

Fitness consequences of delayed maturity in female wood ducks

Madan K. Oli,^{1*} Gary R. Hepp² and Robert A. Kennamer³

¹Department of Wildlife Ecology and Conservation, University of Florida, 303 Newins-Ziegler Hall, Gainesville, FL 32611, ²School of Forestry and Wildlife Sciences, Auburn University, 108 M. White Smith Hall, Auburn, AL 36849-5418 and ³Savannah River Ecology Laboratory, The University of Georgia, PO Drawer E, Aiken, SC 29802, USA

ABSTRACT

Age at maturity has been suggested to be an important life-history trait with substantial potential for influencing the evolution of life histories. Using known reproductive histories of 90 female wood ducks (*Aix sponsa*) from a long-term study (1982–96), we investigated the fitness consequences of changes in age at maturity. Female wood ducks that attained sexual maturity as yearlings had a significantly shorter lifespan than those that delayed reproduction until 2 years of age or later. However, females that delayed reproduction neither produced a larger number of ducklings during their first reproductive event, nor did they have a greater number of successful lifetime breeding attempts than those maturing as yearlings. Females that attained sexual maturity as yearlings had the greatest individual fitness; the results indicated a directional selection for early maturity. These results are consistent with life-history theory predictions and suggest that reduced lifespan in female wood ducks is the primary cost associated with early maturity; however, costs of early maturity are outweighed by the associated benefits in fitness currency. Regression of individual fitness on age at maturity indicated strong directional selection for early maturity. These results suggest that attaining sexual maturity as yearlings may be an evolutionarily stable strategy in our study population, and that females delaying reproduction do so because they are genetically or environmentally constrained, not because of the potential fitness benefits of delayed maturity.

Keywords: age at maturity, *Aix sponsa*, cost of reproduction, demography, fitness, individual fitness, life-history evolution, life-history trade-offs, lifetime reproductive success, wood duck.

INTRODUCTION

The age at which reproduction begins (hereafter, age at maturity) has been suggested to be an important life-history trait with substantial potential for influencing fitness (Cole, 1954; Lewontin, 1965; Caswell and Hastings, 1980; Oli and Dobson, 1999). Within species, a genotype that attains sexual maturity early often has a greater probability of realizing fitness because its offspring start reproducing sooner, and thus is expected to have a higher

* Author to whom all correspondence should be addressed. e-mail: olim@wec.ufl.edu
Consult the copyright statement on the inside front cover for non-commercial copying policies.

fitness than a late-maturing genotype (e.g. Cole, 1954; Lewontin, 1965; Bell, 1980; Caswell and Hastings, 1980; Roff, 1992; Stearns, 1992; Oli and Dobson, 1999). However, fitness benefits of earlier maturity may be balanced due to associated costs if earlier reproduction inhibits growth, survival or future reproduction, reduces quality or survival propensity of offspring, or if delaying maturity allows additional growth or experience and thus substantially increases future reproductive output (Stearns, 1989, 1992). Despite an apparent high selection pressure on age at maturity, reduction in age at maturity may be environmentally constrained in some species, even if it were genetically possible (Dobson and Oli, 2001; Oli *et al.*, 2001). Because of the high sensitivity of fitness to changes in age at maturity in some organisms (Cole, 1954; Lewontin, 1965; Oli, 1999b; Oli and Dobson, 1999), fitness consequences of delayed maturity have recently received substantial attention in the life-history literature (Caswell and Hastings, 1980; Saitoh, 1981; Stearns and Crandall, 1981; Vandenbergh, 1987; Wooten, 1987; Charnov, 1990; Kokko and Ranta, 1996; Tkadlec and Zejda, 1998; also see Clutton-Brock, 1988; Newton, 1989). The results of such studies, however, have been equivocal. Using lifetime reproductive success as a measure of fitness, Wallin (1988) found that delayed maturity had no significant fitness consequences in tawny owls (*Strix aluco*). Similar results were reported for Florida scrub jays (*Aphelocoma coerulescens*; Fitzpatrick and Woolfenden, 1988), pied flycatchers (*Ficedula hypoleuca*; Sternberg, 1989), lesser snow geese (*Anser caerulescens caerulescens*; Viallefont *et al.*, 1995) and Western gulls (*Larus occidentalis*; Pyle *et al.*, 1997). Newton (1988) investigated fitness consequences of delayed maturity in sparrowhawks (*Accipiter nisus*) but found no evidence that early maturity conferred higher fitness. However, re-analysis of these data led McGraw and Caswell (1996) to suggest that using lifetime reproductive success to quantify fitness may obscure patterns of the fitness consequences related to delayed maturity. Using estimates of individual fitness (cf. McGraw and Caswell, 1996) to quantify fitness, they showed that fitness of female sparrowhawks was negatively associated with age at maturity. Brommer *et al.* (1998), who used both lifetime reproductive success and individual fitness as measures of fitness, found no fitness consequences of delayed maturity in Ural owls (*Strix uralensis*). Pärt (1995) obtained conflicting results about the effects of prior breeding experience (which is determined by age at maturity) on reproductive performance of collared flycatchers (*Ficedula albicollis*). Authors of studies that have failed to detect fitness consequences of earlier maturity have suggested that benefits of earlier maturity may be offset or outweighed by costs of early maturity (e.g. Pyle *et al.*, 1997).

The wood duck (*Aix sponsa*) is a North American waterfowl species that is distributed primarily east of the Mississippi River drainage system and nests from the Maritime Provinces of Canada to southern Florida (Hepp and Bellrose, 1995). Many aspects of its life history and management have been studied thoroughly (Bellrose and Holm, 1994). Wood ducks are socially monogamous, but only females care for the precocial young (Fredrickson, 1990). They nest in natural cavities but will readily use nest boxes (Bellrose *et al.*, 1964), and breeding females exhibit a high degree of fidelity to natal areas and previous nest sites (Hepp *et al.*, 1987, 1989; Hepp and Kennamer, 1992). Female wood ducks generally attain sexual maturity as yearlings, but some may defer breeding until 2 or 3 years of age (Heusmann, 1975; Kennamer and Hepp, 2000).

Using data from a long-term study, we investigated fitness consequences of delayed maturity in female wood ducks. Specifically, we asked the following questions: (1) Do females that attain sexual maturity as yearlings produce fewer ducklings in their lifetimes? (2) Do females that attain sexual maturity as yearlings have shorter lifespans than those

attaining sexual maturity later? (3) What are the fitness consequences of delayed maturity in female wood ducks? Furthermore, we quantified fitness in terms of both lifetime reproductive success and individual fitness for comparative purposes.

MATERIALS AND METHODS

Study area and field methods

The study was conducted from 1982 to 1996 on the United States Department of Energy's Savannah River Site in west-central South Carolina (33.1° N, 81.3° W; see White and Gaines, 2000, for details). Approximately 120–140 nest boxes were available to wood ducks annually. Nest boxes were checked weekly during the breeding season (January–July) to obtain information on nesting activity (Kennamer and Hepp, 2000). Frequent checks of nest boxes during the breeding season allowed us to find nests before egg laying was completed. Date of nest initiation was estimated by subtracting the number of eggs in the nest when it was first found from the day (Julian date) after the nest box was checked, assuming a laying rate of one egg per day (Drobney, 1980). Because we checked nest boxes every 7 days, our method of estimating date of nest initiation may have introduced a small bias (*c.* 1–3 days). However, this is unlikely to influence our results substantially, because estimated nest initiation dates were used only to categorize females as early or late nesters (see below).

Female wood ducks frequently engage in intraspecific brood parasitism in which more than one female deposits eggs in a nest (Clawson *et al.*, 1979; Semel and Sherman, 1986). We identified parasitized nests using at least one of the following criteria: (1) egg deposition rate exceeded one egg per day; (2) viable non-term eggs (i.e. eggs laid while host female was incubating) were present at hatching; and (3) clutch size was greater than 16 eggs (Morse and Wight, 1969). Nest initiation dates were estimated similarly for parasitized and non-parasitized nests. Nests parasitized during the laying period of host females contained more eggs than the elapsed number of days between nest box checks. These nests were estimated to have been initiated one day after the previous check of the nest box.

Nests were visited during the first week of incubation to determine clutch size and to estimate the day of incubation by candling eggs (Hanson, 1954; Weller, 1957). Using this information and assuming a 30 day incubation period (Bellrose and Holm, 1994; Manlove and Hepp, 2000), we estimated hatch dates. In 1982–87, 91% (2945/3232) of newly hatched ducklings were marked with serially numbered monel web tags before leaving the nest (Haramis and Nice, 1980). Nests in which ducklings were not web-tagged were visited within one week of hatching to count allantoic membranes remaining, and thus determine the number of ducklings that hatched and departed the nest box (Davis *et al.*, 1998). Successful nests were those in which at least one duckling hatched and exited the nest box; unsuccessful nests fledged no young ('fledging' is defined here as hatching and exiting the nest).

Adult females were captured in nest boxes during incubation. Females were examined for web tags, weighed and banded with US Fish and Wildlife Service leg bands. Recaptures of web-tagged females as breeding adults allowed us to assign them an exact age. Unmarked females were aged (i.e. yearling or older) by using wing feather characteristics (Harvey *et al.*, 1989). Capture probability (p_i) was estimated for female wood ducks using the Jolly-Seber capture–recapture model for open populations (Jolly, 1965; Seber, 1965), where p_i is the

probability that a female alive and in the population in year t will be captured. During the study period, p_t averaged 0.895, indicating that most surviving females that did not permanently emigrate returned to nest boxes and were captured (Kennamer and Hepp, 2000). A comparison of Jolly-Seber model survival estimates for our population with survival estimates based on wood duck band recovery data in the southeastern USA indicated that permanent and temporary emigration from our population was low and thus fidelity to nest boxes was high (Hepp *et al.*, 1987). We also have no reason to believe that emigration or capture probabilities differed with respect to female age or breeding status. We assumed that complete reproductive histories of females were known because: (1) capture probabilities were high, (2) emigration was low and (3) there was a minimum of 8 consecutive years during which lifetime reproduction could be quantified for every female. From 1982 through 1996, only one female was known to have survived to breed beyond 8 years of age (R.A. Kennamer, unpublished data). No females included in this study were known to have nested in the last year of study.

Data analysis

Of 90 females with known age at maturity and complete reproductive histories, 68 had been web-tagged as ducklings and 22 more had been aged as yearlings in 1987 and 1988 using wing feather characteristics (Harvey *et al.*, 1989). Only these birds were used in our analyses.

We used the matrix method of McGraw and Caswell (1996) to estimate individual fitness of females. Data for estimating individual fitness consist of ages at first and last reproduction and age-specific reproductive output for each individual in a population. A population projection matrix is then constructed for each individual, with age-specific fertility rates estimated from the reproductive data, and survival rates of 1. Age-specific annual fertility rate (F_i ; first row of the matrix) was estimated as the number of ducklings that left the nest per year multiplied by 0.5 to account for the genetic contribution of each parent to each offspring (McGraw and Caswell, 1996). Using the estimated annual fertility rate and an annual survival probability of 1 (lower subdiagonal of the matrix) until the female was no longer in the breeding population, a projection matrix ($\mathbf{A}_{(\text{duckling})}^{(m)}$) was constructed for each female m with known age at maturity, and individual fitness was calculated as the dominant eigenvalue of the projection matrix (McGraw and Caswell, 1996). The dominant eigenvalue of the projection matrix is the 'population growth rate of the individual' (McGraw and Caswell, 1996: 49). For example, if the number of ducklings fledged by female 2424 was 5, 6, 4, 8 and 12 in years 1988, 1989, 1990, 1991 and 1992, respectively, the projection matrix would be:

$$\mathbf{A}_{(\text{duckling})}^{(2424)} = \begin{bmatrix} 2.5 & 3 & 2 & 4 & 6 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

The individual fitness for female 2424 ($\lambda_{(\text{duckling})}^{(2424)}$), calculated as the dominant eigenvalue of the above projection matrix, would be 3.606. Individual fitness of zero was assigned to any female that did not survive beyond the first year of life to successfully nest at least once (see below).

Intraspecific brood parasitism occurs frequently in wood ducks and presents a challenge when estimating the annual fertility rate. We could not determine the number of fledglings in parasitized nests that were produced by the incubating female. Therefore, we used our long-term data to estimate the mean number of ducklings fledged in non-parasitized nests, and used these values for parasitized nests. Number of ducklings fledged varied ($F_{3,306} = 17.93$; $P < 0.0001$) with nesting date (early vs late) and wetland condition (wet, normal or dry; Kenamer, 2001), so we computed the mean number of ducklings produced in each of three categories: (1) early nests in wet, normal and dry years (10.13 ± 0.21 ducklings; mean ± 1 standard error), (2) late nests in wet and normal years (8.73 ± 0.22) and (3) late nests in dry years (7.31 ± 0.36). For parasitized nests, it was impossible to know the exact number of ducklings produced by the biological mother. Our only choice was to estimate this number using our long-term data as described above. This could have influenced the estimates of fertilities and some of the potential variation in estimates of individual fitness may have been masked. However, our approach is unlikely to have had a substantial influence on the mean fitness estimates because (1) estimates of the number of ducklings fledged from parasitized nests were based on our long-term data, and (2) we took into account two important factors (wetland condition and nesting date) that influence number of ducklings produced by females in our study population.

Females of parasitized nests were assigned values appropriate to their nesting date and wetland condition, except when the estimated brood size was greater than the number of ducklings known to have been fledged; in this case, we used the number of ducklings fledged. Early nests were initiated ≤ 53 days from the start of the nesting season, and late nests were those that were initiated > 53 days from the beginning of the nesting season. A female was excluded from the analyses if her last known nest was unsuccessful due to our research activities. However, if a female nested multiple times and a nest other than her last nest was unsuccessful due to our research activities, we assumed that nest would have been successful otherwise and estimated the number of ducklings that should have exited the nest based on wetland condition and time of nesting as described above ($n = 17$).

Female wood ducks can contribute to their fitness by being brood parasites. Because we captured and identified only incubating females, there was no way to quantify this contribution to overall fitness. At least some females that began nesting as 2-year-olds may have contributed to reproduction as yearlings by parasitizing the nests of other females. But this also is true of females that nested as yearlings. For example, it has been reported that females of all ages can engage in brood parasitism early in the breeding season before establishing nests of their own (Clawson *et al.*, 1979; Heusmann *et al.*, 1980). Our estimates of individual fitness, therefore, should be viewed as conservative because we did not consider the potential contribution of brood parasitism.

Lifetime reproductive success (LRS) was calculated for each female in two ways: (1) as the lifetime number of successful nests ($LRS_{(nest)}$) and (2) as the total number of ducklings estimated to have been fledged by a female in her lifetime ($LRS_{(duckling)}$; Clutton-Brock, 1988; Newton, 1989).

Some females that survived the first year without having nested undoubtedly died while waiting to reproduce as 2- or 3-year-olds. Because these females were never recaptured, we had no way of estimating their true rate of survival. Thus, we assumed that survival of females that nested as yearlings was similar to females of the same age that waited until 2 years of age or later to nest. We used actual return rates (i.e. adjusted for capture probability) of web-tagged females between their first and second years (0.712 ± 0.058 ;

mean \pm standard error) and their second and third years (0.767 ± 0.051) as estimates of survival for females that did not nest until they were 2- or 3-year-olds. Using these adjusted return rates, we estimated the number of females that did not attain sexual maturity as yearlings and did not survive to reproduce the following year ($n = 6$); these females were assigned an individual fitness or lifetime reproductive success of zero. Similar adjustments were made for females that delayed reproduction as 2-year-olds and did not survive ($n = 4$). We recognize that our assumption of equal survival rates for females that nested as yearlings and those that waited until 2 years of age or later to nest may have resulted in an overestimation of the number of females that might have died while waiting to nest as 2- or 3-year-olds if nest initiation was associated with a reduced survival. However, our data did not allow estimation of survival rates for females that did not initiate nesting as yearlings, and our estimates of individual fitness should be viewed as conservative. Survival from fledging to one year of age was assumed to be equal for all females regardless of the age at which reproduction began, so it was not necessary to make these adjustments for females that attained maturity as yearlings.

We estimated individual fitness and lifetime reproductive success separately for females that attained sexual maturity as yearlings ($\alpha = 1$), 2-year-olds ($\alpha = 2$) and 3-year-olds ($\alpha = 3$). Bootstrap means of individual fitness and lifetime reproductive success were calculated for each of these groups following the methods of Manly (1991). We used two-sample *t*-tests to determine if individual fitness and lifetime reproductive success differed significantly between females that attained sexual maturity as yearlings and those that did not. We used regression of individual fitness or lifetime reproductive success on age at maturity to evaluate the direction and intensity of selection on age at maturity (Lande and Arnold, 1983). First, linear regression was performed to estimate the forces of directional selection, β , and its standard error. Typically, the sign of the linear regression coefficient indicates direction of selection and the magnitude of the absolute value of the regression coefficient indicates intensity of selection on age at maturity. A quadratic regression was then performed to estimate the forces of stabilizing selection, γ (regression coefficient for the quadratic term), and its standard error. Standard errors of the estimates of directional selection and stabilizing selection were estimated as the standard error of β and γ , respectively. Regression coefficients (β and γ) that are not statistically different from zero would indicate no evidence of directional or stabilizing selection on age at maturity (Lande and Arnold, 1983).

RESULTS

Of 90 females used in our analyses, 70 began reproduction as yearlings ($\alpha = 1$), 15 as 2-year-olds ($\alpha = 2$) and 5 as 3-year-olds ($\alpha = 3$). On average, females that deferred reproduction as yearlings (and survived to reproduce at least once) lived longer (4.25 ± 0.51 years; mean \pm standard error) than those that nested in their first year (2.54 ± 0.20 years; *t*-test, $t_{88} = -3.68$, $P = 0.0004$). However, an estimated 28.8% of females that did not attain sexual maturity as yearlings died while waiting to breed as 2-year-olds, and an additional 23.3% of females died while waiting to breed as 3-year-olds. Because females that delayed reproduction lived longer, they tended to initiate nests more frequently (2.85 ± 0.50) than those first breeding as yearlings (2.43 ± 0.18), but the difference was not statistically significant (*t*-test, $t_{88} = -0.97$, $P = 0.334$). The number of ducklings fledged at first breeding did not differ between females that deferred reproduction as yearlings (7.14 ± 1.10) and those that did not

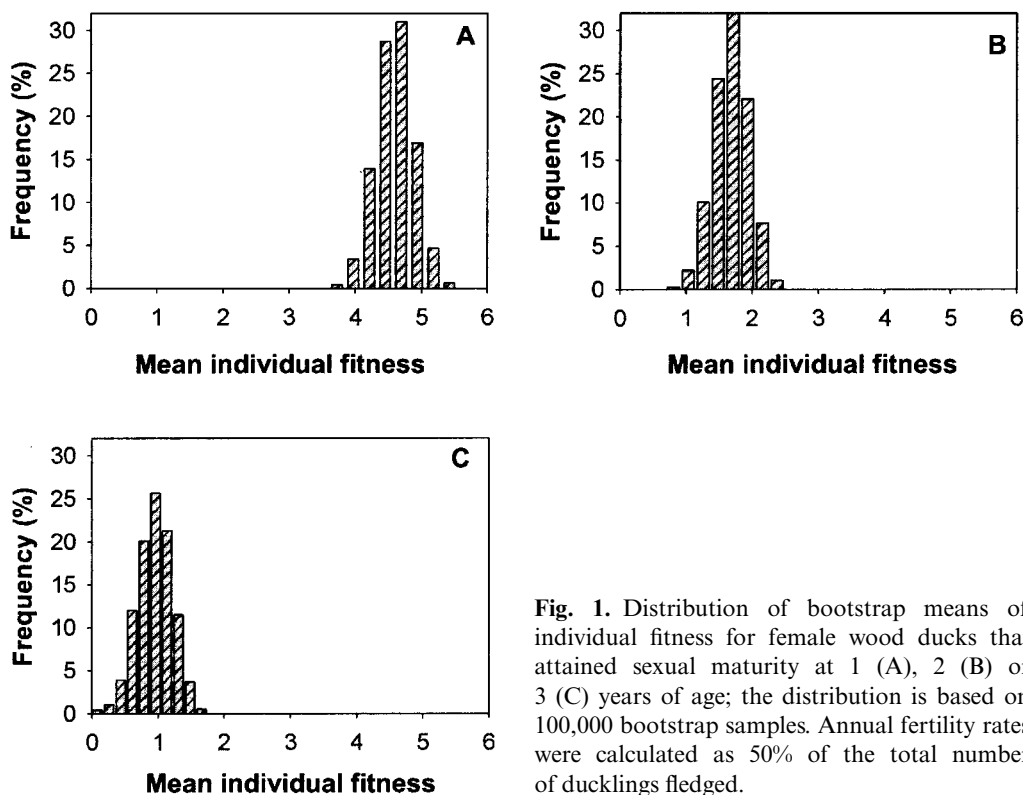


Fig. 1. Distribution of bootstrap means of individual fitness for female wood ducks that attained sexual maturity at 1 (A), 2 (B) or 3 (C) years of age; the distribution is based on 100,000 bootstrap samples. Annual fertility rates were calculated as 50% of the total number of ducklings fledged.

(7.30 ± 0.72 ; t -test, $t_{41} = 0.09$, $P = 0.92$; data from non-parasitized nests only), and there was no significant difference between the two groups in the average number of ducklings fledged per nesting attempt ($\alpha = 1$: 7.60 ± 0.59 ; $\alpha > 1$: 7.81 ± 0.73 ; t -test, $t_{60} = -0.17$, $P = 0.867$; data from non-parasitized nests only).

Individual fitness

The mean individual fitness ($\lambda_{(\text{duckling})}^{(m)}$) of females that began reproduction as yearlings, 2-year-olds and 3-year-olds was 4.60 ± 0.29 , 1.68 ± 0.27 and 0.92 ± 0.29 , respectively (Fig. 1). Female wood ducks that attained sexual maturity as yearlings had a significantly greater individual fitness than those that waited to begin reproduction [t -test (unequal variances) comparing individual fitness of females with $\alpha = 1$ vs $\alpha \geq 2$; $t_{96,1} = -8.66$, $P = 0.0001$]. Linear regression of $\lambda_{(\text{duckling})}^{(m)}$ on age at maturity indicated directional selection for early maturity ($\beta = -2.17 \pm 0.34$, $P < 0.0001$, $R^2 = 0.30$). Quadratic regression indicated that evidence for stabilizing selection was weak ($\gamma = 1.07 \pm 0.60$, $P = 0.08$, $R^2 = 0.32$; Fig. 2).

Lifetime reproductive success

Using number of successful nests, mean $\text{LRS}_{(\text{nest})}$ of females that attained sexual maturity as yearlings, 2-year-olds and 3-year-olds was 2.30 ± 0.23 , 2.81 ± 0.68 and 0.67 ± 0.23 ,

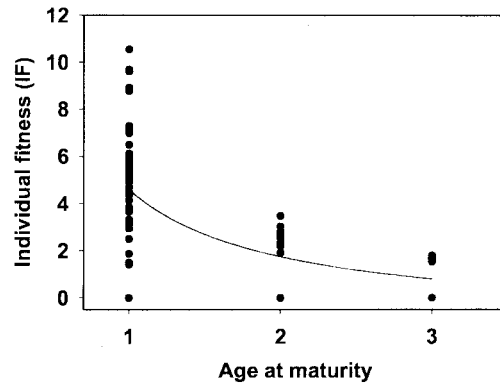


Fig. 2. The relationship between age at maturity and individual fitness in female wood ducks. Annual individual fertility rates were calculated as 50% of the total number of ducklings fledged by each female. Each solid circle may represent more than one data point.

respectively. $LRS_{(nest)}$ of females that attained sexual maturity as yearlings did not differ from $LRS_{(nest)}$ of those not maturing until the second year of life or later [*t*-test (unequal variances) comparing $LRS_{(nest)}$ of females with $\alpha = 1$ vs $\alpha \geq 2$; $t_{41.5} = -0.24$, $P = 0.82$]. Similar results were obtained when total number of ducklings produced was used to estimate $LRS_{(duckling)}$. The mean $LRS_{(duckling)}$ of females that began reproduction as yearlings, 2-year-olds and 3-year-olds was 21.38 ± 2.26 , 25.34 ± 6.12 and 5.54 ± 1.95 , respectively. $LRS_{(duckling)}$ did not differ between females that attained sexual maturity as yearlings and those that did not (*t*-test comparing $LRS_{(duckling)}$ of females with $\alpha = 1$ vs $\alpha \geq 2$; $t_{98} = -0.43$, $P = 0.67$). There was no significant linear relationship between age at maturity and lifetime reproductive success estimated from nest data as well as fledgling data and, therefore, no evidence of directional selection on age at maturity when lifetime reproductive success was used as a measure of fitness ($LRS_{(nest)}$ vs age at maturity: $\beta = -0.41 \pm 0.34$, $P = 0.23$, $R^2 = 0.01$; $LRS_{(duckling)}$ vs age at maturity: $\beta = -4.28 \pm 3.22$, $P = 0.187$, $R^2 = 0.02$; Fig. 3). Quadratic regression indicated stabilizing selection on age at maturity, but only a small proportion of variance in lifetime reproductive success was explained by age at maturity ($LRS_{(nest)}$ vs age at maturity: $\gamma = -1.33 \pm 0.61$, $P = 0.03$, $R^2 = 0.06$; $LRS_{(duckling)}$ vs age at maturity: $\gamma = -11.88 \pm 5.78$, $P = 0.04$, $R^2 = 0.06$; Fig. 3). Qualitatively, the relationship between age at maturity and individual fitness suggested that optimum age at maturity (the age at maturity that maximizes individual fitness) in our study population was 1 year, whereas that between age at maturity and lifetime reproductive success indicated optimum age at maturity to be 2 years (Figs 1–3).

DISCUSSION

All else being equal, life-history theory predicts that earlier maturity should be favoured by natural selection because early-maturing organisms have a greater probability of realizing reproduction and thus improved fitness (Bell, 1980; Roff, 1992; Stearns, 1992). However, the fitness benefits of early maturity may be balanced by associated costs if delaying maturity permits better survival and/or an increase in fecundity or reproductive lifespan (Reznick, 1985; Stearns, 1989, 1992). If age at maturity influences survival rates strongly enough,

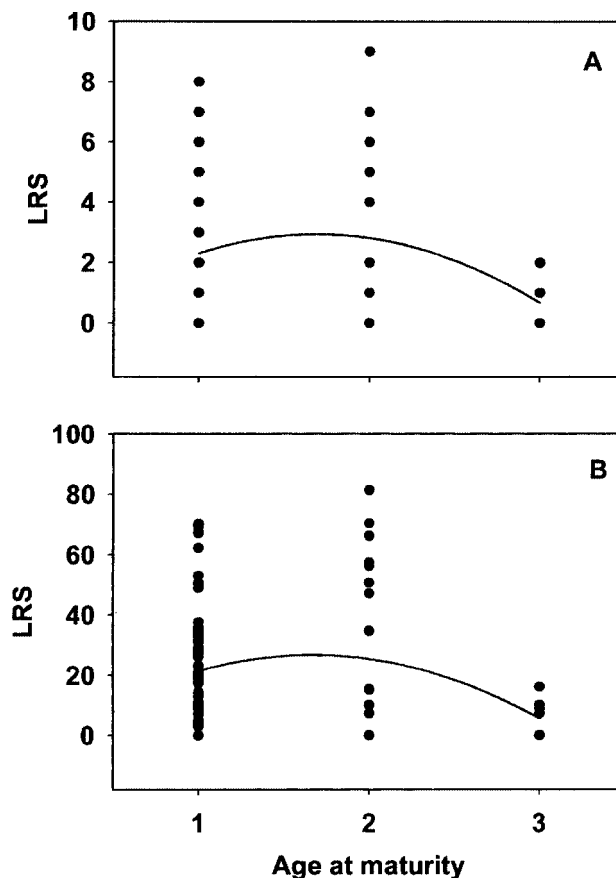


Fig. 3. The relationship between age at maturity and lifetime reproductive success (LRS) in female wood ducks. LRS was estimated as: (A) lifetime total number of successful nests initiated by a female and (B) lifetime total number of ducklings fledged by a female. Each solid circle may represent more than one data point.

delaying maturity can increase the probability that an organism will have more offspring than those that attain sexual maturity earlier. However, fitness also increases with a decrease in generation time, and earlier maturity will cause an increase in fitness by reducing the generation time. In the face of this conflict, theory suggests that a population should be dominated by a genotype with optimum age at maturity, because optimum age at maturity maximizes fitness (Stearns and Koella, 1986).

Female wood ducks that delayed reproduction as yearlings and survived to realize reproduction at an older age had a longer average lifespan than those that started their reproductive careers as yearlings. However, we estimated that 28.8% of females that did not mature as yearlings did not survive to realize reproduction as 2-year-olds and that 23.3% died before they could initiate nesting as 3-year-olds. Females that delayed maturity neither fledged more ducklings during first breeding attempts, nor did they have more successful lifetime reproductive events. Our results suggest that the primary cost of yearling

maturation in wood ducks is a reduced lifespan, but that such costs may be outweighed by fitness benefits associated with early maturity. Females that attained sexual maturity as yearlings had higher individual fitness than those that delayed reproduction until the second or third years of life (Figs 1 and 2). These results are consistent with life-history theory as they deal with the timing of sexual maturity (Cole, 1954; Lewontin, 1965; Stearns, 1992).

When individual fitness was used as a measure of fitness, our results suggested strong directional selection for early maturity. However, no evidence of directional selection on age at maturity was found when lifetime reproductive success was used as a measure of fitness, although quadratic regression indicated a weak but significant stabilizing selection. Similar to the present study, McGraw and Caswell (1996) found strong evidence of directional selection favouring early maturity in sparrowhawks and blue tit (*Parus caeruleus*), but again no evidence of selection on age at maturity when lifetime reproductive success was used as a measure of fitness. The lack of a relationship between lifetime reproductive success and age at maturity may be due to the inadequacy of lifetime reproductive success alone to quantify fitness (Partridge, 1989; McGraw and Caswell, 1996), because it only considers total number of offspring produced and does not adequately consider the timing of both reproduction and the generation time. Individual fitness, in contrast, integrates the timing and quantity of reproduction as well as survival into a projection of the rate at which individuals propagate their genes into the future generations (assuming generational stability in the vital rates) and, therefore, serves as a more appropriate measure of fitness (Partridge, 1989; McGraw and Caswell, 1996). However, we recognize the role of environmental variation in destabilizing the components of the individual fitness over time, which may add to the complexity of estimating the true fitness.

Results of studies investigating fitness consequences of delayed maturity have been inconclusive, despite the prediction that age at maturity is a very influential life-history trait (Cole, 1954; Lewontin, 1965). McGraw and Caswell (1996), Ribble (1992) and Dhondt (1989) all reported a negative relationship between age at maturity and fitness; however, others have found no clear relationship between fitness and age at maturity (Fitzpatrick and Woolfenden, 1988; Sternberg, 1989; Viallefont *et al.*, 1995; Brommer *et al.*, 1998). Why the conflicting results? One possible reason may be associated with the difficulty in obtaining vital life-history data for individuals over their lifetimes. In this study, our success was, at least in part, related to high levels of fidelity to nesting sites and apparent low levels of emigration from the population. Conflicting results also may be a consequence of interactions of life-history traits. Oli (1999) recently found that, in mammals, the proportional sensitivity (i.e. elasticity) of fitness, which also quantifies the selection pressure, to changes in age at maturity depended on the magnitude of reproduction relative to the age at onset of reproduction (i.e. the F/a ratio, where F = average fertility rate and a = age at maturity). Specifically, Oli (1999) found that the sensitivity of fitness to changes in age at maturity increased as the F/a ratio increased, with age at maturity having a large influence on fitness for $F/a \geq 0.57$. To test this idea, we determined our study population's average fertility rate using fledgling data (4.56 ± 0.14) and age at maturity (1.54 ± 0.08). Calculations yielded an F/a ratio of 2.96, which is substantially greater than 0.57. Our results are consistent with the findings of Oli (1999) for mammalian populations and confirmed that age at maturity is currently under substantial selection pressure in our study population. It is possible that the F/a ratio was smaller than 0.57 in the avian studies that reported no relationship between age at maturity and fitness, although methodological differences could be the cause of the conflicting results.

Despite our results illustrating the fitness benefits for female wood ducks that first breed as yearlings and relatively strong selection to breed as yearlings, approximately 28% of females in our South Carolina population still deferred breeding until sometime after their first year of life (Kennamer and Hepp, 2000: table 2). When adjusting for females that defer breeding but do not survive beyond the first year of life to initiate breeding in later years, Kennamer (2001) recently reported that the proportion of females that defer breeding averages about 25% annually. In Massachusetts, 52% of yearlings deferred breeding (Heusmann, 1975: table 1). Environmental or physiological constraints may reduce the number of yearling females that are energetically prepared for reproduction. Yearling females at northerly locations, for example, may defer breeding more frequently due to costs associated with an extended migration that is typically not experienced by southern-breeding wood ducks. Moreover, in years with harsh winter conditions, young wood ducks migrate longer distances than older birds (Hepp and Hines, 1991), suggesting the possibility for annual variation in deferred breeding by yearlings at all latitudes. On the Savannah River Site, most deferred breeding by yearlings occurred in 2 years (i.e. 1985 and 1988; Kennamer and Hepp, 2000: table 2) that coincided with poor wetland conditions brought on by periods of drought. Poor environmental conditions may adversely influence the physiological state of females; initiating breeding under such circumstances may compromise survival potential and thus limit future reproduction for some yearlings (Hepp *et al.*, 1990; McNamara and Houston, 1996). Although yearling maturity appeared to be favoured by natural selection in our study population, plasticity in age at maturity might allow wood ducks to cope with unpredictable changes in the quality of breeding habitats (cf. Stearns and Koella, 1986). The option to defer breeding as a yearling may offer individuals an opportunity to enhance short-term survival while minimizing effects on lifetime reproduction and fitness, particularly when the quality of breeding habitat is poor.

In conclusion, females that did not mature until the second year of their lives or later survived longer, but did not fledge more ducklings at each reproductive attempt or during their lifetimes. Additionally, delayed maturity caused a reduction in fitness in female wood ducks, which is consistent with life-history theory predictions (Cole, 1954; Lewontin, 1965). Given the strong directional selection for early maturity, it is reasonable to assume that natural selection in wood ducks should favour a genotype that attains sexual maturity as yearlings over those that defer reproduction until 2 years of age or later. This was clearly so in our study population; we estimated that fewer than 25% of females deferred breeding until sometime after their first year of life. These results suggest that beginning a breeding career as a yearling may be an evolutionarily stable strategy in wood ducks, and that females of this species that delay the onset of reproduction do so because they are genetically or environmentally constrained, not because of any possible fitness benefits of delayed maturity. We suspect that similar patterns may exist in other bird populations where $F/a > 0.57$ (Oli, 1999), if changes in age at maturity are not genetically or environmentally constrained.

ACKNOWLEDGEMENTS

We thank W.F. Harvey IV, R.T. Hoppe, W.L. Stephens, Jr., L.D. Vangilder, H.S. Zippler and others who have contributed to this study throughout the years. We are especially grateful to I.L. Brisbin, Jr., J.W. Gibbons and M.H. Smith for understanding the value of long-term studies and supporting our efforts. I.L. Brisbin, Jr., J.D. Congdon, F.S. Dobson, J.B. Grand, J.D. Nichols, D.A. Roff and

M.E. Sunquist critically reviewed an earlier draft of the manuscript and provided helpful comments. Much of the field research was supported by US Department of Energy contract DE-AC09-76SROO-819 with the University of Georgia's Savannah River Ecology Laboratory. Preparation of the manuscript was supported by Florida Agricultural Experiment Station, University of Florida, Gainesville and Financial Assistance Award Number DE-FC09-96SR18546 from the US Department of Energy to the University of Georgia Research Foundation.

REFERENCES

- Bell, G. 1980. The costs of reproduction and their consequences. *Am. Nat.*, **116**: 45–76.
- Bellrose, F.C. and Holm, D.J. 1994. *Ecology and Management of the Wood Duck*. Mechanicsburg, PA: Stackpole Books.
- Bellrose, F.C., Johnson, K.L. and Meyers, T.U. 1964. Relative value of natural cavities and nesting houses for wood ducks. *J. Wildl. Manage.*, **28**: 661–676.
- Brommer, J.E., Pietiäinen, H. and Kolunen, H. 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *J. Anim. Ecol.*, **67**: 359–369.
- Caswell, H. and Hastings, A. 1980. Fecundity, developmental time, and population growth rate: an analytical solution. *Theor. Popul. Biol.*, **17**: 71–79.
- Charnov, E. 1990. On the evolution of age of maturity and the adult lifespan. *J. Evol. Biol.*, **3**: 139–144.
- Clawson, R.L., Hartman, G.W. and Fredrickson, L.H. 1979. Dump nesting in a Missouri wood duck population. *J. Wildl. Manage.*, **43**: 347–355.
- Clutton-Brock, T.H., ed. 1988. *Reproductive Success*. Chicago, IL: University of Chicago Press.
- Cole, L.C. 1954. The population consequences of life-history phenomena. *Q. Rev. Biol.*, **29**: 103–137.
- Davis, J.B., Kaminski, R.M. and Stephens, S.E. 1998. Wood duck eggshell membranes predict duckling numbers. *Wildl. Soc. Bull.*, **26**: 299–301.
- Dhondt, A.A. 1989. Blue tit. In *Lifetime Reproduction in Birds* (I. Newton, ed.), pp. 15–33. London: Academic Press.
- Dobson, F.S. and Oli, M.K. 2001. The demographic basis of population regulation in Columbian ground squirrels. *Am. Nat.*, **158**: 236–247.
- Drobney, R.D. 1980. Reproductive bioenergetics of wood ducks. *Auk*, **97**: 480–490.
- Fitzpatrick, J.W. and Woolfenden, G.E. 1988. Components of lifetime reproductive success in the Florida scrub jay. In *Reproductive Success* (T.H. Clutton-Brock, ed.), pp. 305–320. Chicago, IL: University of Chicago Press.
- Fredrickson, L.H. 1990. Wood duck behavior: fall courtship to egg-laying. In *Proceeding of the 1988 North American Wood Duck Symposium* (L.H. Fredrickson, G.V. Burger, S.P. Havera, D.A. Graber, R.E. Kirby and T.S. Taylor, eds), pp. 35–43, St. Louis, MO.
- Hanson, H.C. 1954. Criteria of age of incubated mallard, wood duck, and bob-white quail eggs. *Auk*, **71**: 267–273.
- Haramis, G.M. and Nice, A.D. 1980. An improved web-tagging technique for waterfowl. *J. Wildl. Manage.*, **44**: 898–899.
- Harvey, W.F., IV, Hepp, G.R. and Kennamer, R.A. 1989. Age determination of female wood ducks during the breeding season. *Wildl. Soc. Bull.*, **17**: 254–258.
- Hepp, G.R. and Bellrose, F.C. 1995. Wood duck (*Aix sponsa*). In *The Birds of North America*, No. 169 (A. Poole and F. Gill, eds), pp. 1–24. Philadelphia, PA: The Academy of Natural Sciences/Washington, DC: The American Ornithologists' Union.
- Hepp, G.R. and Hines, J.E. 1991. Factors affecting winter distribution and migration distance of wood ducks from southern breeding populations. *Condor*, **93**: 884–891.
- Hepp, G.R. and Kennamer, R.A. 1992. Characteristics and consequences of nest-site fidelity in wood ducks. *Auk*, **109**: 812–818.

- Hepp, G.R., Hoppe, R.T. and Kenamer, R.A. 1987. Population parameters and philopatry of breeding female wood ducks. *J. Wildl. Manage.*, **51**: 401–404.
- Hepp, G.R., Kenamer, R.A. and Harvey, W.F., IV. 1989. Recruitment and natal philopatry of wood ducks. *Ecology*, **70**: 897–903.
- Hepp, G.R., Kenamer, R.A. and Harvey, W.F., IV. 1990. Incubation as a reproductive cost in female wood ducks. *Auk*, **107**: 756–764.
- Heusmann, H.W. 1975. Several aspects of the nesting biology of yearling wood ducks. *J. Wildl. Manage.*, **39**: 503–507.
- Heusmann, H.W., Bellville, R. and Burrell, R.G. 1980. Further observations on dump nesting by wood ducks. *J. Wildl. Manage.*, **44**: 908–915.
- Jolly, G.M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika*, **52**: 225–247.
- Kenamer, R.A. 2001. Relating climatological patterns to wetland conditions and wood duck production in the Southeastern Atlantic Coastal Plain. *Wildl. Soc. Bull.*, **29**: 1193–1205.
- Kenamer, R.A. and Hepp, G.R. 2000. Integration of long-term research with monitoring goals: breeding wood ducks on the Savannah River Site. *Stud. Avian Biol.*, **21**: 39–49.
- Kokko, H. and Ranta, E. 1996. Evolutionary optimality of delayed breeding in voles. *Oikos*, **77**: 173–175.
- Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**: 1210–1226.
- Lewontin, R.C. 1965. Selection for colonizing ability. In *The Genetics of Colonizing Species* (H.G. Baker and G.L. Stebins, eds), pp. 79–94. London: Academic Press.
- Manlove, C.A. and Hepp, G.R. 2000. Patterns of nest attendance in female wood ducks. *Condor*, **102**: 286–291.
- Manly, B.F.J. 1991. *Randomization and Monte Carlo Methods in Biology*. New York: Chapman & Hall.
- McGraw, J.B. and Caswell, H. 1996. Estimation of individual fitness from life history data. *Am. Nat.*, **147**: 47–64.
- McNamara, J.M. and Houston, A.I. 1996. State-dependent life histories. *Nature*, **380**: 215–221.
- Morse, T.E. and Wight, H.M. 1969. Dump nesting and its effect on production in wood ducks. *J. Wildl. Manage.*, **33**: 284–293.
- Newton, I. 1988. Age and reproduction in the sparrowhawks. In *Reproductive Success* (T.H. Clutton-Brock, ed.), pp. 201–219. Chicago, IL: University of Chicago Press.
- Newton, I., ed. 1989. *Lifetime Reproduction in Birds*. London: Academic Press.
- Oli, M.K. 1999. Demographic mechanisms of population dynamics in mammals. Doctoral dissertation, Auburn University, Auburn, AL.
- Oli, M.K. and Dobson, F.S. 1999. Population cycles in small mammals: the role of age at sexual maturity. *Oikos*, **86**: 557–566.
- Oli, M.K., Slade, N.A. and Dobson, F.S. 2001. Effect of density reduction on Uinta ground squirrels: analysis of life table response experiments. *Ecology*, **82**: 1921–1929.
- Pärt, T. 1995. Does breeding experience explain increased reproductive success with age? An experiment. *Proc. R. Soc. Lond. B*, **360**: 113–117.
- Partridge, L. 1989. Lifetime reproductive success and life-history evolution. In *Lifetime Reproduction in Birds* (I. Newton, ed.), pp. 421–440. London: Academic Press.
- Pyle, P., Nur, N., Sydeman, J. and Emslie, S.D. 1997. Cost of reproduction and the evolution of deferred breeding in the western gull. *Behav. Ecol.*, **8**: 140–147.
- Reznick, D.N. 1985. Cost of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**: 257–267.
- Ribble, D.O. 1992. Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. *J. Anim. Ecol.*, **61**: 457–468.
- Roff, D.A. 1992. *The Evolution of Life Histories*. New York: Chapman & Hall.

- Saitoh, T. 1981. Control of female maturation in high density populations of the red backed vole, *Clethrionomys rufocanus bedfordiae*. *J. Anim. Ecol.*, **50**: 79–87.
- Seber, G.A.F. 1965. A note on the multiple-recapture census. *Biometrika*, **52**: 249–259.
- Semel, B. and Sherman, P.W. 1986. Dynamics of nest parasitism in wood ducks. *Auk*, **103**: 813–816.
- Stearns, S.C. 1989. Trade-offs in life history evolution. *Funct. Ecol.*, **3**: 259–268.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stearns, S.C. and Crandall, R.E. 1981. Quantitative predictions of delayed maturity. *Evolution*, **35**: 455–463.
- Stearns, S.C. and Koella, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution*, **40**: 893–913.
- Sternberg, H. 1989. Pied flycatcher. In *Lifetime Reproduction in Birds* (I. Newton, ed.), pp. 55–74. London: Academic Press.
- Tkadlec, E. and Zejda, J. 1998. Density-dependent life histories in female bank voles from fluctuating populations. *J. Anim. Ecol.*, **67**: 863–873.
- Vandenbergh, J.G. 1987. Regulation of puberty and its consequences on population dynamics of mice. *Am. Zool.*, **27**: 891–898.
- Viallefont, A., Cooke, F. and Lebreton, J.D. 1995. Age-specific costs of first time breeding. *Auk*, **112**: 67–76.
- Wallin, K. 1988. Life-history evolution and ecology in the Tawny owl (*Strix aluco*). Doctoral dissertation, University of Gothenburg, Sweden.
- Weller, M.W. 1957. A simple field candler for waterfowl eggs. *J. Wildl. Manage.*, **20**: 111–113.
- White, D.L. and Gaines, K.F. 2000. The Savannah River Site: site description, land use and management history. *Stud. Avian Biol.*, **21**: 8–17.
- Wooten, J.T. 1987. The effects of body mass, phylogeny, habitat and trophic level on mammalian age at first reproduction. *Evolution*, **41**: 732–749.