



Research Article

Simulations of Wood Duck Recruitment from Nest Boxes in Mississippi and Alabama

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ABSTRACT Since the early 20th century, wildlife managers have deployed artificial nesting structures for wood ducks (*Aix sponsa*) to increase availability of nest sites and local reproduction of the species. However, knowledge is lacking of the effects of nest structure size (i.e., large vs. small; Stephens et al. 1998) and reproductive data (e.g., clutch size, hatch date, duckling survival) on recruitment of wood ducks. We used stochastic simulation analyses to predict recruitment of wood ducks into late summer by analyzing data from a 6-year study of box-nesting wood ducks, and 4-year (Mississippi) and 2-year (Alabama) studies of radio-marked female wood ducks and their ducklings. Our index of recruitment was the number of radio-marked ducklings per nest box that survived until 1 September. Ducklings hatched after 1 June exhibited a 30-day survival probability of 0.29, which was nearly 3 times greater than those hatched before 1 June. In east-central Mississippi, 68% and 65% of total wood duck recruits from large and small boxes, respectively, were hatched and reared from June to August. In western Mississippi, 91% of recruits from each box size also were hatched and reared from June to August. Mean number of wood duck recruits produced from large boxes was greater than small boxes at each study site; each large box in western Mississippi produced approximately 4 recruits on average, whereas small boxes in east-central Mississippi produced approximately 1 recruit. Wood duck recruits in our study resulted primarily from late spring and summer hatched birds in contrast to most Nearctic ducks with adaptive, early nesting to promote recruitment. In Mississippi and similar southern environments, we recommend use of large boxes and cleaning boxes around 1 May after completion of initial nests, and emphasize the importance of late spring and summer duckling production to wood duck recruitment. © 2015 The Wildlife Society.

KEY WORDS *Aix sponsa*, artificial nesting structure, duckling survival, Mississippi, nest box, recruitment, simulation, wood duck.

Wood ducks are forested wetland birds and indigenous to eastern North America, but the species also presently inhabits parts of the Central and Pacific flyways (Phillips 1925, Jones and Leopold 1967, Bellrose 1980). Wood ducks comprise over 8% of the total annual duck harvest in the United States, so they are ecologically and economically important in North America (Raftovich et al. 2010, Grado et al. 2011). However, population management of the wood duck has inherent challenges because it is a cavity nester and typically uses densely vegetated wetlands year around, which hampers accurate surveys of species abundance (Bellrose

1980, Cowardin and Blohm 1992, Sherman et al. 1992, Kelley 1996, Pearse et al. 2009).

Managers have used nest boxes to increase available nest sites for wood ducks for nearly a century (Bellrose 1953, Bellrose and Holm 1994:461, Davis et al. 2007), although researchers have challenged the efficacy of nest boxes in the midwestern United States, where natural cavity abundance was estimated adequate for breeding populations (Soulliere 1990, Roy Nielsen et al. 2007). In the mid-1990s, there were an estimated 100,000 nest boxes in North America that produced approximately 300,000 wood duck ducklings annually (Bellrose and Holm 1994, Utsey and Hepp 1997). Some portions of the wood duck's range are largely agricultural landscapes that lack suitable natural cavities, but adequate food and cover may exist to sustain these populations (Jones and Leopold 1967, Lowney and Hill 1989, Bellrose and Holm 1994, Davis et al. 1999b). Thus, nest boxes may compensate for lack of forestland with suitable cavities in predominantly agricultural, deforested

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landscapes (e.g., Lowney and Hill 1989). Additionally, nest boxes may enhance production by southern populations of wood ducks, especially if boxes are managed during extended breeding seasons in the southern United States (Lowney and Hill 1989, Davis et al. 2007). For example, nest boxes cleaned of abandoned eggs and down at 5 sites in South Carolina produced 35% more ducklings than those managed once during spring (Utsey and Hepp 1997). Wood duck nest boxes placed openly overwater may induce brood parasitism from wood ducks or other cavity nesters, which can cause nest abandonment and decreased egg hatch (Jones and Leopold 1967, Semel et al. 1988, Stephens et al. 1998, Davis et al. 1999*b*, Roy Nielsen et al. 2006). To ameliorate excessive nest parasitism, a nest box approximately half the size of conventional boxes was developed to accommodate a normal-sized clutch of approximately 15 wood duck eggs (Bellrose 1980, Semel and Sherman 1992, Stephens et al. 1998). However, the effect of small and conventional (hereafter, large) boxes on wood duck recruitment into late summer is currently unknown. Although brood parasitism is commonly identified with nest box programs (Semel et al. 1988, Semel and Sherman 1992, Pöysä et al. 2014), as much as 85% of wood duck nests in natural cavities also may be parasitized in some regions (Roy Nielsen et al. 2006). Hence, clutch and brood size may have important influences on recruitment into late summer.

Research that examines duckling production and survival toward late summer recruitment is rare but relevant for understanding population dynamics and management of wood ducks (Johnson et al. 1992, Davis et al. 2007). Therefore, we studied nesting and brood-rearing female wood ducks and duckling survival in 2 physiographic regions in Mississippi and 1 area in Alabama. We used daily stochastic simulation analyses of data from a 6-year study of box-nesting wood ducks (Stephens et al. 1998, Davis et al. 1999*b*) and 4- and 2-year studies of radio-marked females and ducklings in Mississippi and Alabama, respectively (Davis et al. 2007, 2009), to examine how nest box use, box size, clutch size/box, nest box success, and survival of ducklings influenced simulated recruitment of wood ducks to 1 September.

STUDY AREA

Our primary study areas were the Sam D. Hamilton Noxubee and Teddy Roosevelt Yazoo National Wildlife Refuges (hereafter, NNWR and YNWR) located in the Interior Flatwoods (eastern) and the Mississippi Alluvial Valley (MAV; western) regions of Mississippi, respectively (Pettry 1977, Reinecke et al. 1989). Our third study area was the backwaters of the Tennessee-Tombigbee Rivers Waterway (TTRW) in west-central Alabama (Davis et al. 2007). The NNWR (19,424 ha; 33°15'N, 88°46'W) is nearly all forested and surrounded by upland and lowland forest, and pastureland. Little agricultural land has existed in the region since the late 1980s when much cropland was enrolled in the Conservation Reserve Program (Twedt and Uihlein 2005). The YNWR (5,237 ha; 33°06'N, 90°59'W) is located in the MAV, is approximately 38% forestland (Nuttall and Burger

2005, Twedt and Uihlein 2005), and is surrounded predominately by row crop agriculture. Aliceville Lake was our primary study area in the TTRW (3,320 ha; 33°14'N, 88°15'W). The United States Army Corps of Engineers created the lake in 1979 by constructing locks and dams along the Tennessee and Tombigbee Rivers. Once primarily riverine forested bottomlands with associated uplands, the lake and its backwaters are dominated by native and exotic emergent and floating vegetation and contained little bottomland-hardwood and scrub-shrub habitats (Davis et al. 2007).

METHODS

Model Overview

Our simulation model of recruitment into late summer used reproductive data that included clutch size/box, hatch date, and survival of radio-marked ducklings from wood ducks nesting in boxes. At NNWR (eastern Mississippi), we used clutch size and hatch date data from 1994 to 1999, and duckling survival data from 1996 to 1999 (Davis et al. 2007). At YNWR (western Mississippi), we studied reproduction by box nesting females, but not duckling survival from 1994 to 1997 (Stephens et al. 1998, Davis et al. 1999*b*). We collected all reproductive data at TTRW in 1998 and 1999 (Davis et al. 2007, 2009), but only large boxes were available there so we could not simulate effects of small boxes at TTRW (Davis et al. 2007).

Nest boxes were our analytical unit for duckling production, not individual female wood ducks because 1) we did not have complete demographic data on females, such as birds' annual survival rates, and 2) we frequently discovered variably shaped and colored eggs apparently laid by different females within individual boxes. Our metrics associated with reproductive data of nesting wood ducks included the probability that a nest box was used, clutch size/box, and nest box success. Additionally, we estimated daily survival rates of ducklings to 30 days of age (Davis et al. 2007) and then used stochastic simulations to estimate duckling recruitment (Wisdom et al. 2000).

Model Covariates

We classified nest boxes as either large or small wooden nest boxes. The large box is representative of the conventional wooden nest box used in nesting programs for decades in North America (Bellrose 1980:191). Inside dimensions of large boxes measured 25 × 25 × 55 cm and small boxes were 13.75 × 25 × 37.5 cm. Further information on nest box allocation among wetlands and nest box, duckling, and brood monitoring is presented elsewhere (Stephens et al. 1998; Davis et al. 1999*b*, 2007, 2009).

To calculate clutch size (CLUTCH), we included only data from clutches with known fates (i.e., successful, depredated, or abandoned) and followed established protocol for determining nest fates (Klett et al. 1986, Greenwood et al. 1995). We did not determine fertility of eggs in nest boxes; thus, for all nest boxes with successful hatches, we calculated the hatching probability of an individual egg (HATCH) as either the number of egg shell membranes

remaining in the nest divided by total number of eggs per nest (Davis et al. 1998) or direct counts of hatched ducklings in a box divided by number of eggs present in incubated nests.

Because we simulated our model on a daily time step, we needed to estimate the probability a clutch hatched from a nest box on any given day. For instance, a box that produced a clutch on any day in month t could not realistically produce another clutch until a day in month $t + 1$. Therefore, we used our data to estimate the probability a box produced a clutch (i.e., at least 1 duckling) on any given day in a given month.

We calculated the probability a clutch (eggs) hatched from a nest box on a given day (HDAY) as:

$$\text{HDAY} = (\text{NESTS}_{ijk} / \text{BOX}_{ijk}) / \text{DAYS}_i,$$

where NESTS_{ijk} = total number of successful nests observed in month i in box type j at site k , BOX_{ijk} = total number of boxes monitored in month i in box type j at site k , and DAYS_i = number of days in month i . If all monitored boxes produced a clutch ($P = 1.0$) in a given month with 31 days, the maximum probability a single box containing a clutch ultimately produced a clutch on any given day in that month = 3.2% (i.e., $1.0/31 = 0.032$).

We calculated daily survival of ducklings <30 days old (S_d) and birds ≥ 30 days old (i.e., late summer recruit; S_f); we assumed these metrics culminated in duckling recruitment to 1 September (Fig. 1). We used these data to index recruitment because we did not know how many ducklings actually fledged after the brood rearing period. However, natural mortality of young ducks after 30 days of age is acknowledged as low and not a critical influence on fall recruitment (Kirby and Sargeant 1999, Beaudoin, 2010).

Duckling Survival

In a previous study, we estimated interval (e.g., spring-summer) duckling survival during 4 breeding seasons (1996–1999) at NNWR and TTRW (Davis et al. 2007). To refine these results, we used a daily time-step model and estimated seasonal variation (e.g., early vs. late hatched) in the daily survival of ducklings. Unlike Davis et al. (2007), we allowed

the estimates of survival probabilities to vary among time periods and study sites, in part resulting from environmental stochasticity. Seasonal data allowed us to predict recruitment between cohorts (e.g., hatched in spring or summer) and among sites. We used Program MARK to estimate duckling survival based on duckling age. We analyzed survival of radio-marked ducklings based on interval survival estimation and right-censored ducklings when transmitters were lost or failed (Davis et al. 2007).

We conducted known-fate modeling in Program MARK (White and Burnham 1999) to estimate 30-day survival of wood duck ducklings after hatch and exodus from nest boxes. Survival of radio-marked ducklings is commonly monitored for about 30 days because of transmitter longevity and because duckling mortality is typically low once ducklings reach 30 days of age (Rotella and Ratti 1992, Davis et al. 2007). Wood duck ducklings fledge in 75–85 days after hatch (Bellrose and Holm 1994:341). Because survival between 30 days and fledging is likely not 100% (Beaudoin 2010), we assigned a constant daily survival in our simulations of 0.9985 (Nichols and Johnson 1990).

We used an information-theoretic approach to make inferences regarding a priori hypotheses about potential influences on survival rates (Burnham and Anderson 2004). We first assigned all ducklings ($n = 497$) to 12 groups based on calendar year (4 years; 1996–1999), site (NNWR and TTRW), and time period (early- and late-hatched). This scenario created 8 and 4 duckling groups at NNWR and TTRW, respectively. Because wood duck duckling survival increased as the breeding season progressed (Davis et al. 2007), we divided ducklings into 2 groups representing their relative hatch periods. Ducklings hatched before 1 June were early hatched and ducklings hatched ≥ 1 June were late hatched. We used 1 June as a cutoff date because sample sizes between early and late-hatched groups were approximately equal, and this date coincided with nearly half of ducklings that hatched, departed boxes, and were monitored. We did not include specific Julian date in our models because we were not concerned with how survival rates varied among individuals relative to hatch date. This resulted in 8 a priori

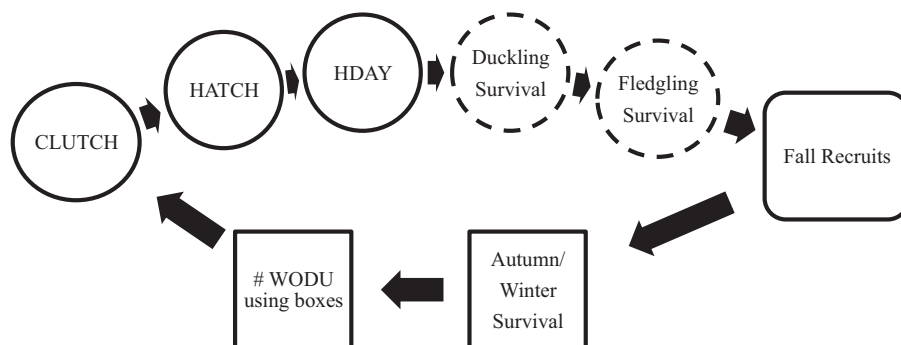


Figure 1. Time-step model flowchart to predict number of wood duck (WODU) recruits to 1 September (late-summer recruits) for small and large nest boxes. Solid line circles represent parameters that varied monthly, whereas dashed circles represent parameters that varied daily. Parameters were derived from 3 study sites during 1994–1999 in Mississippi and Alabama, USA. The parameter CLUTCH was the number of wood duck eggs in a box, HATCH was the probability that an egg hatches, and HDAY was the probability a duckling exited a nest box on a given day. We did not estimate parameters in the 2 square boxes because we did not have 1) complete demographics on nesting females, so the nest box was our analytical unit, or 2) survival estimates for wood ducks in autumn and winter.

candidate models. Each model contained a survival structure (time-dependent or constant across time) and a grouping structure (study year, site, hatch season, or null).

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to select the best models (i.e., models $\leq 2.0 AIC_c$ of $\Delta AIC_c = 0$; Burnham and Anderson 2004). We modified AIC_c to correct for overdispersion by using the quasi-likelihood variance inflation factor (median \hat{c}) to yield $QAIC_c$ (Cooch and White 2011). We evaluated strength of evidence of models based on Akaike weights (w_i) and assessed model fit by calculating \hat{c} . We calculated \hat{c} using a bootstrapping procedure on our most complex model (number of parameters [K] = 116) by dividing observed deviance by mean deviances of the simulated data (1,000 replicates; Cooch and White 2011:5–27). Our models were only slightly over dispersed ($\hat{c} = 1.280$) indicating relatively good model fit (Cooch and White 2011).

We believe our study met the assumptions for known-fate analyses in Program MARK for the following reasons. First, our radio-marked ducklings were a random sample of ducklings within broods and nest boxes (Davis et al. 2007). Second, we assumed intra-brood survival was independent for individual ducklings because when Davis et al. (2007) accounted for broods in their analyses, they found intra-brood dependence did not influence survival estimates substantially. Moreover, wood ducks do not form crèches, which could enhance dependence of survival (Bellrose and Holm 1994). Bishop et al. (2008) also concluded that treating siblings as independent sample units resulted in limited overdispersion (i.e., sibling dependence). Finally, we assumed left-censored individuals (i.e., radio-marked birds introduced into the sample population through time with staggered entry) had survival distributions similar to birds radiomarked previously, and survival of all birds was not affected by capture, handling, or radiomarking (Pollock et al. 1989, Davis et al. 1999a).

Recruitment

Our stochastic simulations projected the dynamics of duckling subpopulations from 1 April through 1 September. We did not field monitor duckling survival beyond 30 days nor did we estimate overwinter survival of >30-day-old ducklings. Therefore, we converted annual survival rates from Nichols and Johnson (1990) to daily survival rate and applied them to S_f . We deemed S_f as the daily survival rate of ducklings older than 30 days. Because of different hatch dates, the number of additional exposure days differed for each duckling. Nichols and Johnson (1990) reported annual survival of yearling wood ducks of 0.625 (southern) for males and 0.538 (southern) for females. We converted annual survival to daily survival (e.g., $\sqrt[365]{\text{annual survival}}$) for males and females and used the mean (0.9985) as S_f . This procedure was necessary because we did not estimate annual survival of these wood ducks. Thus, we considered a duckling a recruit if it lived to 1 September. We used stochastic simulations of 5 time-dependent demographic processes to project numbers of wood duck recruits that hatched in 2 different sizes of nest boxes. We used stochastic simulations

to model parameters CLUTCH (i.e., number of eggs in box), HATCH (probability an egg hatches), HDAY (probability a box produced a clutch on a given day), survival (S_d) of ducklings <30 days old, and survival (S_f) of >30-day-olds, all culminating in duckling recruitment (Fig. 1).

We implemented our simulations in a daily time step in Program R 2.8.1 (R Development Core Team 2009) and our simulation spanned 153 iterations (i.e., days, from 1 Apr to 1 Sep). Daily time steps allowed us to account for the effects of seasonality on recruitment with seasonally varying duckling daily survival. Again, because we did not account for egg laying among individual female wood ducks, the nest box was our unit of analysis. We used actual daily survival rates of known-aged birds, which is more refined and precise than interval rates (Davis et al. 2007), and we applied our estimates of duckling survival from NNWR and TTRW to YNWR because we did not study duckling survival at YNWR. Nonetheless, nest and duckling survival data were temporally representative as they shared overlapping years (1996–1997). We parameterized our stochastic models using monthly estimates averaged across 4 years for CLUTCH, HATCH, and HDAY for small and large nest boxes at NNWR and YNWR (Table 1).

We constructed a stochastic daily time-step model to project number of wood duck recruits for each study site and nest box type (small vs. large; Fig. 1). We allowed parameter values used in simulations to fluctuate based on the distributions of the data. For example, some processes were binomial and others had Poisson distributions. We assigned $n = 100$ for each box size and study site. For egg laying and hatching, we simulated CLUTCH with a Poisson distribution, and HATCH, HDAY, S_d , and S_f with binomial distributions as follows:

$$Nd_{1,i} = \sum_{j=1}^{Nb_i} \text{bin}(CS_{i,j}, \%HATCH), \quad (1)$$

$$Nb_i = \text{bin}(Nb, HDAY), \quad (2)$$

$$CS_{i,f} = \text{Poisson}(CLUTCH), \quad (3)$$

where $Nd_{1,i}$ is the number of 1-day-old ducklings produced from Nb_i nest boxes on day i , $CS_{i,j}$ is the clutch size from box j on day i , Nb is total number of nest boxes available, Nb_i is number of boxes producing ducklings on day i , $\text{bin}(n, p)$ represents a binomial distribution with parameters n (total number of trials) and p (probability of success), and $\text{Poisson}(\lambda)$ is for a Poisson distribution with the parameter λ .

For duckling survival and recruitment, we used the following formulas:

$$Nd_i = \sum_{a=1}^{29} \text{bin}(Nd_{a,i-1}, S_{a,i-1}), \quad (4)$$

$$Nf_i = \text{bin}(Nd_{30,i-1}, S_f) + \text{bin}(Nf_{i-1}, S_f), \quad (5)$$

where Nd_i is total number of ducklings surviving to day i from day $i - 1$, $Nd_{a,i}$ is number of day-old ducklings that

Table 1. Parameters used in stochastic simulation to predict wood duck recruits from 2 study sites and small versus large nest box sizes at 2 National Wildlife Refuges (NWR) in Mississippi, USA, 1994–1997. Parameter estimates are mean values across 4 years.

Parameter ^a _(month)	Sam D. Hamilton Noxubee NWR						Teddy Roosevelt Yazoo NWR					
	Small box			Large box			Small box			Large box		
	<i>n</i>	\bar{x}	Range ^b	<i>n</i>	\bar{x}	Range ^b	<i>n</i>	\bar{x}	Range ^b	<i>n</i>	\bar{x}	Range ^b
CLUTCH _(April)	20	13.2	11.2–16.1	68	16.6	14.0–19.4	3	8.8	1.0–16.5	19	21.5	14.9–27.0
CLUTCH _(May)	33	12.2	10.7–14.6	39	16.6	14.3–20.5	19 ^c	18.2 ^c	n/a	16	28.8	22.6–40.0
CLUTCH _(June)	26	10.9	10.5–11.3	58	12.1	11.3–13.4	27	15.0	10.3–19.4	47	30.1	23.4–34.6
CLUTCH _(July)	7	8.8	8.0–10.4	16	10.7	8.8–12.4	44	9.9	7.8–11.0	76	14.6	8.8–19.4
HATCH _(April)	20	76.9%	67.7–84.5	68	66.8%	57.9–71.7	3	84.4%	68.9–100.0	19	43.6%	30.6–60.4
HATCH _(May)	33	74.0%	66.9–81.6	39	68.2%	62.7–71.0	19 ^c	44.2% ^c		16	58.0%	47.9–76.2
HATCH _(June)	26	85.0%	79.2–92.2	58	83.4%	77.5–90.9	27	59.4%	53.2–65.2	47	49.1%	38.7–63.5
HATCH _(July)	7	75.3%	50.0–87.5	16	86.4%	72.1–100.0	44	79.1%	74.6–85.7	76	67.2%	63.6–74.2
HDAY _(April)	225	0.294%	0.179–0.460	231	0.982%	0.747–1.170	141	0.077%	0.000–0.208	147	0.432%	0.000–0.721
HDAY _(May)	223	0.490%	0.396–0.601	233	0.538%	0.334–0.765	144	0.549%	0.000–1.613	147	0.349%	0.000–0.610
HDAY _(June)	224	0.380%	0.128–0.632	230	0.840%	0.575–1.149	141	0.645%	0.278–0.860	147	1.058%	0.556–1.667
HDAY _(July)	52 ^d	0.321% ^d		59 ^d	0.601% ^d		87	1.880%	1.457–2.823	103	2.519%	1.792–3.047

^a Sample sizes for CLUTCH and HATCH were based on total number of successful clutches over the 4 years. CLUTCH was the number of wood duck eggs in a box and HATCH was the probability that an egg hatches; only data from clutches with known fates (i.e., successful, depredated, or abandoned) were used. Sample sizes for HDAY were based on total number of boxes monitored and available for wood ducks over the 4 years. HDAY was the probability a duckling exited a nest box on a given day.

^b Refers to the range of estimates over the 4 years.

^c Only used data from 1994; sample sizes from 1995 to 1997 were too small for reliable estimate.

^d Only used data from 1997; sample sizes from 1994 to 1996 were too small for reliable estimate.

survived through day $i-1$, $S_{a,i-1}$ is the daily survival probability of a day-old duckling from days $i-1$ to i , Nf_i is number of fledglings (>30 days) on day i , and S_f is the probability of fledgling survival defined above. We generated random numbers using eqs. (1) – (5) and the R functions `rbinom()` and `rpois()` to project daily number of ducklings and fledglings for a period of 153 days (from 1 Mar to 1 Sep) with 2,000 repetitions for each combination of study site and box size. We calculated means and 95% confidence intervals for the cumulative number of recruits produced per box for each box size and study site. We plotted total recruits over the entire simulation period to examine changes over time. Finally, we calculated mean daily growth rate, or the population at day t /the population at day $t-1$. We estimated daily growth rate for each month by dividing total number of recruits produced in a given month by days in that month.

Perturbation

We used modified perturbation analyses to examine the influence CLUTCH, HATCH, HDAY, and early and late S_d had on recruitment for each box type and site (Caswell, 2001). We could not calculate formal sensitivities and elasticities (Caswell, 2001) in life-stage population matrix because 1) we could not account for nest parasitism among conspecific females and 2) our goal was to predict total recruits not changes in annual population. Because we used a daily time step, we adjusted CLUTCH, HATCH, and HDAY by 10% for the days corresponding to April–July. We adjusted early and late S_d by 10% for the days corresponding to early and late time periods. For a given iteration, we adjusted 1 variable by 10% while holding all other variables constant (control). For each iteration, we compared number of recruits surviving to 1 September given no adjustments to

parameters and after adjusting a given parameter. We repeated for 2,000 iterations and ranked each parameter, within box size and site, based on the proportion of times the adjusted number of recruits exceeded the control by 10 recruits. The overall rank was the average of within box type and study site ranks.

RESULTS

Survival

Our best-supported model estimated survival on a daily basis compared to constant survival, and survival estimates differed for early- and late-hatched birds (Table 2). Survival to 30 days for late-hatched ducklings was 0.298 (95% CI = 0.049–0.562) and 0.100 (95% CI = 0.002–0.359) for early-hatched ducklings. We did not consider any other models competitive, because the next best model was >2 QAIC_c units from the leading model (Table 2). Duckling survival increased with offspring age during spring and summer (Fig. 2). Daily survival differences were most pronounced for 2-day-old ducklings (early hatched = 0.66, 95% CI = 0.56–0.74; late hatched = 0.87, 95% CI = 0.82–0.91) followed by 3-day-old ducklings (early hatched = 0.72, 95% CI = 0.60–0.81; late hatched = 0.89, 95% CI = 0.84–0.93; Fig. 2).

Recruitment

Cumulative recruits per box for an entire breeding season were greatest for large boxes at YNWR (\bar{x} = 3.7 ducks, 95% CI = 3.0–4.5), followed by small boxes at YNWR (\bar{x} = 1.9, 95% CI = 1.5–2.4), large boxes at NNWR (\bar{x} = 1.6, 95% CI = 1.2–2.1), and small boxes at NNWR (\bar{x} = 0.7, 95% CI = 0.4–1.0). Total recruits hatched per day was positive (i.e., reproduction > mortality) for the entire breeding season for both box sizes and study sites, and recruitment rate

Table 2. Candidate models used to assess variation in survival of 429 radio-marked wood duck ducklings using nest boxes in Mississippi and Alabama in 1996–1999. Models are ranked by Akaike’s Information Criterion corrected for small sample size and overdispersion (QAIC_c). Also included are the number of estimable parameters (*K*), model weight (ω_i), and Quasi-deviance (QDeviance).

Survival structure	Grouping structure	ΔQAIC_c	ω_i	<i>K</i>	QDeviance
Daily	Time-period ^a	0.0 ^b	0.987	58	371.2
Daily	Null	8.8	0.012	29	439.1
Daily	Site	14.5	0.001	58	385.7
Constant	Time-period	102.0	0.000	2	586.7
Daily	Year	121.9	0.000	116	372.5
Constant	Site	148.0	0.000	2	632.7
Constant	Null	159.2	0.000	1	645.9
Constant	Year	162.1	0.000	4	642.8

^a Time-period relates to hatch dates of ducklings in a given year. Ducklings hatched before 1 June were early hatched and ducklings hatched ≥ 1 June were late hatched.

^b QAIC_c of top model: 1,821.1.

increased for ducklings produced in late spring and summer (i.e., Jun–Aug). Based on non-overlapping confidence intervals, we inferred that recruits per day differed among box sizes and study sites. At YNWR, recruits per day from large boxes ranged from 6.5 (95% CI = 5.8–7.0) in August to 0.4 (95% CI = 0.1–0.8) in May, whereas recruits per day from small boxes at YNWR ranged from 3.9 (95% CI = 3.3–4.6) in August to 0.1 (95% CI = 0.0–0.2) in May. At YNWR, 54% of recruits from large boxes and 63% of recruits from small boxes hatched in June and July. At NNWR, recruits per day from large boxes ranged from 2.3 (95% CI = 1.7–2.8) in July to 0.7 (95% CI = 0.50–0.8) in June, whereas recruits per day from small boxes ranged from 0.9 (95% CI = 0.7–1.3) in July to 0.3 (95% CI = 0.1–0.6) in May at this site. At NNWR, 44% of recruits from large boxes hatched in June, as did 43% of recruits from small boxes. Collectively, the months of June–August were critical to wood duck recruitment at YNWR because 91% of all recruits from each box type were hatched and reared during those

months. At NNWR, 68% of all recruits from large boxes and 65% of all recruits small boxes were hatched and reared during June–August. Overall, only about 10% of all ducklings hatched prior to June at YNWR were estimated to survive until 1 September compared to 32–35% of all ducklings hatched at NNWR.

Perturbation Analysis

Daily survival rate, HATCH, and HDAY had the most influence on recruitment for each box size and study site (Table 3). Increasing late-hatched duckling survival by 10% elevated simulated recruitment 10% and 8% for large and small boxes, respectively, at both YNWR and NNWR (Table 3). The next most influential recruitment parameters were box size and study site, but parameters for June and July always were more influential than parameters for April and May. Increasing HDAY_{July} by 10% increased simulated recruitment by 2% for small boxes and 4% for large boxes at NNWR, and 6% for small boxes and 7% for large boxes at

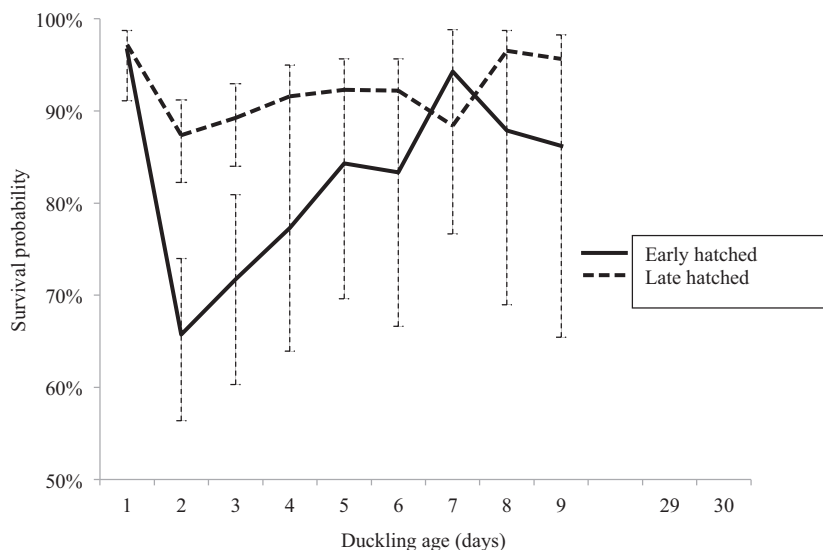


Figure 2. Probability of survival to 30 days for early- (solid line) and late-hatched (dashed line) wood duck ducklings radiomarked in Mississippi (1996–1999) and Alabama (1998–1999), USA. Early- and late-hatched ducklings correspond to a hatch date before and after 1 June, respectively. We derived survival estimates from the most parsimonious model using a known-fate model in Program MARK. Confidence intervals overlapped for daily survival rates for all duckling ages except 2 and 3 days old; after 9 days, estimates were nearly identical, so we plotted survival estimates only to day 9. The known-fate model estimated survival at duckling age 29 and 30 at 100% with no variance (dash on top right).

Table 3. The relative effect of parameters influencing recruitment growth rate of wood ducks using small and large nest boxes at Sam D. Hamilton Noxubee and Teddy Roosevelt Yazoo National Wildlife Refuges in Mississippi, 1994–1997, as measured by percentage change (% Δ) in recruitment by increasing a parameter while holding all others at their means. The % Δ was calculated relative to baseline growth rate (all parameters held at mean values). Results are based on 2,000 stochastic iterations and parameters are ranked within a box size and study site. Asterisks indicate the top 4 most influential variables overall.

Rate	Noxubee						Yazoo						Overall rank ^b
	Small box			Large box			Small box			Large box			
	% Δ	σ	Rank ^a	% Δ	σ	Rank ^a	% Δ	σ	Rank ^a	% Δ	σ	Rank ^a	
CLUTCH ^c (April)	0.4	197	14	1.5	539	9	0.6	592	14	0.3	1,457	14	14
CLUTCH ^c (May)	1.5	196	12	1.6	500	11	1.5	620	8	0.6	1,441	13	11
CLUTCH ^c (June)	3.5	209	3	4.2	546	4	2.7	632	7	3.8	1,677	6	5
CLUTCH ^c (July)	2.6	210	7	3.0	545	6	2.8	607	4	5.7	1,639	4	6
HATCH ^c (April)	1.2	182	13	2.3	534	7	0.5	593	12	0.7	1,475	11	10
HATCH ^c (May)	1.6	202	10	1.4	514	13	1.5	593	10	0.6	1,395	12	12
HATCH ^c (June)*	4.1	214	2	4.7	574	2	2.9	631	5	4.0	1,626	5	3
HATCH ^c (July)*	2.2	198	5	2.9	519	8	7.1	712	3	6.0	1,572	3	4
HDAY ^d (April)	1.0	202	11	1.5	491	12	0.1	595	13	0.7	1,509	10	13
HDAY ^d (May)	1.4	192	8	1.1	524	14	0.7	602	11	0.7	1,490	7	9
HDAY ^d (June)	4.0	204	4	4.1	533	5	2.9	614	6	0.7	1,543	8	7
HDAY ^d (July)*	2.4	212	6	4.0	526	3	7.3	643	2	6.3	1,548	2	2
S _d ^e (early)	2.0	199	9	2.3	555	10	1.2	610	9	0.7	1,515	9	8
S _d ^e (late)*	7.7	219	1	7.8	600	1	10.1	696	1	10.3	1,892	1	1

^a Ranks are based on proportion of times (from 2,000 stochastic iterations) adjusted number of recruits exceeded the simulations when all other parameters were held at their mean values.

^b Average of within box type and study site ranks.

^c CLUTCH was the number of wood duck eggs in a box and HATCH was the probability that an egg hatches; only data from clutches with known fates (i.e., successful, depredated, or abandoned) were used.

^d HDAY was the probability a duckling exited a nest box on a given day.

^e Survival of wood duck ducklings hatched early (before 1 Jun) and late (≥ 1 Jun) in a breeding season.

YNWR (Table 3). For HATCH_{June} and HATCH_{July}, simulated recruitment increased 2–7% across box types and study sites (Table 3).

DISCUSSION

Biological events related to the timing of hatch and duckling survival were more important to simulated wood duck recruitment than clutch size. Regardless of box size and study site, our stochastic simulations predicted a similar trend of increased recruitment through the breeding season but especially during late spring and summer. We cannot affirm the mechanisms promoting positive seasonal duckling survival in our study. However, seasonal survival of northern prairie mallard (*Anas platyrhynchos*) ducklings generally contrast with our results because temporary and seasonal wetlands important to prairie duck broods typically decrease in availability with progressing spring and summer (Krapu et al. 2000, Stafford et al. 2002). Lake wetlands in our study areas contained water year around, and wetland vegetation increased during spring and summer. Moreover, mallard duckling survival varied little over the breeding season in the Great Lakes region, where broods primarily used semi-permanent and permanent ponds, marshes, and other relatively stable wetlands (Simpson et al. 2005). Important resources (e.g., brood cover, invertebrates) in our wetlands may have increased seasonally and were important to later-hatching wood duck ducklings (Arner et al. 1974; Davis et al. 2007, 2009).

Our perturbation analysis demonstrated that late-season duckling survival was most important in influencing recruitment from each box size and study site. Because

ducklings hatched later in the breeding season have enhanced 30-day survival, our simulations predicted that most recruits were hatched and reared from June through August. Despite the apparent advantages to late-season hatching and recruitment (Davis et al. 2007), there may be selective pressures for wood ducks to nest early, allowing some birds to renege if necessary, and some females raise 2 broods in a season (Fredrickson and Hansen 1983, Kennamer and Hepp 1987, Hepp et al. 1989). The subtropical climate and environment in Mississippi and Alabama provided an extended breeding and brood-rearing season generally from February through August (Davis et al. 1999b, 2007).

Recruitment From Large and Small Nest Boxes

Both large and small nest boxes at YNWR consistently produced as many or more recruits than did large boxes at NNWR, but small boxes produced <1 recruit at NNWR. The differences between sites may be related partly to the open, agricultural landscape surrounding YNWR, perhaps stimulating wood duck females to use boxes because relatively few natural cavities exist in and around YNWR (Lowney and Hill 1989). Intuitively, availability of natural cavities for wood ducks in NNWR may be greater than at YNWR, because the former area is largely composed of upland and lowland forests (Lowney and Hill 1989). Lowney and Hill (1989) estimated 0.19 suitable cavities/ha in bottomland hardwood forests at NNWR and 0.23 cavities/ha in the 24,000-ha Delta National Forest, the largest bottomland hardwood forest in Mississippi and <40 km from YNWR. Although contemporary estimates of natural cavities are not available for YNWR, an estimated 2,301 ha of lowland and bottomland hardwood forest existed at

YNWR compared to 17,200 ha of upland and lowland forest at NNWR during our study (<http://www.fws.gov/refuge/Noxubee/about.html>, accessed 17 Jun 2014). The above estimates of natural cavities suitable for wood ducks were some of the lowest recorded in North America (Soulliere 1990, Denton et al. 2012). Therefore, disparities in overall wood duck recruitment between YNWR and NNWR cannot be explained, but nest boxes seem important to wood duck production especially at YNWR amid the lack of forested habitat in this agrarian region.

Differences between study sites in probability of producing a successful clutch on a given day (i.e., HDAY) were evident, particularly in June and July, which may have been a primary mechanism influencing increased nest success and recruitment from that time period, particularly at YNWR. Although HDAY remained relatively constant for large and small boxes at NNWR, it increased substantially at YNWR in June and July. Indeed, there was increased nest success later in the year at YNWR compared to earlier in the breeding season. We do not know if seasonal patterns in nest success occur elsewhere in the wood ducks' range, but it seems possible, particularly in agricultural and other open landscapes with nest boxes but few natural cavities. In contrast, wood ducks did not demonstrate a seasonal fluctuation in nesting efficiency at NNWR. Decreased nest box occupancy and nest success, especially in small boxes at NNWR, may have resulted from ≥ 7 species of passerines that used small boxes generally in May and later annually (Davis et al. 1999b). At NNWR, use of small boxes by passerines ranged from 14% to 65% and generally increased over the first 4 years after small boxes were established (Davis et al. 1999b). In contrast, $\leq 15\%$ of large boxes at NNWR were used by passerines, and passerines never used large boxes at YNWR. Although passerines occupied as much as 56% of small boxes at YNWR, those structures still yielded more duckling recruits than large boxes at NNWR consistent with our hypothesis of limited suitable cavities in and around YNWR.

We did not experimentally evaluate duckling production relative to different maintenance schedules of nest boxes (e.g., Utsey and Hepp 1997); however, we monitored boxes monthly and removed non-hatched eggs and down feathers of terminated nests (Davis et al. 2007). Although smaller clutch sizes likely helped to increase late-season nesting efficiency, we posit that duckling production would have been substantially less without nest box maintenance (Utsey and Hepp 1997). At YNWR particularly, layers of abandoned eggs and down would have persisted in nest boxes had we not removed them. These boxes likely would have been less desirable than cleaned boxes to nest-site prospecting females. We recognize that total recruitment was the sum of surviving ducklings from early- and late-season nests. However, given the increased survival of late-hatched ducklings, nest-box maintenance conducted throughout the breeding season was presumably fundamental to enhancing recruitment of box-nesting wood ducks, especially at YNWR, and it is likely important elsewhere in the species' range (Utsey and Hepp 1997, Davis et al. 2007).

MANAGEMENT IMPLICATIONS

Large boxes consistently produced more wood duck recruits into late summer than small structures. Nest boxes were most effective in an agricultural landscape where suitable natural cavities may have been limited (Lowney and Hill 1989). In addition, passerines rarely used large boxes. Assuming waterfowl managers' primary goal for use of nest boxes is to recruit wood ducks, we recommend large over small structures. In Mississippi and Alabama, based on phenology of wood duck nesting, we suggest 1 May as a reasonable date for inspecting and cleaning boxes of abandoned eggs and down feathers. Southern latitudes promote extended breeding seasons for wood ducks (Kenamer and Hepp 1987, Bellrose and Holm 1994). Second broods produced by wood ducks may be important to fall recruitment, although successful second nests only may comprise 10% of all successful nests in a season (Kenamer and Hepp 1987). Double brooding, late-hatching nests, and positive seasonal duckling survival may be important to fall recruitment in southern wood duck populations, but this should be investigated comparatively among different geographic populations.

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