

## EFFECTS OF BROOD SIZE AND AGE ON SURVIVAL OF FEMALE WOOD DUCKS<sup>1</sup>

FRANK C. ROHWER

*School of Forestry, Wildlife and Fisheries, Louisiana State University, Baton Rouge, LA 70803*

H. W. HEUSMANN

*Division of Fisheries and Wildlife, Westborough, MA 01581*

**Abstract.** During a 13-year study of Wood Ducks (*Aix sponsa*) nesting in eastern Massachusetts, 43.3% of nests were parasitized by conspecifics. Early season nests were more frequently parasitized than were late nests. First-nesting females were less frequently parasitized than experienced breeders, partially because first-nesting females nest later in the season when parasitism declines. Nest parasitism created clutch size variation that allowed us to investigate the effect of clutch size and brood size on survival of Wood Ducks. Females that hatched large broods had a minor delay in nesting the following year. Brood size had no influence on the survival rate of female Wood Ducks. Survival rates averaged 52.8% over all year and age classes. Survival rates declined by 6.1% per year of breeding experience.

**Key words:** *Age-specific survival; brood size; clutch size; intraspecific nest parasitism; reproductive effort; Wood Duck; Aix sponsa.*

### INTRODUCTION

A great deal of life-history theory is devoted to relationships between patterns of mortality and reproductive effort. Two tenets concerning patterns of mortality and fecundity are central. First, parental survival should be inversely related to reproductive effort (Williams 1966, Charnov and Krebs 1974), though the relationship may be nonlinear (Pianka and Parker 1975). Second, animals should show senescence (Hamilton 1966), expressed as declining survival or reproductive efficiency in old-age classes. Both tenets have important ramifications on optimal patterns of reproductive effort, yet they have not been adequately tested, particularly for precocial birds.

The relationship between parental effort and parental survival in birds is best studied by manipulating brood size and recording effects on parents' survival and future reproduction (Alerstam and Högstädt 1984). Brood enlargements decreased parental return rates in some studies (Askenmo 1979, Nur 1984, Reid 1987, Dijkstra et al. 1990), but not in others (Harris 1970, De Steven 1980, Røskaft 1985, Lessells 1986, Hegner and Wingfield 1987, Gustafsson and Sutherland 1988, Korpimäki 1988, Pettifor et al. 1988, Wiggins 1990). In two of the above studies (Askenmo 1979, Korpimäki 1988), brood enlarge-

ments did not increase the number of fledglings, so parental effort may not have been substantially increased.

Patterns of age-specific survival rates also are expected to influence reproductive effort. Declining survival should increase reproductive effort as animals age, because residual reproductive value is declining (Pianka and Parker 1975, Stearns 1976). Studies of age-related mortality patterns among birds have produced a variety of results. Some analyses suggest that old-aged individuals show reduced likelihood of survival (e.g., Coulson 1984, Loery et al. 1987, Bradley et al. 1989), whereas others find little evidence that survival probabilities decline with age (e.g., Buckland 1982, Parkin and White-Robinson 1985). If senescence is real, it may partially explain the increase in clutch size and reproductive output of older birds (Curio 1983, Pugesek 1983, Winkler and Walters 1983). To help understand the factors influencing optimal reproductive effort we examined the effect of age and prior reproductive effort on survival of female Wood Ducks (*Aix sponsa*).

### METHODS

Data were derived from a 13-year study of females nesting in artificial nest boxes at 25 sites in eastern Massachusetts (see Heusmann and Bellville 1982). Females were captured at the nest during incubation and were banded or had

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prior band numbers recorded. A few birds were initially banded during late summer. Most females were captured as breeding adults, so analyses of survival are based on years since first breeding. Breeding philopatry is strong in female waterfowl (Johnson and Grier 1988, Rohwer and Anderson 1988), including Wood Ducks (Grice and Rogers 1965, Hepp et al. 1987). Only 11 marked females (4.0%) were recorded nesting at two different sites. This is important because large scale movements would cause experienced females to be assigned to the first-year age class. The sedentary nature of females means that return rates are reliable indices of survival (Hepp et al. 1987), though they may represent underestimates of survival.

We examined the influence of brood size on parental survival by comparing return rates of females with normal-sized broods to females with enlarged broods resulting from the frequent occurrence of intraspecific nest parasitism (Rohwer and Freeman 1989). Clutches of more than 13 eggs have almost always been enlarged by parasitism (Morse and Wight 1969, Semel and Sherman 1986), so we used that clutch size as our criterion for identifying parasitized nests. We assumed that the occurrence and intensity of parasitism would be independent of host attributes (i.e., inherent survival probability). For 256 females we recorded clutch size for two or more years, so we could examine the frequency of repeated parasitism for individual females. We used observed rates of nest parasitism in a binomial expansion to generate expected frequencies of repeated parasitism over the years of observation.

Our measure of brood size in all analyses was the number of young leaving the nest, which positively correlated with the number of young that survived (Heusmann 1972). Initial brood size was correlated with clutch size ( $r = 0.81$ ,  $n = 901$ ,  $P < 0.0001$ ); thus, our analyses evaluate the combined effect on parents of incubating eggs and caring for broods. However, we cannot assess the effects on parents of producing eggs.

Our survival analyses used a methodology outlined in Seber (1982) and Loery et al. (1987). Analyses were cohort-based, and involved 1,021 captures and recaptures of 471 female Wood Ducks. We marked birds for two years before we assigned new captures to the first-breeding age category. We only calculated an age-specific sur-

vival rate for a cohort if we had at least three years to observe the return of its members.

Nesting dates were recorded as Julian dates coded so that 1 April equals day 1. To control for variation in nesting phenology, we adjusted each years' hatch dates so that they matched the pattern for the data pooled over all years. Nest dates for each year were scaled so the date by which 10% of nests had hatched was day 45. We matched yearly data at the tenth percentile because that is reasonably good indicator of the initiation of nesting, but, unlike first nest dates, is not overly influenced by sample size and the earliest nesting individuals. Scaling by median hatch date would have produced practically the same effect.

Statistical analyses were based on the SAS system (SAS Institute Inc. 1985). Two and three way contingency tables were analyzed using log-linear models (Proc Catmod). Analyses of categorical and continuous data were analyzed using logistic regression (Proc Catmod).

## RESULTS

### EFFECTS OF REPRODUCTIVE EFFORT

The frequency distribution of returning versus nonreturning female parents was independent of brood size (Table 1). That result was consistent for any grouping of brood sizes. We also expanded the contingency table analyses to include an age dimension, with classes of 1-year, 2-years, and  $\geq 3$ -years of breeding experience. The interaction of brood size, breeding age, and survival was not significant ( $\chi^2 = 4.2$ ,  $P > 0.10$ ). If incubation or brood care were costly, then we might expect female survival to systematically decline with increased brood size. Contrary to this prediction, females did not show a decline in survival associated with increased brood size (ranging from 8 to 22 ducklings); in fact, the slope of the survival vs. brood size relationship was positive, though non-significant (ANCOVA weighted by brood size samples,  $F = 0.06$ ,  $P > 0.10$ ). The interaction term in the above analysis was also nonsignificant ( $F = 0.79$ ,  $P > 0.10$ ), indicating that neither yearling nor experienced females were negatively influenced by brood size.

Experienced females nested earlier than younger females. Nests of second-year females hatched 13.8 days earlier than first-year females; similarly, as birds entered the 3-year and  $\geq 4$ -year

TABLE 1. Fate of female Wood Ducks attending broods of different sizes.

	Initial brood size			
	<13	14-16	17-19	>20
Disappeared	299	74	34	13
Returned	419	81	34	24

$G = 4.2$   $P > 0.10$ .

classes their hatch dates were 2.4 and 1.4 days earlier than each prior year. These hatch dates were significantly different ( $F_{3,574} = 52.6$ ,  $P < 0.0001$ ), but the Tukey-Kramer multiple range test distinguished only two classes of birds with respect to hatch date, namely first-year and experienced birds.

We also examined the relationship between brood size and nesting date the next year. We controlled for individual variation in nest dates by examining change in hatch dates for individual females between years  $X$  and  $X + 1$ . We corrected for the age-related changes in nesting time by subtracting the mean advance in hatch date for that age class (given above) from the individual hatch date. Increasing brood size by one duckling caused less than a one day delay in hatch date the following year (Fig. 1, hatch date in year  $X + 1 = 0.9$  (brood size in year  $X$ )  $- 11.4$  days,  $F_{1,224} = 11.5$ ,  $P < 0.001$ ). Restricting the analysis

to broods hatching from parasitized nests ( $>13$  eggs) resulted in a non-significant regression between brood size and change in hatch date the following year (Fig. 1, hatch date in year  $X + 1 = 0.5$  (brood size in year  $x$ )  $- 3.9$  days,  $F_{1,95} = 1.5$ ,  $P > 0.10$ ).

#### NEST PARASITISM

Nest parasitism occurred in 43.3% of nests, but was not equally distributed among females. First-year females were parasitized less frequently (30.8%) than were older females (56.0%) ( $G = 60.8$ ,  $P < 0.0001$ ). Parasitism rates among experienced birds did not vary with age since first breeding ( $G = 0.6$ ,  $P > 0.10$ ). Logistic regression indicated that nest date had a strong influence on rates of parasitism, with early nests more frequently parasitized than late-season nests ( $\chi^2 = 41.7$ ,  $P < 0.0001$ ). First-year and experienced females had similar rates of seasonal declines in parasitism (hatch date  $\cdot$  age interaction,  $\chi^2 = 2.2$ ,  $P > 0.10$ ). However, the age class term was significant ( $\chi^2 = 4.0$ ,  $P < 0.05$ ), which means that experienced breeders had a higher probability of being parasitized than first-year females, even after controlling for the earlier nesting of experienced breeders.

Parasitism was nearly equally distributed among females with multiple nest records (Table

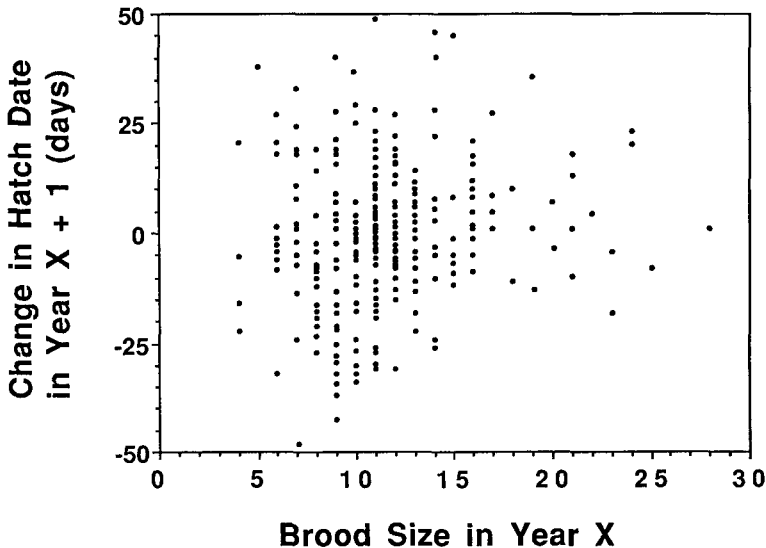


FIGURE 1. The relationship between brood size and hatch date in the following year. Change in hatch date equals hatch date in year  $X + 1$ , minus hatch date in year  $X$ , plus a correction for age effects (see text). A negative value for change in hatch date indicates earlier nesting, positive means later nesting.

TABLE 2. Actual and expected numbers of female Wood Ducks showing multiple parasitism events.

Frequency of parasitic events per individual	2 nests/female		3 nests/female		4 nests/female	
	Actual	Expected	Actual	Expected	Actual	Expected
0	46	43.5	16	8.2	4	1.7
1	65	74.8	17	24.4	6	7.3
2	32	23.7	17	22.5	8	11.2
3	—	—	11	5.9	8	7.2
4	—	—	—	—	3	1.6
	$\chi^2 = 4.14$ $P > 0.1$		$\chi^2 = 15.6$ $P < 0.05$		$\chi^2 = 5.6$ $P > 0.1$	

2). Only the set of females where we had records of three nests showed deviations from the expected distribution of nests being parasitized. In that case, greater than expected numbers of females were repeatedly parasitized or consistently escaped parasitism.

#### SURVIVAL

Wood Duck survival declined with age and breeding experience (Table 3). Regressions of survival upon years of breeding experience (weighted by numbers of birds) produced four negative slopes and three positive slopes (Table 3). The regression of average survival versus breeding experience projected that yearly survival rate drops by 6.1% each year ( $P < 0.05$ ). We calculated survival for five breeding years, because there were few survivors past that age and survival estimates became highly variable in the older age classes (Table 3).

Cohort-based analyses can be faulted because they compare survival estimates obtained under different conditions. Survival estimates for waterfowl are known to fluctuate on a yearly basis (Nichols et al. 1984). One way to avoid those problems is to compare different aged individ-

uals over the same one year interval. Such analyses, of necessity, combine data from different cohorts. Complete data were available for seven yearly comparisons; the data run diagonally from top-right to bottom-left in Table 3. For example, one comparison would be the survival of novice females in 1976, second-year females from the 1975 cohort, 3-year-females from 1974, and so on. Yearly regressions of survival produced five negative and two positive slopes, with two of the negative slopes significant (both  $P < 0.05$ , regressions weighted by numbers of birds).

#### DISCUSSION

Our data on return rates suggest that incubation of enlarged clutches and care of enlarged broods do not have negative consequences for female Wood Ducks. Similar results have been obtained for other waterfowl (Dow and Fredga 1984, Lessells 1986, Rockwell et al. 1987, Hepp et al. 1990). Such results are not unexpected, because the young of waterfowl find their own food and are quite independent at an early age. Descriptions of waterfowl behavior show that parental investment increases with brood size in some species (Afton 1983, Lessells 1987, Schindler and

TABLE 3. Age-specific survival rates for cohorts of Wood Ducks. Ages are from the first known breeding attempt.

Age period	Year of first breeding											Average $\bar{x} \pm SD$
	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	
1-2	.50	.61	.81	.54	.53	.67	.66	.52	.69	.67	.73	.63 $\pm$ 0.09
2-3	.53	.53	.73	.54	.39	.77	.59	.50	.48	.43	—	.55 $\pm$ 0.12
3-4	.56	.78	.44	.43	.77	.50	.41	.56	.40	—	—	.54 $\pm$ 0.15
4-5	0.0	.57	.71	1.0	.80	.30	.45	.40	—	—	—	.53 $\pm$ 0.31
5-6	0.0	.75	.60	.33	.25	.33	0.0	—	—	—	—	.32 $\pm$ 0.28
Slope <sup>1</sup>	-.081	.026	-.074	.001	.009	-.106	-.118	—	—	—	—	-.061
<i>P</i>	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	<0.05	—	—	—	—	<0.05

<sup>1</sup> Slopes from regression weighted by number of females or number of survival estimates.

Lamprecht 1987, Sedinger and Raveling 1990), but not in others (Lazarus and Inglis 1978, Scott 1980, Guinn and Batt 1985). It is unclear, however, whether changes in the time spent in alert postures or other such inactive and nonrisky parental behaviors affect parental survival in waterfowl and thereby influence optimal fecundity levels.

Increased effort in one year could manifest itself in poorer reproduction in later years (e.g., Røskaft 1985). Lessells (1986) noted that Canada Geese (*Branta canadensis*) with enlarged broods delayed laying the following spring. Such delays could negatively influence clutch size and survival of young (Rohwer, in press). After controlling for individual variation (Batt and Prince 1979) and parental age (Grice and Rogers 1965, Afton 1984, Dow and Fredga 1984), we found a minor delay in nesting associated with larger brood sizes. This effect was largely the result of females with small clutches in one year initiating nesting substantially earlier in the following year. Such females may lose or abandon their brood, so they nest earlier because of reduced parental effort. A more parsimonious explanation is that the large advance in nesting dates was a result of comparing hatch dates of replacement nests (re-nests have small clutches) with hatch dates of first-nests in the subsequent year. Nest dates were not influenced by prior brood sizes for the sample of birds that had parasitically enlarged clutches. That is the sample of birds where parental quality and brood size were probably uncoupled by parasitism. Wood Ducks, unlike Canada Geese, do not extend parental care past fledging, so a strong association between brood size and subsequent nesting date would be surprising.

Natural and experimental manipulations of brood size in waterfowl show that brood size does not influence duckling survival (Morse and Wight 1969, Heusmann 1972, Clawson et al. 1979, Dow and Fredga 1984, Rohwer 1985, Lessells 1986, Rockwell et al. 1987). Such results coupled with the independence of parental survival from brood size suggest that post-hatching factors have little influence on optimal reproductive output in waterfowl.

Late-season nests were less frequently parasitized than early nests in our population and in several other studies (Morse and Wight 1969, Clawson et al. 1979, Dow and Fredga 1984, Lank et al. 1989). We assume that the higher level of parasitism of early nesters reflects higher levels

of parasitic laying early in the season, and is not simply due to a greater time of exposure (i.e., both laying and incubation) of early nests (Lank et al. 1989, Hepp et al. 1990). After controlling for date effects, we found a weak, but significant, relationship between host age (categorized as experienced vs. inexperienced breeders) and the frequency of parasitism. Older females may experience greater nest parasitism due to natal philopatry of their offspring (Andersson 1984). Alternatively, the age effect may simply be a dominance effect, such that when two females are both using the same nest box the older (dominant) female eventually incubates the jointly produced clutch.

Repeated observations on individuals show that parasitism is relatively equally distributed among females. Only in the set of females for which we had three nest records was there a deviation from the expected distribution of multiple parasitisms. In that case, a greater than expected number of females experienced no parasitism or frequent parasitism. This may be a nest site effect. Females show consistency in nest site, and some sites are much more susceptible to parasitism than other sites (Semel et al. 1988).

Much ornithological literature suggests that survival rates are not significantly related to age (Richdale 1957, Ludwig 1967, Kadlec and Drury 1968, Henny and Wight 1969, Potts 1969, Bulmer and Perrins 1973, Richdale and Warham 1973, Coulson and Horobin 1976, Buckland 1982, Dow and Fredga 1984, Woolfendon and Fitzpatrick 1984, Parkin and White-Robinson 1985, Nol and Smith 1987, Gibbs and Grant 1987, Curry and Grant 1989). However, our data on Wood Ducks suggest that survival declines in older age classes, as reported in some recent studies (Coulson 1984, Dunnet and Ollason 1978, Ainley and DeMaster 1980, Loery et al. 1987, Bradley et al. 1989, Aebischer and Coulson 1990). The main group of birds that show declining age-specific survival are long-lived seabirds, where small declines in age-specific survival could be an important selective force shaping age-related variation in reproductive effort (Charlesworth 1980). Unfortunately, it is questionable whether declining age-specific survival represents an intrinsic decline in survival (Pianka and Parker 1975). For example, in California Gulls (*Larus californicus*) the age-specific decline in survival (Pugesek 1983) may be extrinsic; that is, caused

by their high reproductive effort. Old-aged birds that failed early in the reproductive stage had the same survival rates as middle-aged birds (Pugesek and Diem 1990). We believe the effects of changing age-specific survival on reproductive patterns are not clear and should be the subject of further study.

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