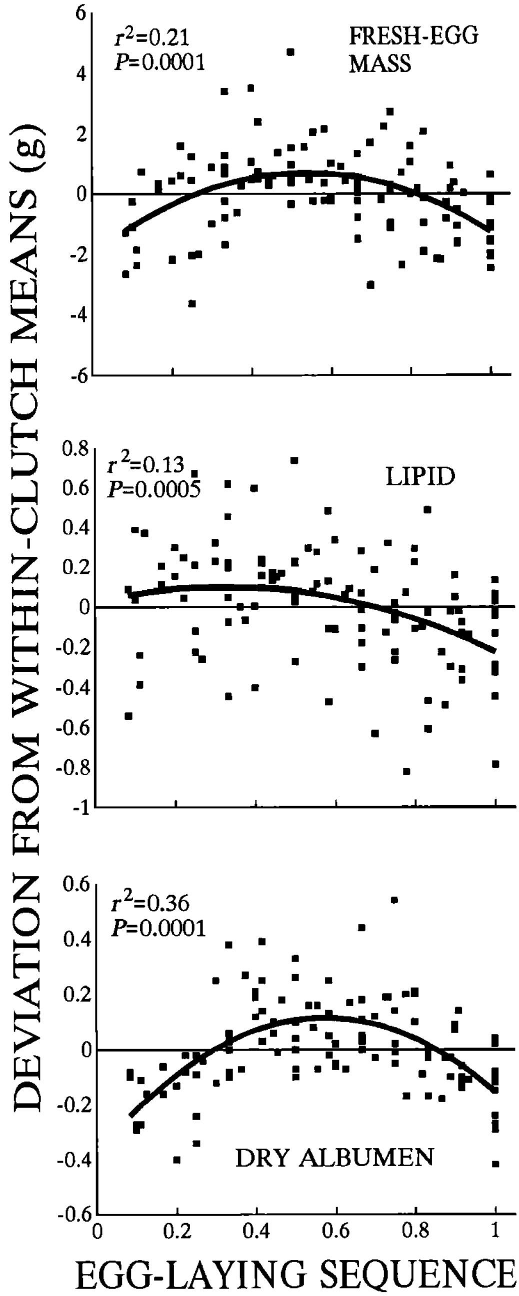

FIGURE 3. Relations between fresh-egg, yolk lipid, and dry albumen masses (deviations from within-clutch means) and laying sequence (standardized for different clutch sizes) for 11 first clutches of Wood Ducks from the Savannah River Site in South Carolina, 1991–1992. Figures are taken from Kennamer et al. (1997).

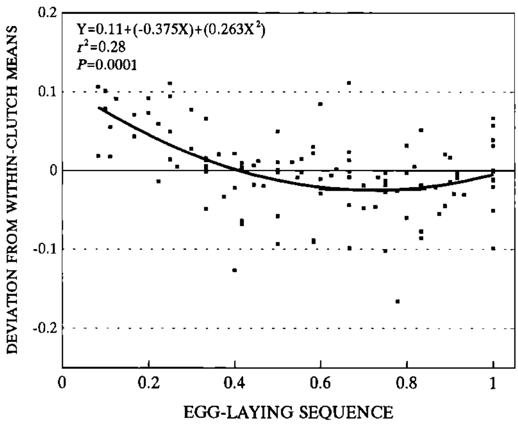

FIGURE 4. Relation between lipid indices (lipid mass/lean-dry egg-content mass; deviations from within-clutch means) and laying sequence (standardized for different clutch sizes) for 11 first clutches of Wood Ducks from the Savannah River Site in South Carolina, 1991–1992. Figure is taken from Kennamer et al. (1997).

component specific; for neutral lipids (comprising 65.5% of dry yolk), near-average absolute levels were evident until about 75% of the clutch was completed and then declined (Fig. 3, middle). Mass of dry albumen tended to increase sharply initially and then decrease as with fresh-egg mass (Fig. 3, bottom). We further found that fat indices (g egg lipid/g lean-dry egg contents) indicated that first-laid eggs of Wood Ducks were proportionately better provisioned with lipids than all other eggs in the clutch (Fig. 4), containing about 2.5 kJ more energy per gram of lean-dry egg contents than even the largest eggs in the clutch. These extra lipids could provide the energy necessary for the young of first-laid eggs to delay hatching while later-laid eggs complete incubation. Our results thus support the idea that intraclutch variation in egg size and composition may enable female Wood Ducks to initiate incubation before clutch completion and still allow for a synchronous hatch without compromising the hatching success of first-laid eggs (Kennamer et al. 1997).

CONCLUSIONS

Potential impacts on wetland habitats from reactivating a nuclear production reactor provided the initial motivation and funding for the study of Wood Duck breeding on the Savannah River Site. The work originally was designed simply to monitor breeding by this species and compare reproduction in areas affected versus not affected by thermal effluent from the reactor. Although the proposed habitat changes were never fully realized, Wood Duck reproductive data have been collected for 15 years. We have used these data to produce descriptive studies and to test specific hypotheses using retrospective analyses (Nichols 1991) where questions were formulated a priori.

Using nest boxes to monitor reproduction of Wood Ducks had two clear advantages. First, females used nest boxes extensively, so the time-consuming activity of searching for nests was eliminated; nest boxes made it easy to examine nests and to collect reproductive data. Second, females and their ducklings could be captured more easily in nest boxes and marked through vigilant efforts. Marking and recapturing individuals were key aspects of both the long-term monitoring and research, because it enabled us to estimate important population parameters and to study within population movements of females. Because recapture probabilities were high, we showed that precise parameter estimates could be obtained by marking relatively small numbers of breeding females. Identifying methods that allowed precise estimation of important population parameters with which to establish baseline information on the population was one of the most important outcomes of our research.

Long-term studies are essential for answering questions about slow processes and rare events (Likens 1989). However, duration of many population-level studies is relatively short (1–3 yrs) because of funding constraints. Results from short-term studies may be misleading, especially if the biological phenomena of interest are linked to processes with high annual variation. The intent of many of our analyses was to explore sources of variation in female survival and reproduction. Thus, the long-term aspect of our research was important because it allowed us to measure the natural range of variation likely to be found in the system. Survival of adult females, for example, was not constant but varied annually, ranging from 41 to 77%. Reproductive variables (e.g., length of the nesting season, clutch size, and frequency of producing a second brood) also showed significant annual variation. Using data encompassing numerous years and different environmental conditions provided for more powerful tests of specific hypotheses. Our long-term work provided more meaningful and effective monitoring because of the insight gained through examination of the factors related to and/or responsible for the wide range of natural variation in population characteristics. In the future, continued monitoring will allow SRS natural resource managers to better project population responses to different habitat management scenarios by taking into consideration the full range as well as the causes of this natural variation.

Field experiments are generally the best way to test hypotheses in ecology because the variable(s) of interest can be manipulated while controlling other factors or allowing them to vary independently of main effects (Hairston 1989). However, it frequently is impossible to adequately conduct manipulative field experiments. Long-term mensurative data (like ours) allow testing of hypotheses in situations where manipulative field experiments are impractical (Krebs 1991). For example, we were able to separately test the effects of age and breeding experience of females on their reproductive success by simply posing appropriate a priori questions that the long-term data could answer (Hepp and Kennamer 1993). Although a controlled experiment that manipulated breeding experience of similar aged females may have provided a stronger test of the age-experience hypothesis, it would have been extremely difficult to accomplish under field conditions.

We believe that our research illustrates some of the beneficial aspects of ecological research derived from long-term rigorous monitoring efforts: they generate baseline data and the comparative data essential for resource managers to continually assess effects of management practices, provide answers to important ecological questions that cannot be easily addressed using experimental methods, and establish a foundation for formulating and testing new hypotheses.

ACKNOWLEDGMENTS

We thank the many people who generously contributed so much time and energy involved with keeping such a long-term project functioning. Our thanks to R. K. Chesser, B. L. Cockerel, Jr., J. B. Coleman, P. A. Consolie, D. R. Eggeman, K. F. Gaines, J. W. Gibbons, W. F. Harvey, III, S. Henry, R. T. Hoppe, L. Janecek, J. J. Mayer, W. D. McCort, E. Megonigal, R. Sarno, R. R. Sharitz, M. H. Smith, D. J. Stangohr, W. L. Stephens, Jr., B. Thompson, L. D. Vangilder, T. Walton, H. S. Zippler, and others. A special acknowledgment of I. L. Brisbin, Jr., is offered for his persistent support of this work dating to the mid-1970s, and for valuable comments on this manuscript and earlier papers referred to herein. We also thank S. M. Pearson for his critical reading of this manuscript. Much of this research was supported by U.S. Department of Energy contract DE-AC09-76SROO-819 with the University of Georgia's Savannah River Ecology Laboratory. Preparation of this manuscript was supported by Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation.