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RESEARCH ARTICLE

Effects of current reproductive success and individual heterogeneity on survival and future reproductive success of female Wood Ducks

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ABSTRACT

Estimates of vital rates and their sources of variation are necessary to understand the population dynamics of any organism. These data have been used to test predictions of life history theory as well as to guide decisions of wildlife managers and conservation biologists. Life history theory predicts tradeoffs among life history traits, such that current reproductive effort will be negatively correlated with survival and/or future reproduction. Many studies support this prediction, but others report positive covariation between fitness traits, and attribute positive correlations to differences in individual quality. In this study, we used 11 yr of capture–mark–recapture data of breeding female Wood Ducks (*Aix sponsa*), along with their breeding histories, to examine sources of variation in annual survival rates and to assess the impact of current reproductive success on probabilities of survival and future reproductive success. Cormack-Jolly-Seber models indicated that apparent survival of female Wood Ducks did not vary annually and was only weakly affected by age class and breeding habitat conditions, but that there was a strong positive relationship between survival and the number of successful nests (0, 1, or 2). Next, we used a multistate analysis to examine the importance of female nest fate (successful or failed) on the probability of surviving and of nesting successfully the next year. Early incubation body mass was used to assess the nutritional status and quality of females. Females that nested successfully in year t were not less likely to nest successfully in year $t+1$ than females that had nested unsuccessfully in year t. We also found strong positive covariation between nest success in year t and the probability of surviving. However, being in relatively good or poor condition had no effect on these relationships. Our results are consistent with the idea that female quality is heterogeneous, but body mass was not a good proxy of quality. Therefore, the existence of tradeoffs between female reproductive success and survival or future reproduction was less clear because of our inability to identify and control for differences in female quality.

Keywords: life history tradeoffs, capture–mark–recapture, apparent survival, reproductive success, female quality, *Aix sponsa*

Efectos del éxito reproductivo actual y de la heterogeneidad entre individuos en la supervivencia y el éxito reproductivo futuro en hembras de *Aix sponsa*

RESUMEN

Los estimados de las tasas vitales y de sus fuentes de variación son necesarios para entender la dinámica poblacional de cualquier organismo. Estos datos han sido usados para poner a prueba predicciones de la teoría de historias de vida y también para informar decisiones de gestores ambientales y biólogos de la conservación. La teoría de historias de vida predice compromisos entre rasgos de la historia de vida, de modo que el esfuerzo reproductivo actual está negativamente correlacionado con la supervivencia y/o la reproducción en el futuro. Muchos estudios sustentan esta predicción, pero otros reportan que rasgos de la aptitud covarían positivamente y atribuyen estas correlaciones positivas a diferencias en la calidad de los individuos. En este estudio usamos 11 años de datos de captura-marcado-recaptura de hembras reproductoras de *Aix sponsa*, en conjunto con sus historias reproductivas, para examinar las fuentes de variación en las tasas anuales de supervivencia y para determinar el impacto del éxito reproductivo actual en la probabilidad de supervivencia y en el éxito reproductivo futuro. Los modelos de Cormack-Jolly-Seber indicaron que la supervivencia aparente de las hembras de *A, sponsa* no varió anualmente y sólo fue débilmente afectada por la clase de edad y las condiciones del hábitat reproductivo, pero hubo una fuerte relación positiva entre la supervivencia y el número de nidos exitosos (0, 1 y 2). A continuación usamos un análisis multi-estado para examinar la importancia del destino de los nidos de las hembras (éxito o fracaso) en sus probabilidades de supervivencia y de anidación exitosa el año siguiente. La masa corporal durante el inicio de la incubación se usó para determinar el estado nutricional y la calidad de las hembras. Las hembras que anidaron exitosamente en el año t no tuvieron menor probabilidad de anidar exitosamente en el año $t+1$ que las hembras que habían fracasado en la anidación en el año t. También encontramos

una fuerte correlación positiva entre el éxito de los nidos en el año *t* y la probabilidad de supervivencia. Sin embargo, estar en relativamente buena o mala condición no tuvo un efecto en estas relaciones. Nuestros resultados concuerdan con la idea de que la calidad de las hembras es heterogénea, pero el tamaño corporal no fue un buen indicador de su calidad. Por esto, la existencia de compromisos entre el éxito reproductivo de las hembras y su supervivencia o reproducción futura fue menos clara dada nuestra dificultad para identificar y controlar las diferencias en la calidad de las hembras.

Palabras clave: Aix sponsa, calidad de las hembras, captura-marcado-recaptura, compromisos de historia de vida, éxito reproductivo, supervivencia aparente

INTRODUCTION

Estimates of vital rates and their sources of variation are essential to understanding the population dynamics of any organism (e.g., Sæther and Bakke 2000, Stahl and Oli 2006, Koons et al. 2014). These data have been used to test predictions of life history theory (Reznick 1985, Stearns 1992, Lescroël et al. 2009), as well as to guide decisions of wildlife managers and conservation biologists (Beissinger et al. 2006, Mills 2013). Population growth of Mallards (*Anas platyrhynchos*) in the midcontinent of North America, for example, is strongly influenced by nest success and breeding female survival (Cowardin et al. 1985, Hoekman et al. 2002, Arnold et al. 2012). Therefore, managers have focused conservation efforts on improving the quality of nesting habitat and on reducing the density of nest predators to increase nest success and female survival and thus to enhance population growth (Reynolds et al. 2001, Hoekman et al. 2002, Devries et al. 2003, Brasher et al. 2006, Pieron and Rohwer 2010; but see Amundson et al. 2013, Pieron et al. 2013). Similarly, demographic data are fundamental to the conservation and recovery of threatened and endangered species such as the Red-cockaded Woodpecker (*Picoides borealis*; Letcher et al. 1998, Walters et al. 2002) and Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*; Lockwood et al. 2001, Boulton et al. 2009).

Life history theory predicts tradeoffs among life history traits, so that the allocation of limited resources is balanced among various competing biological processes to maximize fitness (Stearns 1992). Reproduction is one of these key life history variables, and current reproductive effort is predicted to be negatively correlated with survival and future reproduction (Reznick 1985, Stearns 1989). Many studies support this predicted tradeoff, and show that increased reproductive effort is indeed associated with a reduced probability of survival (Visser and Lessels 2001, Blomberg et al. 2013) and future reproduction (Viallefont et al. 1995, Hanssen et al. 2005, Stoelting et al. 2015). However, other studies report positive covariation between these fitness traits and have attributed positive relationships to differences in individual quality (Cam et al. 1998, Cam and Monnat 2000, Sanz-Aguilar et al. 2008, Lescroël et al. 2009). Individual quality often is poorly defined, but

can be related to differences in morphology, behavior, and demography (Lewis et al. 2006, Moyes et al. 2009, Wilson and Nussey 2009). High-quality individuals, for example, may compensate for increased reproductive costs by being able to secure more resources (Blums et al. 2005). Therefore, it is necessary either to experimentally manipulate reproductive investment or to somehow account for individual heterogeneity when examining evidence for tradeoffs in life histories (Reznick 1985, Hamel et al. 2009, Moyes et al. 2011).

The Wood Duck (*Aix sponsa*) is a relatively small species of Anatidae that nests in cavities and is socially monogamous. Most females at southern latitudes generally begin nesting as yearlings (Hepp et al. 1989), and females that defer first reproduction until 2 or 3 yr of age live longer but have reduced individual fitness compared with females that nest in their first year (Oli et al. 2002). Breeding females show a high degree of fidelity to natal areas and previous nest sites (Hepp et al. 1987, Hepp and Kennamer 1992). The Wood Duck is the only species of duck in North America to regularly produce 2 broods in a single breeding season (Kennamer and Hepp 1987), and females are solely responsible for incubation and brood rearing (Hepp and Bellrose 2013). Incubation takes ~32 days (Hepp et al. 2005). Incubating females lose body mass and are generally in poorer condition at the end of incubation than at the beginning (Harvey et al. 1989b). Low body mass at the end of incubation can affect female survival to the next breeding season (Hepp et al. 1990). Nesting later in the season, when temperatures are warmer and conditions are more benign, helps females to mediate the costs of incubation (Hepp and Kennamer 2011). Evidence also suggests that caring for broods reduces the survival of postnesting female Wood Ducks, but being in good condition may help to lessen these costs (Hartke et al. 2006).

In this study, we used 11 yr of capture–mark–recapture data for breeding female Wood Ducks, along with their breeding histories, to examine sources of variation in annual survival rates and to assess the impact of current reproductive success on the probability of future reproductive success and survival. First, we used Cormack-Jolly-Seber (CJS) models to examine sources of variation in apparent annual survival. We included female age and breeding habitat quality as covariates, and predicted that

the apparent annual survival of females would decline as reproductive investment changed with the number of successful nests (0, 1, or 2).

Next, we used multistate models to examine the importance of current reproductive success and female quality on the probability of future reproductive success and of survival (Nichols et al. 1994). We assumed that reproductive costs would be greater for females that nested successfully compared with those that nested unsuccessfully because of increased investments associated with incubation and parental care (Hepp et al. 1990, Hartke et al. 2006, Arnold et al. 2012, Blomberg et al. 2013). Therefore, we predicted that females that nested successfully in year t would have reduced probabilities of surviving and nesting successfully in year $t + 1$, but that differences in female quality would affect this relationship. We used body mass as a dynamic trait to assess the nutritional status and quality of female Wood Ducks (Bergeron et al. 2011). If improved nutritional status helps females to mitigate reproductive costs, then the probabilities of survival and future reproductive success of females that are relatively heavy at the start of incubation should be less affected by the increased costs of nesting successfully than those of lighter females.

METHODS

Study Area
Our study was conducted from 1986 to 1996 on the Department of Energy's Savannah River Site (SRS; 78,000 ha) in west-central South Carolina, USA (33.1°N, 81.3°W). The SRS contains several blackwater streams and a variety of wetland habitats, including extensive forested wetlands, beaver ponds, Carolina bays, and other types of palustrine wetlands (Schalles et al. 1989, Kennamer 2001). Approximately 150 nest boxes, distributed among 19 sites, were available to Wood Ducks each year. Cypress nest boxes (inside dimensions: 48 cm [front] × 50 cm [back] × 25 cm [width]) were attached to trees or aluminum poles, and ~50% of nest boxes were equipped with predator guards.

Field Methods
We checked nest boxes each week during the breeding season (January–July) to monitor nesting activity. We captured females in nest boxes during early incubation (<day 15) and banded unmarked females with U.S. Fish and Wildlife Service leg bands or recorded the band numbers of previously marked individuals. Unmarked females were aged as yearlings (SY: hatched in the calendar year preceding the year of banding) or adults (ASY: hatched earlier than the calendar year preceding the year of banding) using wing feather characteristics (Harvey et al. 1989a), and body mass was measured to the nearest 5 g with a 1,000-g Pesola scale. Clutch size also was determined at this time, and we candled eggs to age embryos and estimate the day of incubation

(Hanson 1954). Females were returned to the nest box after capture. The fate of nests was checked weekly, and we visited nests within 1 week of hatching to determine the number of ducklings that hatched and left the nest box. Successful nests were those in which at least 1 duckling hatched and exited the box, and unsuccessful nests fledged no young.

Each year, we measured surface water levels (to the nearest 0.5 cm) weekly (February–June) at several wetlands (9 of 19 sites) that contained nest boxes. These sites ranged from seasonal wetlands that frequently dried out in mid to late summer and in some years remained dry, to semipermanent wetlands that rarely dried. We also monitored the water level of an undisturbed blackwater stream. Water levels each month were averaged for each site, and monthly mean water levels were averaged within years for each site. Yearly averages for each site were ranked across years, and ranks were summed across sites each year to produce a value to represent the hydrologic condition of SRS wetlands. Values of wetland condition were positively related to annual duckling production (Kennamer 2001), and we used these values in the CJS analysis to represent annual variation in habitat quality experienced by female Wood Ducks.

Data Analyses
We used the Live Recapture module in program MARK (White and Burnham 1999), which uses a CJS approach to estimate apparent survival (φ) and capture (p) probabilities. Survival probability is the apparent survival of marked individuals, because CJS does not differentiate between deaths and permanent emigration (White and Burnham 1999). Capture probability is the likelihood of capturing marked females given that they are alive and in the population. We began by building a global model that allowed each age class to have a unique survival and capture probability during each year of the study (φ(Age*Year) p(Age*Year)). We used this model to test models of capture probability based on the effects of age class, year, wetland condition, and their additive and interactive effects. The highest-ranking model of capture probability was used to test the effects of age class, year, wetland condition, and number of successful nests (0, 1 or 2) on survival probability. We tested models using both additive and interactive effects of these variables. We tested the goodness-of-fit of the global model with program RELEASE 3.0 (Burnham et al. 1987) and estimated the amount of overdispersion ($\hat{c} = \chi^2/df$; Burnham and Anderson 2002). We used an information-theoretic approach for model selection and used model-averaging of competitive models to estimate survival ($\pm$ SE) and parameter coefficients (β; Burnham and Anderson 2002). Using a difference in second-order Akaike's Information Criterion (ΔAIC_c) > 2 to guide model selection is the same as using an α-level of 0.15

TABLE 1. Summary of captures and recaptures of breeding female Wood Ducks at the Savannah River Site, South Carolina, USA, 1986–1996.

	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
New captures	61	43	42	25	44	44	53	58	37	52	28
Recaptures	0	43	45	43	42	48	52	55	60	50	55
Total encounters	61	86	87	68	86	92	105	113	97	102	83

instead of $\alpha = 0.05$. Therefore, we present 85% confidence intervals of parameter coefficients, which are fully compatible with information-theoretic methods, rather than 95% confidence intervals. We considered covariates to be important if 85% confidence intervals did not overlap 0.0 (Arnold 2010).

Next, we developed multistate capture–mark–recapture models with the Multistate Recaptures Only module in program MARK (White and Burnham 1999, White et al. 2006) to investigate the effects of female nest success and relative body mass on the probability of future nest success. This is an extension of the CJS model that estimates the probabilities of capture (p) and apparent survival (φ), and also the probability of transitioning among states (ψ). Transition probability is the likelihood that an individual moves from one state to another state in consecutive years.

For this analysis, we classified the nest fate of females each year as either successful or unsuccessful. We grouped females with 1 or >1 successful nests because of the small number of females with >1 successful nest. Only 11% (86 of 780) of successful females had >1 successful nest, and there were no double-brooded females in 4 of 11 yr. We used early incubation body mass of the female's first nesting attempt each year as an index of female body condition and quality, and classified females as being either ≥ (heavy) or < (light) the median value. We assumed that females with body mass above the median level would be less affected by reproductive success than females below the median level. Body mass adjusted for variation in structural size is frequently used as an index of body condition (i.e. lipid reserves), and has been linked to female quality and reproductive success (Blums et al. 2005, Devries et al. 2008). However, condition indices often are no better at predicting the nutritional status of a bird than using body mass alone, and sometimes are worse (Schamber et al. 2009, Labocha and Hayes 2011). Hipes and Hepp (1995), for example, found no relationship between structural size and lipid mass of breeding male Wood Ducks. Thus, we used body mass rather than a condition index to reflect female condition.

We defined 4 states based on nest fate and early incubation body mass: heavy and successful (HS), heavy and unsuccessful (HN), light and successful (LS), and light and unsuccessful (LN). We used a stepwise process for building our models. Capture probability (p) was modeled first, followed by transition probability (ψ), and the highest-ranking models of p and ψ were used to model survival probability (φ; Lescroël et al. 2009). We began by building a global model that hypothesized that survival and transition probabilities varied by state and year, and capture probability varied by female body mass (heavy or light) and year (φ(State*Year), p(Body mass*Year), ψ(State*Year)). We used this global model to test 5 models of capture probability in which capture probability was held constant or allowed to vary by year, body mass, year + body mass, and year*body mass. We captured females on the nest during early incubation before nest fate was determined; therefore, it was not appropriate to use the fate of nests to model capture probability. We used the highest-ranking model of capture probability to compare models of transition probability. We predicted that females that nested successfully would be more likely to transition to an unsuccessful state the next year compared with females that had nested unsuccessfully. However, we also predicted that this relationship would be influenced by body mass: If female body mass was above the yearly median (heavy), then successful females would be more likely to transition to another successful nest than successful females that were light (less than median body mass). We used the highest-ranking of these models to compare 11 models of survival. These models were designed to test the effects of nesting successfully on annual survival and whether relative female body mass helped to mitigate increased reproductive investment, such that the survival of relatively heavy females would be less affected than that of light females. Models allowed survival to be constant or to vary by state, female body mass, nest success, and year, and included interactive and additive effects.

We used an information-theoretic approach for model selection using Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002). Goodness-of-fit of the global model was evaluated with Program U-CARE (Choquet et al. 2005). We used the JollyMove (JMV) model to test for overdispersion ($\hat{c}$) and adjusted AIC$_c$ if $\hat{c} > 1$ (Brownie et al. 1993).

RESULTS

We captured and banded 487 breeding female Wood Ducks (236 yearlings and 251 adults) that were encountered on 980 occasions during 1,129 nesting attempts in 1986–1996 (Table 1). Average annual nest success was 76%

TABLE 2. Cormack-Jolly-Seber (CJS) models of apparent annual survival of breeding female Wood Ducks at the Savannah River site, South Carolina, USA, 1986–1996. Models were ranked by the difference from the top model in Akaike's Information Criterion corrected for small sample size (ΔAIC_c). K = number of model parameters; w_i = Akaike model weight.

Model [a]	ΔAIC_c	w_i	K	Deviance
φ(Age + Number of nests), p(Wetland condition)	0.00 [b]	0.39	5	1384.79
φ(Number of nests + Wetland condition), p(Wetland condition)	1.29	0.20	5	1386.08
φ(Age*Number of nests), p(Wetland condition)	1.72	0.16	6	1384.48
φ(Number of nests), p(Wetland condition)	2.14	0.13	4	1388.95
φ(Number of nests + Wetland condition + Number of nests*Wetland condition), p(Wetland condition)	2.58	0.11	6	1385.34
φ(Year + Number of nests), p(Wetland condition)	9.48	0.00	13	1377.92
φ(Year*Number of nests), p(Wetland condition)	21.89	0.00	22	1371.59
φ(.), p(Wetland condition)	56.89	0.00	3	1445.73
φ(Age), p(Wetland condition)	58.46	0.00	4	1445.27
φ(Wetland condition), p(Wetland condition)	58.65	0.00	4	1445.46
φ(Age + Wetland condition), p(Wetland condition)	60.26	0.00	5	1445.05
φ(Year), p(Wetland condition)	62.02	0.00	12	1432.52
φ(Age*Wetland condition), p(Wetland condition)	62.08	0.00	6	1444.84
φ(Age + Year), p(Wetland condition)	63.95	0.00	13	1432.40
φ(Year + Wetland condition), p(Wetland condition)	64.08	0.00	13	1432.52
φ(Age*Year), p(Wetland condition)	76.43	0.00	22	1426.13
φ(Year*Wetland condition), p(Wetland condition)	77.09	0.00	22	1426.79

[a] Age = SY (second-year, or yearling) or ASY (after-second-year, or adult); number of nests = 0, 1, or 2; wetland condition = annual hydrologic condition of wetlands at the Savannah River Site.
[b] The AIC_c value = 1394.86 for the highest-ranking model. Overdispersion, $\hat{c}$ = 1.15.

± 1% SE (range = 70%–83%), and median values of female body mass each year ranged between 560 g and 595 g. Yearly values of wetland condition ranged from 16 to 110 (dry to wet; Kennamer 2001). There was a positive relationship between nest success and wetland condition (Pearson correlation: r = 0.65, P = 0.03, n = 11).

In the CJS analysis, the goodness-of-fit test (χ^2 = 42.70, df = 37, P = 0.24) suggested that the data were not overdispersed ($\hat{c}$ = 1.15), so we used AIC_c for model selection. Capture probability (p) was positively related to wetland condition (β = 0.28; 85% CI = 0.02 to 0.54). The top-ranked model (w_i = 0.39) of survival probability (φ) included an additive effect of age class and number of successful nests (Table 2). The second-best model (w_i = 0.20) showed an additive effect of wetland condition and number of successful nests on φ (Table 2). Parameter likelihood values indicated that the number of successful nests (1.0) had greater relative importance than age class (0.55) and wetland condition (0.31). We model-averaged parameter estimates using the top 5 models ($\Delta AIC_c \leq 2.6$), which contained >99% of the cumulative model weight (Table 2). Apparent survival was positively related to the number of successful nests (β = 1.31; 85% CI = 0.94 to 1.68), but was only weakly influenced by female age class (β = −0.20; 85% CI = −0.42 to 0.02; Figure 1) and wetland condition (β = −0.02; 85% CI = −0.05 to 0.01).

The CJS analysis showed a strong positive response between apparent annual survival and the number of successful nests, which was in opposition to our prediction but supported the idea that the quality of female Wood Ducks was heterogeneous. Female age, wetland condition, and year were found to be much less important for explaining variation in annual survival.

In the multistate analysis, the goodness-of-fit test (χ^2 = 109.04, df = 118, P = 0.71) indicated that the data were not overdispersed ($\hat{c}$ = 0.92), so we used AIC_c. The model of capture probability with the most support (w_i = 0.82)
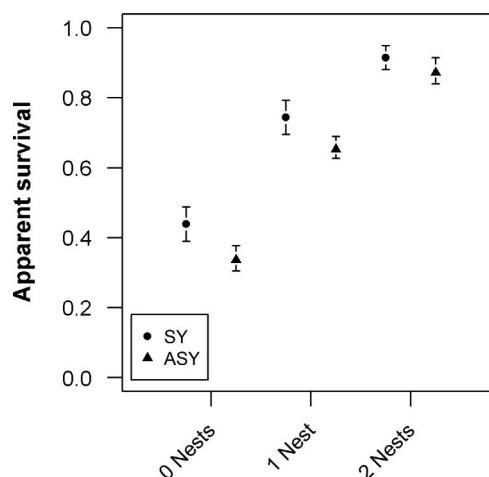

FIGURE 1. Relationships between the number of successful nests and female age and estimates of apparent annual survival (± SE) of breeding female Wood Ducks at the Savannah River Site, South Carolina, USA, 1986–1996. SY = second-year or yearling; ASY = after-second-year or adult.

TABLE 3. Model selection table of multistate capture–mark–recapture analysis modeling capture (p), transition (ψ), and survival (φ) probabilities of breeding female Wood Ducks at the Savannah River Site, South Carolina, USA, 1986–1996. Models were ranked by the difference from the top model in Akaike's Information Criterion corrected for small sample size (ΔAIC_c). K = number of model parameters; w_i = Akaike model weight.

Model [a]	ΔAIC_c	w_i	K	Deviance
Capture probability				
φ(State*Year) p(.) ψ(State*Year)	0.00 [b]	0.82	161	2134.77
φ(State*Year) p(Body mass) ψ(State*Year)	2.97	0.18	162	2134.76
φ(State*Year) p(Year) ψ(State*Year)	15.44	0.00	170	2123.09
φ(State*Year) p(Body mass + Year) ψ(State*Year)	18.49	0.00	171	2123.09
φ(State*Year) p(Body mass*Year) ψ(State*Year)	39.09	0.00	180	2115.83
Transition probability				
φ(State*Year) p(.) ψ(Body mass)	0.00 [c]	0.96	47	2239.18
φ(State*Year) p(.) ψ(State)	6.20	0.04	53	2231.90
φ(State*Year) p(.) ψ(Body mass + Year)	15.37	0.00	59	2227.40
φ(State*Year) p(.) ψ(Body mass*Year)	73.78	0.00	104	2176.70
φ(State*Year) p(.) ψ(State + Year)	112.71	0.00	125	2160.35
φ(State*Year) p(.) ψ(.)	139.96	0.00	42	2390.23
φ(State*Year) p(.) ψ(Nest success)	142.55	0.00	47	2381.73
φ(State*Year) p(.) ψ(Nest success + Year)	177.65	0.00	68	2368.81
φ(State*Year) p(.) ψ(State*Year)	189.24	0.00	161	2134.77
φ(State*Year) p(.) ψ(Nest success*Year)	238.42	0.00	104	2341.34
Survival probability				
φ(Nest success) p(.) ψ(Body mass)	0.00 [d]	0.74	9	2298.61
φ(State) p(.) ψ(Body mass)	2.30	0.23	11	2296.81
φ(Nest success + Year) p(.) ψ(Body mass)	7.03	0.02	18	2287.07
φ(State + Year) p(.) ψ(Body mass)	9.41	0.01	20	2285.26
φ(Nest success*Year) p(.) ψ(Body mass)	16.18	0.00	27	2277.25
φ(State*Year) p(.) ψ(Body mass)	21.69	0.00	47	2239.18
φ(.) p(.) ψ(Body mass)	49.21	0.00	8	2349.86
φ(Body mass) p(.) ψ(Body mass)	51.24	0.00	9	2349.85
φ(Year) p(.) ψ(Body mass)	55.43	0.00	17	2337.54
φ(Body mass + Year) p(.) ψ(Body mass)	57.71	0.00	18	2337.54
φ(Body mass*Year) p(.) ψ(Body mass)	60.53	0.00	27	2321.60

[a] Nest success = successful or unsuccessful; Body mass = heavy ($\geq$ median body mass) or light ($<$ median body mass); State = heavy and successful, heavy and unsuccessful, light and successful, or light and unsuccessful; (.) = constant.
[b] The AIC_c value of the top capture probability model = 2527.74.
[c] The AIC_c value of the top transition probability model = 2338.50.
[d] The AIC_c value of the top survival probability model = 2316.81.

indicated that capture probability was constant and high ($p = 0.90 \pm 0.02$; Table 3). Therefore, we used p(.) to model ψ and φ. The best-supported model by far for transition probability (ψ; $w_i = 0.96$) showed that the probability of transitioning to 1 of 4 states varied with female body mass (Table 3). Females that were relatively heavy or light in year t were very likely to remain heavy (H: $\psi_{HS + HN} = 0.85$) or light (L: $\psi_{LS + LN} = 0.69$) in year $t + 1$ (Figure 2). Furthermore, the probability of nesting successfully was high in year $t + 1$, and female body mass in year t had little effect on the probability of nesting successfully the following year (H: $\psi_{HS + LS} = 0.89$; L: $\psi_{HS + LS} = 0.84$; Figure 2). Importantly, we found no support for the transition model that included nest success, ψ(nest success), which indicated that females that nested successfully in year t were not less likely to nest successfully again in year $t + 1$ compared with females that had nested unsuccessfully in year t (Table 3).

In the top-ranked model of survival ($w_i = 0.74$), φ was influenced by nest success (Table 3). Females that nested successfully had a greater probability of surviving (0.64 $\pm$ 0.02) than females that nested unsuccessfully (0.34 $\pm$ 0.04). The next-best model ($w_i = 0.23$) had $\sim$3 times less support than the top model and indicated that survival varied by state, but it is clear that the relative body mass of females had little effect on survival. Apparent survival did not differ between heavy (0.65 $\pm$ 0.03) and light (0.64 $\pm$ 0.03) females that nested successfully or between heavy (0.28 $\pm$ 0.05) and light (0.38 $\pm$ 0.05) females that nested unsuccessfully.

In the multistate analysis, we found no evidence that females that nested successfully in year t had lower probabilities of either nesting successfully or surviving to year $t + 1$ than females that nested unsuccessfully. In fact, there was strong positive covariation between nest success in year t and the probability of surviving and nesting
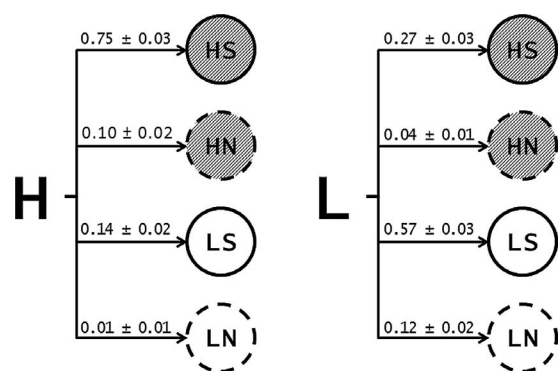
FIGURE 2. Transition probabilities ($\psi \pm$ SE) from the top-ranked model ($w_i = 0.96$; Table 3) of heavy (H) and light (L) female Wood Ducks in year t transitioning to different states in year $t + 1$ at the Savannah River Site, South Carolina, USA, 1986–1996. Heavy females had $\geq$ median body mass, and light females had $<$ median body mass. States were heavy and nested successfully (HS), heavy and nested unsuccessfully (HN), light and nested successfully (LS), and light and nested unsuccessfully (LN).

successfully in year $t + 1$. There was little evidence that the relative body mass of females, which we used as an index of quality, influenced these relationships.

DISCUSSION

In our study, the apparent survival of female Wood Ducks increased with the number of successful nests but did not vary annually and was only weakly related to age class and wetland condition. The multistate analysis showed strong positive relationships between the nest success of females in year t and their probabilities of surviving and nesting successfully again the following year. However, relative body mass, which was used as an index of female quality, had little effect on life history tradeoffs. These results were the opposite of our predictions, but were consistent with the idea that the quality of female Wood Ducks was heterogeneous and independent of body mass. Inferences about life history tradeoffs were weakened because we were unable to control for differences in female quality (Hamel et al. 2009).

It is clear that reproductive tradeoffs are best examined using experiments that manipulate reproductive investment (Reznick 1985). However, long-term correlative studies such as ours can be useful for investigating tradeoffs and have provided evidence of reproductive costs, usually for young, inexperienced breeders or in years of poor environmental conditions (Viallefont et al. 1995, Cam and Monnat 2000). However, we found no indication that breeding habitat conditions or female age interacted strongly with reproductive success to influence annual survival of female Wood Ducks. Instead, the lengthy breeding season of females at the SRS and their use of nest boxes likely reduced the costs of nesting successfully (i.e.

incubating eggs and raising broods). We suggest that the large differences in mortality between females that nested successfully and unsuccessfully occurred mostly outside the breeding season.

Female Age, Wetland Condition, and Survival

Annual survival in ducks generally is lower for hatch-year birds than for older individuals (Johnson et al. 1992). Age-specific differences in survival tend to be strongest during the first fall–winter period and become less evident afterward (Nichols and Hines 1987). However, age-specific differences in breeding propensity and accompanying reproductive costs also can influence the survival of females during the breeding season. Reduced survival of adult female Mallards compared with yearling females, for example, was attributed to the greater breeding propensity and reproductive costs of adult females (Reynolds et al. 1995, Dufour and Clark 2002). In Latvia, the breeding propensities of Common Pochards (*Aythya ferina*) and Northern Shovelers (*Anas clypeata*) also were greater for adult females than for yearling females (Blums et al. 1996). However, active predator control reduced the predation risks of nesting females and was thought to be responsible for the high survival rates of adult females (Blums et al. 1996). Breeding propensity did not differ in our study because we marked and recaptured only females that were already nesting, and female age had little effect on annual survival. Similarly, in a study of radio-tagged Wood Ducks, age was not important for explaining variation in daily survival of breeding females from preincubation to postnesting (Hartke et al. 2006). In ducks, especially ground-nesting species, the mortality risk of females increases greatly during reproduction. For example, Arnold et al. (2012) estimated that 80% of the annual mortality of female Mallards occurred during the breeding season. Therefore, evidence supports the idea that age-specific differences in breeding propensity are largely responsible for variation in female survival.

Reproduction by prairie-nesting ducks increases in wet years when there is an abundance of wetland habitat (Baldassarre and Bolen 2006). However, female survival rates often decline after wet breeding years because increased nesting activity puts females at greater mortality risk (Nichols et al. 1982, Arnold and Clark 1996). In our study, several factors supported the use of wetland condition as an index of breeding habitat quality for Wood Ducks at the SRS. First, the capture probability of female Wood Ducks, possibly an indicator of breeding propensity, was positively related to wetland condition. Second, the body mass of incubating females declined less in wet years than in dry years (Harvey et al. 1989b, Hepp et al. 1990), and productivity (i.e. number of ducklings per female) increased during wet years (Kennamer 2001). Finally, overall nest success each year at the SRS was

positively related to wetland conditions. However, unlike prairie-nesting ducks, there was only a weak negative relationship between wetland conditions and annual survival of female Wood Ducks. This suggests that costs associated with nesting successfully were not as great for females using nest boxes at southern latitudes, or perhaps these females simply were better at managing reproductive costs than prairie-nesting females.

Nest Success and Brood Care

Cavity-nesting birds, such as Wood Ducks, generally have reduced predation risk and greater nest success compared with bird species that do not use cavities (Martin and Li 1992). Incubation is energetically expensive for birds and can be costly for Wood Ducks (Hepp et al. 1990, Tinbergen and Williams 2002). Female Wood Ducks generally are able to mitigate these costs and provide an optimal thermal environment for developing embryos (Hepp and Kennamer 2011, McClintock et al. 2014). For example, even when the number of incubation days was manipulated (range = 22–44 days), females did not alter incubation constancy or experience greater mass loss with more days of incubation (Hepp and Kennamer 2011). Prairie-nesting ducks generally have low nest success (<5%–36%) and high mortality, and females are especially vulnerable during egg laying and incubation (Klett et al. 1988, Sargeant and Raveling 1992, Beauchamp et al. 1996). For example, the mortality risk of female Mallards was 2.5 times greater during incubation than in other periods of the breeding season (Arnold et al. 2012). In contrast, Hartke et al. (2006) estimated breeding season survival of female Wood Ducks that used nest boxes and reported no mortality of females during incubation. Predation of females using nest boxes at the SRS occurred in only 0.4% of nests (4 of 1,129 nests). Predation of incubating Wood Ducks was somewhat higher for females using natural cavities (1.7%; 2 of 118 nests), but still was much lower than that of ground-nesting ducks (Roy Nielsen et al. 2006, Arnold et al. 2012).

Unfortunately, most of what is known about the breeding ecology of Wood Ducks originates from studies of populations using nest boxes. There are very few comprehensive studies of Wood Ducks nesting in natural cavities, so any comparison between nest types is challenging. In our study, the nest success of females that had started incubation was high (76%), and predation of nests was low (7%; 84 of 1,129 nests). Bellrose and Holm (1994) summarized several Wood Duck studies from across the U.S. and found that average nest success was higher in nest boxes (67%; range = 44%–80%) than in natural cavities (40%; range = 10%–63%). In an 8-yr study of Wood Ducks using natural cavities in Illinois, nest success varied with flood conditions and habitat type and was generally lower (range = 26%–65%) than success at the

SRS, while nest predation was much higher (28%; 63 of 223 nests; Roy Nielsen and Gates 2007). Use of nest boxes or natural cavities by breeding females certainly puts them at less risk from predators than ducks that do not use cavities. Furthermore, females using nest boxes generally are less affected by predators than females using natural cavities.

Caring for young is an important reproductive cost even for precocial birds (Walters 1982, Milonoff et al. 2004). Annual survival of Greater Sage-Grouse (*Centrocercus urophasianus*), for example, was lower for females that raised broods compared with females that did not, but costs were incurred mostly after the breeding season (Blomberg et al. 2013). In Mallards, survival during the breeding season was high for females that raised broods; however, annual survival was lower for females that raised broods compared with females that nested unsuccessfully (Arnold et al. 2012, Arnold and Howerter 2012). Apparently, the limited time available at northern latitudes to raise broods, molt, and prepare for fall migration adversely affects the postbreeding survival of female Mallards (Arnold and Howerter 2012).

Wood Ducks at southern latitudes have longer breeding seasons (January–July), migrate later, and travel shorter distances than individuals at northern latitudes (Nichols and Johnson 1990, Hepp and Bellrose 2013). Therefore, time constraints associated with breeding successfully are likely to be less important for females breeding at southern latitudes. Similarly, the strong positive effect of early hatching date on offspring survival and recruitment that occurs commonly for birds breeding at northern latitudes is not evident for Wood Ducks breeding at southern latitudes (Hepp et al. 1989). In the southern U.S., overall survival of brood-rearing Wood Ducks was high (0.90; Davis et al. 2001), but daily survival was lower for successful females than for females with failed nests, suggesting that raising broods entails some risk (Hartke et al. 2006). Comparable estimates of breeding season survival are not available for SRS females, but brood care likely entailed similar mortality risks. Annual survival of successful females at the SRS, however, was much greater than that of unsuccessful females, suggesting that differences in mortality occurred outside the breeding season. Many factors influence the mortality risk of females during the nonbreeding season. For example, winter survival and vulnerability to hunting mortality are positively related to body condition in many duck species (Hepp et al. 1986, Conroy et al. 1989, Bergan and Smith 1993). Successful, high-quality female Wood Ducks may experience reduced mortality risk in the nonbreeding season by forming pair bonds early in the fall, thereby increasing their dominance rank and giving them access to better food resources and habitats, from which they are less likely to disperse or migrate than low-quality, unsuccessful females (Hepp and Hair 1984, Hepp 1986).

Reproductive Costs and Female Quality

The use of nest boxes by SRS females certainly increased nest success and reduced, but did not eliminate, mortality risk during incubation. Moreover, time constraints were unlikely to have prevented successful females at the SRS from raising broods, molting, and acquiring sufficient nutrients before fall migration. Therefore, the impacts of using nest boxes and breeding at southern latitudes potentially weakened any negative effects of reproducing successfully on survival and future reproduction. However, annual survival of successful female Wood Ducks at the SRS was almost twice that of unsuccessful females, and the probability of nesting successfully again the following year also was extremely high (0.84–0.89) and was not affected by nest success in the previous year. These results were unexpected but not unique. Positive covariation between life history traits has been reported for a variety of species (Sanz-Aguilar et al. 2008, Hamel et al. 2009, Lescroël et al. 2009), and further emphasizes the need to account for differences in individual quality when examining life history tradeoffs.

Survival estimated with Cormack-Jolly-Seber capture–mark–recapture methods does not differentiate between mortality and permanent emigration. Therefore, if failure to recapture unsuccessful females that were alive was higher than for successful females, then survival estimates of unsuccessful females would be biased low. We think that this is unlikely, but may have occurred, for example, if unsuccessful females were more likely than successful females to permanently change from using nest boxes to using natural cavities, to reproduce as brood parasites and not incubate eggs, or to not reproduce again. We only captured females that had begun incubating eggs in our nest boxes and, therefore, cannot estimate directly the probability of permanent emigration. However, nest-site fidelity was high in our population of Wood Ducks, with ~80% of females returning to nest in the same wetland as they used the previous year (Hepp and Kennamer 1992). A larger percentage of unsuccessful females (27%) than successful females (19%) moved to different wetlands the next year and nested, but differences due to nest success were small, and movements between nest sites were usually short ($\bar{x} = 1.3$ km; Hepp and Kennamer 1992). Furthermore, survival of female Wood Ducks from the southeastern U.S. estimated with band recovery models did not differ from survival of SRS females estimated with capture–mark–recapture analyses, suggesting that SRS females had low rates of permanent emigration (Hepp et al. 1987). Arnold and Clark (1996) also found little evidence for permanent emigration in several species of breeding dabbling ducks in Saskatchewan, Canada. Therefore, we believe that differences in apparent survival between females that nested successfully and unsuccessfully were real and reflect heterogeneity in female quality and not variation in rates of permanent emigration. High-quality female Wood Ducks nested more successfully and had increased probabilities of surviving and nesting successfully in the future. These results are consistent with many long-term studies of birds which show that a small fraction of the population actually contributes to population growth (Newton 1989, Blums and Clark 2004, Murphy 2007).

Individual heterogeneity often is used to structure harvest regulations and manage exploited populations (e.g., ungulates). In North America, waterfowl harvest regulations for the most part do not consider heterogeneity. However, we know that heterogeneity occurs in waterfowl populations and that disproportionate harvests of either high- or low-quality individuals can have important effects on the dynamics and growth of populations (Blomberg et al. 2013, Lindberg et al. 2013, Guillemain et al. 2014). For example, some areas of the U.S. allow Wood Ducks to be harvested in an early season (September) before the regular waterfowl season commences. An early season could disproportionately target high-quality, successful females that have not dispersed from breeding areas and may be more vulnerable, thereby lowering estimates of survival and affecting our perception of the compensatory nature of harvest mortality (Sauer et al. 1990). Future research should further examine individual heterogeneity in wildlife populations and begin to include heterogeneity in conservation and management decisions.

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