INCUBATION AS A REPRODUCTIVE COST IN FEMALE WOOD DUCKS

Gary R. Hepp, Robert A. Kennamer,[1] and
William F. Harvey IV[1,2]

Department of Zoology and Wildlife Science, and Alabama Agricultural Experiment Station,
Auburn University, Auburn, Alabama 36849-5414 USA; and
[1]Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801 USA

ABSTRACT.—We investigated the effects of body mass of incubating female Wood Ducks (*Aix sponsa*) on aspects of their current and future reproduction, and we examined factors that affect length of the incubation period. During three breeding seasons, body mass of female Wood Ducks averaged 578.0 g early and 553.3 g late in the incubation period. Body mass at the start of incubation was not related to either hatching success or length of the incubation period. 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 one year coincided with a greater loss of body mass in that year relative to other years, which indicates that incubation can be an important reproductive cost to female Wood Ducks. There were no relationships between body mass at the end of incubation and date of nesting or clutch size in the next breeding season. Partial correlations between clutch mass and length of incubation that controlled for date of nesting indicated a positive association between clutch mass and incubation length in every year. This relationship was evident only for parasitic nests (i.e. nests in which more than one female was laying eggs). Increased length of the incubation period associated with larger clutch mass represents a potential cost of intraspecific nest parasitism not previously recognized. *Received 26 December 1989, accepted 17 June 1990.*

INCUBATING birds must provide the proper thermal environment for embryonic development. Simultaneously they must maintain their body condition so that survival and subsequent reproduction are not affected adversely. Time for feeding is restricted during incubation, which often makes it difficult for incubating individuals to meet daily metabolic costs (see Drent et al. 1985). Some avian species have adjusted to the demands of incubation by having biparental incubation (Eisner 1960, Feare 1984). In other species, males provide incubating females with food (Lyon and Montgomerie 1985, Nilsson and Smith 1988). In waterfowl (Anatidae), females of large-bodied species generally begin incubation with large energy reserves and are more attentive during incubation than females of small-bodied species, because large-bodied females spend less time feeding (review in Afton and Paulus 1990). Small anatids depend on exogenous foods to meet most metabolic demands during incubation and take two

to three recesses each day to forage (Afton 1980, Hohman 1986).

Successful development of bird eggs occurs within a relatively narrow range of incubation temperatures (White and Kinney 1974). Cooling of eggs increases as ambient temperature decreases, and as time away from the nest by incubating individuals increases (Caldwell and Cornwell 1975, Afton 1979). Short-term declines in egg temperature, however, apparently have little effect on hatching success (Vleck 1981, Haftorn 1988). Nevertheless, a decrease in average egg temperature may lengthen the incubation period, which exposes the nest to greater risk of predation and increases the energy expended by developing embryos (Vleck et al. 1980, Booth 1987). Greater amounts of energy used by embryos of precocial species before hatching may decrease the size of residual yolk reserves that are important to newly hatched chicks for maintenance and growth (Peach and Thomas 1986).

Many species of birds modify activity patterns during incubation in response to variation in weather and food availability (Caldwell and Cornwell 1975, Cartar and Montgomerie 1985,

Drent et al. 1985). Large-bodied species are affected less by environmental factors than small-bodied species (Afton 1980). Flexibility of incubation patterns within and among species suggests there is a tradeoff between maintaining body condition during incubation and providing eggs with a suitable environment for development. If time and energy constraints are important during incubation, then attentiveness at the nest should increase as body condition or food availability increases, assuming that greater attentiveness shortens the incubation period and increases hatching success (Martin 1987). Several studies support this idea. Aldrich and Raveling (1983) reported that female Canada Geese (*Branta canadensis moffitti*) that began incubation in good condition spent more time on the nest and had shorter incubation periods than females in poor condition. In years when food was abundant, European Starlings (*Sturnus vulgaris*) spent less time feeding, and some females were able to incubate without assistance from their mates (Drent et al. 1985). Female Blue Tits (*Parus caeruleus*) that were given a food supplement during incubation had shorter incubation periods and greater hatching success than females that were not provisioned (Nilsson and Smith 1988).

Loss of body mass during incubation may reflect the need to provide constant care for developing embryos (Sherry et al. 1980), or it may enable females to reduce wingloading and to conserve energy during brood rearing (Freed 1981). However, a critical body mass certainly exists for individuals during incubation. Below that threshold, birds either spend more time feeding (Aldrich and Raveling 1983) or they abandon the nest (Drent 1975, Ankney and MacInnes 1978, Jones 1987). Body mass of female waterfowl during the annual cycle typically is lowest at the end of incubation (Afton and Paulus 1990). Ability of individuals to balance the conflicting demands of incubation may influence current and future reproductive success.

Male Wood Ducks (*Aix sponsa*) do not take part in incubation. Females are relatively small (610 g) at the beginning of incubation (Afton and Paulus 1990) and have lipid reserves sufficient to meet energy demands for only five days of an average 30-day incubation period (Drobney 1980). Females typically take two incubation recesses each day to feed (Brecken-

ridge 1956, Bellrose 1980). They lose an average of 1.3 g/day during incubation, but changes in body mass vary greatly within and among females (Harvey et al. 1989). Loss of body mass during incubation may influence the reproductive success of Wood Ducks. Kennamer and Hepp (1987), for example, reported that double-brooded females lost a smaller proportion of body mass during incubation of first nests than females that nested only once. In this study, we tested the effects of body mass of incubating female Wood Ducks on subsequent survival and on aspects of their current and future reproduction. We also examined factors that influence length of the incubation period.

METHODS

The study was conducted from January to July, 1986–1989, on the U.S. Department of Energy's Savannah River Site (SRS) in west-central South Carolina (33.10°N, 81.30°W). Approximately 140 nest boxes were available to Wood Ducks each year, and boxes were checked weekly to provide information on nesting activity.

Nesting data.—Checking nest boxes weekly allowed us to find nests during the egg-laying stage. We estimated the date of nest initiation by subtracting the number of eggs in the nest when it was first found from the date that the nest box was checked (i.e. assumed laying rate of one egg per day [Bellrose 1980]). Female Wood Ducks frequently engage in intraspecific nest parasitism (dump or parasitic nests) where >1 female deposit eggs in a nest (Clawson et al. 1979, Semel and Sherman 1986). We classified nests as *dump nests* if egg deposition rates exceeded one egg per day or if clutch sizes were >16 eggs (Morse and Wight 1969). Nest initiation dates were estimated similarly for parasitic and nonparasitic nests. Dump nests occasionally contained more eggs than the elapsed time (days) between nest-box checks. These nests were estimated to have been initiated one day after the previous check of the nest box.

Length and breadth of eggs were measured (nearest 0.1 mm) with vernier calipers, and measurements were used to estimate fresh egg mass of each egg and clutch mass of every nest (Hepp et al. 1987b).

Duration of incubation.—The *incubation period* was defined as the number of days between the start of incubation and hatching of eggs. Day of hatching was known precisely in 1986 and 1987, because we marked newly hatched ducklings as part of another study (Hepp et al. 1989). In 1988, however, hatch dates were known only for nests (*n* = 19) that were visited on days when the eggs were pipping.

The day that females began incubation was esti-

mated in the following manner. For nonparasitic nests in 1986 and 1987, we assumed that females laid one egg per day and that incubation began on the day the clutch was completed (but see Arnold et al. 1987, Afton and Paulus 1990). It was assumed that females incubating dump nests (i.e. host females) in 1986 and 1987 laid a number of eggs similar to that of females of nonparasitic nests that nested at the same time. We also assumed that incubation began on the day the host laid her final egg. Clutch size of Wood Ducks declines seasonally (Hepp unpubl. data), as it does in other species of waterfowl (see Toft et al. 1984). Therefore, we regressed clutch size of normal nests with the date of nest initiation. Regression equations (**1986**: CLUTCH SIZE = 14.8 − 0.0399(DATE), r^2 = 0.34, P = 0.0002; **1987**: CLUTCH SIZE = 14.5 − 0.0358(DATE), r^2 = 0.30, P = 0.0003) were used to estimate the number of eggs deposited in dump nests by host females. Clutch sizes estimated in this manner were rounded to the nearest integer. To check the suitability of this regression approach for determining first day of incubation, we applied the method to 1988 data for which we also had accurate candling information (see below). A t-test for paired comparisons confirmed that the two methods were similar overall (mean difference = 0.31 days, df = 60, P = 0.24).

In 1988, most (75%) of the eggs in every clutch were candled (Weller 1957) in early incubation (before day 15) to determine the stage of embryo development (see Hanson 1954). From this information, we computed average number of days that eggs had been incubated for both parasitic and nonparasitic nests. We substracted the average day of incubation from the date that the eggs were candled to estimate the day that incubation began.

For analyses involving length of the incubation period, we tested parasitic and nonparasitic nests separately in 1986 and 1987 because of differences in the way the start of incubation was estimated in those years. In 1988 the method for estimating the day when incubation began was the same for all nests.

Body mass and the return of females.—We captured incubating females in nest boxes, banded them with USFWS leg bands, and measured body mass to the nearest 5 g with a 1,000-g Pesola scale. Some females were captured during both early (≤day 15; $\bar{x}$ = day 5) and late (>day 15; $\bar{x}$ = day 30) incubation. Most (88%) females were caught between 0800 and 1200 to minimize any diurnal variation in body mass. In 1987 and 1988, flattened wing length (mm) from the wrist to the end of the longest primary was measured also. Females were returned to the nest box after capture.

Body mass often is a good measure of nutrient reserves (e.g. lipids) in birds. However, adjusting body mass by a measure of structural size may improve this relationship (Johnson et al. 1985). We calculated and used a condition index (body mass/wing length) in analyses of 1987 and 1988 data. Inferences from tests using either body mass or the condition index did

not differ. We, therefore, chose to use body mass for simplicity.

If body mass varies among females at the start of incubation, then changes in body mass expressed as grams per day may not assess accurately the relative costs of incubation. The following statistic was used to compare changes in body mass of incubating females:

$$\lambda = (\text{body mass}_{t+\Delta}/\text{body mass}_t)^{1/\Delta}, \qquad (1)$$

where λ is the relative change in body mass, body mass$_{t+\Delta}$ is the body mass of females during late incubation, body mass$_t$ is the body mass of females during early incubation, and Δ is the number of days between the two measurements of body mass. Values of 1.0 represent no change, <1.0 a loss, and >1.0 a gain in body mass.

Capture probabilities (p_i) of females were estimated with the Jolly-Seber capture-recapture model for open populations (Jolly 1965, Seber 1965). These estimates correspond to the probability that a female alive and in the population during breeding season i will be captured during that period. During the study, $\hat{p}_i$ averaged 0.89, which indicates that most females, if alive, returned to nest boxes and were captured (see Hepp et al. 1987a, 1989).

Analysis.—Return of breeding female Wood Ducks is a binary variable; a female either returns to nest and is recaptured, or she does not. Females were counted as returning if they were captured while incubating a clutch of eggs, regardless of whether the nest was successful. We used logistic regression analysis to examine the relationship between body mass at the end of incubation and return of females to breed in the subsequent year (Cox 1970). A number of ecological studies recently have used this method of analysis (see Haramis et al. 1986, Boyce and Perrins 1987, Hepp et al. 1989).

If θ_i is the probability of return for individual i, then the linear-logistic model provides a reasonable form of the relationship between θ_i and female body mass at the end of incubation (also see Martin 1987: 458):

$$\theta_i = \exp(B_0 + B_1 x_i)/[1 + \exp(B_0 + B_1 x_i)], \qquad (2)$$

where B_0 and B_1 are the model parameters, and their estimates and standard errors are computed using maximum likelihood procedures. In model M_1 (Equation 2), x_i is the body mass of female i at the end of incubation.

We tested whether the body mass of females at the end of incubation influenced their return in the next breeding season by using a null model (M_0) that does not include body mass as an independent variable. In model M_0, θ_i is written:

$$\theta_i = \exp(B_0)/[1 + \exp(B_0)]. \qquad (3)$$

TABLE 1. Means (±SD) of body mass (g) and the relative change in body mass (λ) of female Wood Ducks during incubation. Means in each column not followed by the same letter are significantly different (Duncan's multiple-range test, $P < 0.05$); relative change in body mass (λ) equals (body mass in late incubation/body mass in early incubation)$^{1/\Delta}$, where Δ is the number of days between the two measures of body mass.

Year	n	Early incubation	Late incubation	λ
1986	31	586.6 ± 47.1 A	546.1 ± 45.6 A	0.9970 ± 0.0022 A
1987	64	579.0 ± 43.2 A	548.0 ± 43.5 A	0.9980 ± 0.0020 B
1988	57	572.9 ± 43.7 A	564.5 ± 45.8 A	0.9994 ± 0.0018 C
Weighted average		578.0	553.3	0.9983

The null model assumes that each female has the same probability of return regardless of body mass at the end of incubation. Maximum likelihood estimates of B_0 were calculated, and likelihood ratio tests of model M_0 vs. M_1 provided a test of the hypothesized relationship. Likelihood-ratio test statistics are distributed as Chi-square. Test statistics were computed separately for each year, and composite statistics were calculated that also are distributed as Chi-square.

Wilcoxon rank sum tests provided another method to test the null hypothesis that females returning to nest were not heavier at the end of incubation than females that did not return to nest (Dietz 1985). Years were tested individually, and probabilities were combined to obtain a composite test (Sokal and Rohlf 1981: 780). Composite statistics are distributed as Chi-square with $2n$ degrees of freedom.

If body mass and return rate of females were age specific, then results and interpretation of these analyses might be affected. However, female age was not an important factor in these analyses, because annual return rates of yearling females were not different from adults (Chi-square tests, $P > 0.05$). These results agree with Nichols and Johnson (1990), who reported that survival rates of female Wood Ducks in the southeastern United States were not age-specific.

SAS (SAS Institute 1988) was used for statistical summaries and analyses. With the exception of logistic regressions and Wilcoxon rank sum tests, we used data from successful (i.e. that produced at least one duckling) first nests only. Second-nest attempts and nests that were unsuccessful were excluded. We used initiation date of first nests and clutch size of nonparasitic nests to test relationships between body mass at the end of incubation in year i and the nest initiation date and clutch size in year $i + 1$.

RESULTS

Body mass dynamics.—Body mass of female Wood Ducks early ($\bar{x} = 578.0$ g) and late (553.3 g) in the incubation period did not differ among years (one-way ANOVAs, $P > 0.05$) (Table 1). Heavy females tended to nest earlier in the sea-

son than light females (Table 2). The relative change in body mass during incubation varied significantly among years ($F = 15.7$; df = 2, 149; $P < 0.001$) and was greatest in 1986 (Table 1). There was a decline in body mass for most incubating females in 1986 (87.1%, $n = 31$) and 1987 (81.2%, $n = 64$), but approximately 42% ($n = 57$) of the females in 1988 either gained body mass while incubating or there was no change.

Female return and future reproduction.—In 1986 the $\hat{B}_1$ value of the logistic regression was positive, indicating that heavy females were more likely to return to nest the following year than light females (Table 3). All tests of the relationship were marginally significant ($P < 0.10$) in 1986, but none of the tests were significant in 1987 or 1988.

Body mass of females at the end of incubation was not correlated in any year with either the date of nest initiation ($P > 0.30$) or clutch size ($P > 0.85$) in the next breeding season.

Hatching success and incubation length.—Body mass of females at the beginning of incubation was not correlated in any year with either hatching success ($P > 0.55$) or length of the incubation period ($P > 0.15$). The incubation period was longer in 1987 for females that nested early, but this relationship was absent in other years (Table 4). With the exception of nonparasitic nests in 1986, simple correlation anal-

TABLE 2. Correlations between the body mass of female Wood Ducks during early incubation (< day 15) and the date of nest initiation.

Year	n	r[a]	P
1986	32	−0.30	0.10
1987	64	−0.45	0.0002
1988	58	−0.26	0.05

[a] Pearson's correlation coefficient.

TABLE 3. Logistic regression parameter estimates and test statistics of the relationship between body mass of female Wood Ducks at the end of incubation and the probability of returning to nest in the next breeding season.

Year of return	Model M_1 parameter estimates					M_1 vs. M_0			Rank sum test	
	$\hat{B}_0$	$\widehat{SE}(\hat{B}_0)$	$\hat{B}_1$	$\widehat{SE}(\hat{B}_1)$	P	χ^2	df	P	T	P
1987	−11.44	7.49	+0.024	0.014	0.09	3.67	1	<0.10	1.8	0.08
1988	0.54	3.16	−0.000	0.006	0.95	0.01	1	<0.90	0.4	0.68
1989	−0.09	3.31	−0.000	0.006	1.00	0.00	1	1.00	0.2	0.85
Means and totals	−3.66	7.45	+0.008	0.014	0.50	3.68	3	<0.50	$\chi^2 = 6.16$, df = 6, $P < 0.50$	

yses showed a positive association between length of incubation and clutch mass in all three years (Table 4). Results were significant ($P < 0.05$) in 1986 and 1987, and they were marginally significant ($P = 0.08$) in 1988. Clutch masses of parasitic and nonparasitic nests generally were larger early in the nesting season (Table 4), and this relationship may have contributed to the positive association between clutch mass and length of incubation. After controlling for date of nesting, partial correlation coefficients indicated a significant positive association between clutch mass and incubation length of parasitic nests in 1986 and 1987 (Table 4). This relationship was marginally significant ($P = 0.09$) in 1988 and not significant ($P > 0.20$) for nonparasitic nests in 1986 and 1987 (Table 4).

DISCUSSION

Body mass and incubation costs.—Studies of reproductive costs in birds have emphasized the effects of brood size on survival and future reproduction of the parents. Most research has been done on altricial species. In one of the few studies of a precocial species, Lessells (1986) manipulated brood size of Canada Geese (*Branta canadensis*), and demonstrated that body mass of females caring for large broods was lower during the molt period and that they molted later than females with small broods. Overwinter survival and clutch size in the next breeding season were not affected by brood size, but geese with larger broods nested later the next year. Care of precocial young after hatching generally is not considered a major cost to parents. Lessells' (1986) results emphasize that costs indeed are associated with rearing large broods in species that do not feed their young. The cost of parental care has been shown to increase with brood size in other precocial species (Wal-

ters 1982) and may play an important role in determining clutch size in these species (Winkler and Walters 1983).

In Blue Tits, where parents feed their young, increases in brood size resulted in greater loss of body mass for the adult females (Nur 1984, 1988). Females with low body mass had lower probabilities of surviving to the next breeding season, which suggests that loss of body mass is costly to females (Nur 1984, 1988). Similar results have been reported for male Pied Flycatchers (*Ficedula hypoleuca*) that care for large broods (Askenmo 1979). The basic idea is that parents that care for large broods have less time to devote to self maintenance; hence, they end the breeding period in poorer condition than parents of small broods.

Body mass of female Wood Ducks at the end of incubation had no effect on their date of nest initiation or clutch size in the next breeding season. In 1986, heavy females returned at higher rates than light females. There was no relationship in 1987 and 1988 between body mass of females and their survival to the next breeding season. Reduced survival of light females in 1986 coincided with a greater loss of body mass in that year relative to 1987 and 1988. Changes in body mass vary greatly within and among incubating female Wood Ducks (Harvey et al. 1989). Some females are better at balancing the various costs of incubation than others. Harvey et al. (1989) suggested that annual variation in the amount of local precipitation affected the availability of wetlands and influenced body-mass dynamics of incubating females. The positive relationship between body mass of females at the end of incubation and their survival to the next breeding season suggests that incubation can be an important reproductive cost for Wood Ducks during some years.

Female Wood Ducks that incubate clutches

TABLE 4. Correlations and partial correlations between the length of incubation, clutch mass, and date of nesting of female Wood Ducks.

	Nest type[a]				
	1986		1987		1988
Association	P (*n* = 20)	NP (*n* = 25)	P (*n* = 39)	NP (*n* = 22)	Combined (*n* = 19)
Correlation					
Length of incubation × clutch mass	0.44[b]	−0.11	0.63	0.54	0.41
	0.05[c]	0.59	0.0001	0.009	0.08
Length of incubation × nesting date	0.08	−0.03	−0.52	−0.59	−0.01
	0.75	0.87	0.0007	0.004	0.98
Clutch mass × nesting date	−0.43	−0.57	−0.35	−0.61	−0.18
	0.06	0.003	0.03	0.003	0.45
Partial correlation[d]					
Length of incubation × clutch mass	0.52	−0.16	0.56	0.29	0.42
	0.02	0.45	0.0003	0.21	0.09

[a] Nest type: P = parasitic; NP = nonparasitic; Combined = parasitic and nonparasitic nest types. See the Methods section for a description of nest types.

[b] Correlation coefficient, for *n* < 20 we used Spearman's correlation coefficient (r_s) and for *n* ≥ 20 we used Pearson's correlation coefficient (*r*).

[c] Probability level.

[d] Date of nesting is held constant.

early in the breeding season generally are heavier than females that begin incubation later. Energy reserves of early-nesting females may provide them with an important buffer that can be used when energy expenditures increase or the ability of females to acquire energy decreases. Females that cannot begin incubation in good physical condition may postpone nesting, engage in intraspecific nest parasitism, or both. Clawson et al. (1979), for example, reported that some female Wood Ducks laid eggs parasitically before establishing their own nests later in the season. This type of "mixed reproductive strategy" may depend partly on female body condition (see Lank et al. 1989). Competition for limited nest sites certainly contributes to nest parasitism in the cavity-nesting Wood Duck. However, reproductive success may be improved if females pursue a "mixed strategy" when they cannot begin incubation in good condition. Wood Ducks have a lengthy breeding season (e.g. 122 days in South Carolina), which increases the opportunity for females that are parasitic early in the season to initiate their own nests at a later time.

Length of incubation.—Nest attentiveness during incubation is related positively to body mass within and among species of waterfowl (Afton and Paulus 1990). If Wood Duck response is similar to the response of other waterfowl, then low body mass should lead to reduced nest at-

tentiveness with longer incubation periods and possibly lower hatching success. We found that body mass of female Wood Ducks at the beginning of incubation was not related to either duration of incubation or hatching success. These results contrast with those in Canada Geese where heavy females were at the nest longer than light females, and had shorter incubation periods (Aldrich and Raveling 1983). We have no data on the activity patterns of incubating Wood Ducks, and it is possible that body mass had no effect on nest attentiveness. However, heavy female Wood Ducks tended to nest earlier in the breeding season than light females. Even if small females were less attentive than large females, eggs would cool more slowly later in the season in response to warmer ambient temperatures (Caldwell and Cornwell 1975). Under these circumstances, females nesting later could spend less time at the nest without affecting egg temperature and thus hatching success and incubation duration.

We found that length of the incubation period was inversely related to nesting date in one of three years. Ambient temperatures are cooler early in the nesting season than they are later. Low temperatures cause eggs to cool faster when they are left unattended (Caldwell and Cornwell 1975), and temperature of eggs may decline as ambient temperature declines even with constant incubation (Haftorn and Reinert-

sen 1985). Low egg temperature during incubation may result in longer incubation periods (see Booth 1987). Beginning incubation in good condition, therefore, may be important for female Wood Ducks nesting early in the breeding season. Lipid reserves of female Wood Ducks can provide only a small part of the total energy demands of incubation (Drobney 1980). However, heavy females may be able to provide more constant care to eggs than light females, which is important when ambient temperatures are low. Female Wood Ducks that start incubating at higher body mass, for example, lose mass at a faster rate than light females (Harvey et al. 1989).

Length of the incubation period for Wood Ducks also increased as clutch mass of parasitic nests increased. Larger clutches can result in longer incubation periods (Jones 1987, Coleman and Whittall 1988), and energy expenditure is greater for birds that incubate at temperatures below the thermoneutral zone (Biebach 1984). All eggs in large clutches may not come in contact with the brood patch (Mertens 1977); consequently some eggs cool and need to be rewarmed, which causes a longer incubation period. In our study, the significant relationship between clutch mass and length of incubation for parasitic—but not for nonparasitic—nests suggests that disruption of nesting activity by nest parasites may also contribute to this relationship.

Clutch mass had no effect on the weight loss of incubating Wood Ducks (Harvey et al. 1989). This indicates either that energy expenditures of females were not dependent on clutch mass, or that they were able to adjust nutrient intake so that body mass was not affected. Jones (1987), for example, reported that swallows (*Hirundo rustica*) spent more time incubating experimentally enlarged clutches, but that body mass decreased only during periods when food availability was low.

Intraspecific nest parasitism (dump nesting) is common in Wood Ducks (Clawson et al. 1979, Heusmann et al. 1980, Semel and Sherman 1986), as well as in other species of birds (Rohwer and Freeman 1989). During a nine-year period in Missouri, clutch size of nonparasitic nests averaged 11.4 eggs, while clutch size of parasitic nests averaged 20.2 eggs (Clawson et al. 1979). Potential costs of nest parasitism to host females involve laying fewer of their own eggs (An-

dersson and Eriksson 1982, but see Rohwer 1984) and disruption or abandonment of nesting activity (Pienkowski and Evans 1982, Semel and Sherman 1986). A longer incubation period associated with larger clutch mass is also a potential cost of nest parasitism that has not been previously addressed. Nests taking longer to hatch are at greater risk from predation, and embryos may use more energy as a result of longer developmental time and hatch with smaller residual yolk reserves. Both factors have the potential to reduce the reproductive success of host females.

LITERATURE CITED

AFTON, A. D. 1979. Incubation temperatures of the Northern Shoveler. Can. J. Zool. 57: 1052–1056.
———. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82: 132–137.
———, & S. L. PAULUS. 1990. Incubation and brood care in waterfowl. *In* The ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). Saint Paul, Univ. Minnesota Press. In press.
ALDRICH, T. W., & D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. Auk 100: 670–679.
ANDERSSON, M., & M. O. G. ERIKSSON. 1982. Nest parasitism in Goldeneyes *Bucephala clangula*: some evolutionary aspects. Am. Nat. 120: 1–16.
ANKNEY, C. D., & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95: 459–471.
ARNOLD, T. W., F. C. ROHWER, & T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. Am. Nat. 130: 643–653.
ASKENMO, C. 1979. Reproductive effort and return

rate of the male Pied Flycatcher. Am. Nat. 114: 748–753.

BELLROSE, F. C. 1980. Ducks, geese, and swans of North America. Harrisburg, Pennsylvania, Stackpole Books.

BIEBACH, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating Starlings (*Sturnus vulgaris*). Physiol. Zool. 57: 26–31.

BOOTH, D. T. 1987. Effect of temperature on development of Mallee Fowl *Leipoa ocellata* eggs. Physiol. Zool. 60: 437–445.

BOYCE, M. S., & C. M. PERRINS. 1987. Optimizing Great Tit clutch size in a fluctuating environment. Ecology 68: 142–153.

BRECKENRIDGE, W. J. 1956. Nesting study of Wood Ducks. J. Wildl. Manage. 20: 16–21.

CALDWELL, P. J., & G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard duck. Auk 92: 706–731.

CARTAR, R. V., & R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour 95: 261–289.

CLAWSON, R. L., G. W. HARTMAN, & L. H. FREDRICKSON. 1979. Dump nesting in a Missouri Wood Duck population. J. Wildl. Manage. 43: 347–355.

COLEMAN, R. M., & R. D. WHITTALL. 1988. Clutch size and the cost of incubation in the Bengalese Finch (*Lonchura striata* var. *domestica*). Behav. Ecol. Sociobiol. 23: 367–372.

COX, D. R. 1970. The analysis of binary data. London, Chapman and Hall.

DIETZ, E. J. 1985. The rank sum test in the linear logistic model. Am. Stat. 39: 322–325.

DRENT, R. 1975. Incubation. Pp. 333–420 *in* Avian biology, Vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

———, J. M. TINBERGEN, & H. BIEBACH. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. Netherlands J. Zool. 35: 103–123.

DROBNEY, R. D. 1980. Reproductive bioenergetics of Wood Ducks. Auk 97: 480–490.

EISNER, E. 1960. The biology of the Bengalese Finch. Auk 77: 271–287.

FEARE, C. 1984. The Starling. New York, Oxford Univ. Press.

FREED, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? Ecology 62: 1179–1186.

HAFTORN, S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. Ornis Scandinavica 19: 97–110.

———, & R. E. REINERTSEN. 1985. The effect of temperature and clutch size on the energetic cost of

incubation in a free-living Blue Tit (*Parus caeruleus*). Auk 102: 470–478.

HANSON, H. C. 1954. Criteria of age of incubated Mallard, Wood Duck, and Bob-white Quail eggs. Auk 71: 267–273.

HARAMIS, G. M., J. D. NICHOLS, K. H. POLLOCK, & J. E. HINES. 1986. The relationship between body mass and survival of wintering Canvasbacks. Auk 103: 506–514.

HARVEY, W. F., IV, G. R. HEPP, & R. A. KENNAMER. 1989. Body mass dynamics of Wood Ducks during incubation: individual variation. Can. J. Zool. 67: 570–574.

HEPP, G. R., R. T. HOPPE, & R. A. KENNAMER. 1987a. Population parameters and philopatry of breeding female Wood Ducks. J. Wildl. Manage. 51: 401–404.

———, D. J. STANGOHR, L. A. BAKER, & R. A. KENNAMER. 1987b. Factors affecting variation in the egg and duckling components of Wood Ducks. Auk 104: 435–443.

———, R. A. KENNAMER, & W. F. HARVEY IV. 1989. Recruitment and natal philopatry of Wood Ducks. Ecology 70: 897–903.

HEUSMANN, H. W., R. BELLVILLE, & R. G. BURRELL. 1980. Further observations on dump nesting by Wood Ducks. J. Wildl. Manage. 44: 908–915.

HOHMAN, W. L. 1986. Incubation rhythms of Ringnecked Ducks. Condor 88: 290–296.

JOHNSON, D. H., G. L. KRAPU, K. J. REINECKE, & D. G. JORDE. 1985. An evaluation of condition indices for birds. J. Wildl. Manage. 49: 569–575.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225–247.

JONES, G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J. Anim. Ecol. 56: 229–245.

KENNAMER, R. A., & G. R. HEPP. 1987. Frequency and timing of second broods in Wood Ducks. Wilson Bull. 99: 655–662.

LANK, D. B., E. G. COOCH, R. F. ROCKWELL, & F. COOKE. 1989. Environmental and demographic correlates of intraspecific nest parasitism in Lesser Snow Geese *Chen caerulescens caerulescens*. J. Anim. Ecol. 58: 29–45.

LESSELLS, C. M. 1986. Brood size in Canada Geese: a manipulation experiment. J. Anim. Ecol. 55: 669–689.

LYON, B., & R. D. MONTGOMERIE. 1985. Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? Behav. Ecol. Sociobiol. 17: 279–284.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev. Ecol. Syst. 18: 453–487.

MERTENS, J. A. L. 1977. The energy requirements for

incubation in Great Tits, *Parus major* L. Ardea 65: 184–196.

MORSE, T. E., & H. M. WIGHT. 1969. Dump nesting and its effect on production in Wood Ducks. J. Wildl. Manage. 33: 284–293.

NICHOLS, J. D., & F. A. JOHNSON. 1990. Wood Duck population dynamics: a review. *In* North American Wood Duck Symposium (L. H. Frederickson and G. V. Burger, Ed.). In press.

NILSSON, J. A., & H. G. SMITH. 1988. Incubation feeding as a male tactic for early hatching. Anim. Behav. 36: 641–647.

NUR, N. 1984. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53: 479–496.

———. 1988. The consequences of brood size for breeding Blue Tits: III. Measuring the cost of reproduction: survival, future fecundity and differential dispersal. Evolution 42: 351–362.

PEACH, H. C., & V. G. THOMAS. 1986. Nutrient composition of yolk in relation to early growth of Canada Geese. Physiol. Zool. 59: 344–356.

PIENKOWSKI, M. W., & P. R. EVANS. 1982. Clutch parasitism and nesting interference between Shelducks at Aberlady Bay. Wildfowl 33: 159–163.

ROHWER, F. C. 1984. Patterns of egg laying in prairie ducks. Auk 101: 603–605.

———, & S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. Can. J. Zool. 67: 239–253.

SAS INSTITUTE. 1988. SAS/STAT user's guide, 6.03 Ed. Cary, North Carolina, SAS Inst. Inc.

SEBER, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52: 249–259.

SEMEL, B., & P. W. SHERMAN. 1986. Dynamics of nest parasitism in Wood Ducks. Auk 103: 813–816.

SHERRY, D. F., N. MROSOVSKY, & J. A. HOGAN. 1980. Weight loss and anorexia during incubation in birds. J. Comp. Physiol. Psychol. 94: 89–98.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry, second edition. San Francisco, California, W. H. Freeman.

TOFT, C. A., D. L. TRAUGER, & H. W. MURDY. 1984. Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Aythya*, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol. 53: 75–92.

VLECK, C. M. 1981. Hummingbird incubation: female attentiveness and egg temperature. Oecologia 51: 199–205.

———, C. M. VLECK, & D. F. HOYT. 1980. Patterns of metabolism and growth in avian embryos. Am. Zool. 20: 405–416.

WALTERS, J. R. 1982. Parental behavior in Lapwings (Charadriidae) and its relationship with clutch sizes and mating systems. Evolution 36: 1030–1040.

WELLER, M. W. 1957. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20: 111–113.

WHITE, F. N., & J. L. KINNEY. 1974. Avian incubation. Science 186: 107–115.

WINKLER, D. W., & J. R. WALTERS. 1983. The determination of clutch size in precocial birds. Curr. Ornithol. 1: 33–68.