



RESEARCH ARTICLE

## Winter survival of female American Black Ducks in Tennessee, USA

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### ABSTRACT

Many migratory bird species, including the American Black Duck (*Anas rubripes*; hereafter black duck), face challenges to their survival during winter due to potentially limited resources and high energetic demands. These winter processes can be especially important for the population dynamics of migratory species. Despite stabilization of the overall black duck breeding population, historical declines continue for black ducks wintering in the Mississippi Flyway. It remains unclear if declining abundance in this region reflects high winter mortality. We radio-tagged 111 females in the Tennessee National Wildlife Refuge (TNWR), a major wintering area for mid-continent Mississippi Flyway black ducks, from December to February of 2010–2012 to estimate winter survival and investigate factors that may influence survival rates, including body mass, age, hunting period, and weather. Winter survival (0.83–0.85) was greater than or comparable with previous estimates for black duck populations in North America. Generally, birds with greater body mass had higher survival than birds of lesser body mass; a bird 100 g heavier than one of average body mass had 18% greater interval survival. We also found that body mass had a greater influence on survival during late (nonhunting) periods and a more severe winter, when resources potentially were limited. For example, a bird with a body mass 100 g above average had 9% greater interval survival than one of average body mass during the winter of 2010–2011, but in the subsequent milder winter, the heavier bird had similar survival to the bird of average body mass. Our results suggest that winter mortality is not a primary factor contributing to declining abundance of black ducks in the TNWR. If this reflects the general pattern in the Mississippi Flyway, declining regional abundance may be driven by movement patterns or cross-seasonal effects rather than winter mortality.

**Keywords:** American Black Duck, winter, body mass, weather, hunting, known-fate models, Mississippi Flyway

### Survie hivernale des femelles d'*Anas rubripes* au Tennessee

#### RÉSUMÉ

Plusieurs espèces d'oiseaux migrants, dont *Anas rubripes*, font face à des défis pour leur survie en hiver en raison des ressources limitées et des demandes énergétiques élevées. Ces processus hivernaux peuvent être particulièrement importants pour la dynamique des populations d'espèces migratrices. Malgré la stabilisation de la population reproductrice globale d'*A. rubripes*, des déclins historiques persistent pour les populations hivernant dans la voie migratoire du Mississippi. Il demeure incertain si le déclin de l'abondance dans cette région reflète une mortalité hivernale élevée. De décembre à février 2010–2012, nous avons équipé 111 femelles de radio-émetteurs au Tennessee National Wildlife Refuge (TNWR), un quartier d'hivernage majeur pour les individus de cette espèce de la voie migratoire du Mississippi dans le centre du continent, afin d'estimer la survie hivernale et d'examiner les facteurs qui peuvent influencer les taux de survie, dont la masse corporelle, l'âge, la période de chasse et les conditions météorologiques. La survie hivernale (0,83–0,85) était plus élevée ou comparable à celle des estimations antérieures pour les populations d'*A. rubripes* en Amérique du Nord. Généralement, les oiseaux ayant une plus grande masse corporelle avaient une survie plus élevée que les oiseaux de plus faible masse corporelle; un oiseau plus lourd de 100 g qu'un autre de masse corporelle moyenne avait une survie 18 % plus élevée. Nous avons aussi trouvé que la masse corporelle avait une plus grande influence sur la survie au cours des périodes tardives (sans chasse) et d'un hiver plus rude car les ressources étaient potentiellement limitées. Par exemple, un oiseau avec une masse corporelle de 100 g au-dessus de la moyenne avait une survie de 9 % plus élevée qu'un autre de masse corporelle moyenne au cours de l'hiver 2010–2011, mais lors de l'hiver subséquent, plus doux, l'oiseau le plus lourd avait une survie similaire à celui de masse corporelle moyenne. Nos résultats suggèrent que la mortalité hivernale n'est pas un facteur principal contribuant au déclin de l'abondance d'*A. rubripes* au TNWR. Si cela reflète le patron général de la voie migratoire du Mississippi, le déclin de l'abondance régionale peut être causé par des patrons de mouvements ou des effets trans-saisonniers plutôt que par la mortalité hivernale.

*Mots-clés:* *Anas rubripes*, hiver, masse corporelle, conditions météorologiques, chasse, modèles de destinée connue, voie migratoire du Mississippi

## INTRODUCTION

The nonbreeding period is challenging for many bird species because of potentially limited resources and high energetic demands, and low survival during winter can disproportionately affect fitness and population dynamics (Robinson et al. 2007, García-Pérez et al. 2014, Klaassen et al. 2014, Hostetler et al. 2015, Rogers 2015). For most Nearctic ducks, this period extends nearly 8 mo and includes significant biological and social events (Weller 1988, Robertson and Cooke 1999, Baldassarre and Bolen 2006, Davis et al. 2014). Accessible, quality food and disturbance-free areas are essential resources for wintering waterfowl (Whyte and Bolen 1984, Legagneux et al. 2009, Dooley et al. 2010b). The survival of waterfowl in winter can be greatly affected by age, habitat conditions, body condition, hunting-related effects (e.g., disturbance, direct mortality), and the availability of sanctuary (Krementz et al. 1988, Conroy et al. 1989, Longcore et al. 2000, Dooley et al. 2010a, Davis et al. 2011, 2014).

Once the most harvested and abundant dabbling duck in eastern North America (Blandin 1992, Devers and Collins 2011), the American Black Duck (*Anas rubripes*; hereafter black duck) declined precipitously between the 1950s and 1990s, falling from ~750,000 in 1955 to ~288,800 birds in 2014 in the Mid-winter Waterfowl Survey (MWS; USFWS 2014). Harvest and hunting-related disturbance, competition and introgressive hybridization with Mallards (*A. platyrhynchos*), and loss and degradation of habitat are among the most implicated possible causes (Rusch et al. 1989, Nudds et al. 1996, Conroy et al. 2002a). Research into factors possibly influencing declines in black duck populations is especially important in the Mississippi Flyway, where the steepest declines have occurred. Changes in black duck populations have not been uniform throughout the species' range, and both breeding and winter survey data reveal contrasting population trends, with declines in southern, western, and central sectors of the range, but stabilization or slight increases in north-eastern areas (Link et al. 2006, Brook et al. 2009, Zimmerman et al. 2012). There was a 2-fold decrease in the MWS population index for black ducks in the Atlantic Flyway between 1955 and 2014 (582,453 to 269,000 birds), while the index for the Mississippi Flyway showed a 9-fold decrease during the same period (178,400 to 19,700 birds; Fronczak 2012, USFWS 2014). Despite extensive research on black ducks in North America, limited information exists on factors affecting winter survival of black ducks in the Mississippi Flyway (Krementz et al. 1988, Chipley 1995, Robb 1997). However, there is some evidence to

support differential winter survival between adults and juveniles, and also potential negative effects of body condition, hunting, and weather severity on black duck survival (Krementz et al. 1988, Chipley 1995, Robb 1997).

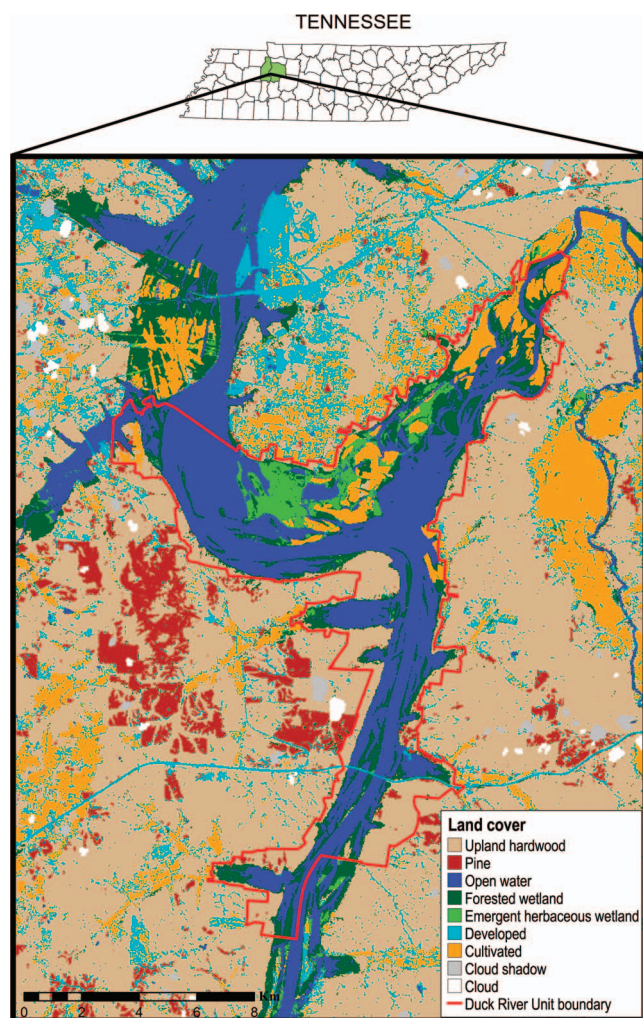
The state of Tennessee has supported the most wintering black ducks in the Mississippi Flyway in more than half of the years from 1955 to 2014, averaging ~33,851 birds from 1955 to 1999, but decreasing 76% to an average of ~8,108 birds for 2000–2013 (Fronczak 2012, USFWS 2014). Tennessee National Wildlife Refuge (TNWR) and Cross Creeks National Wildlife Refuge historically held the most wintering black ducks in Tennessee (Sanders 1995), with the TNWR having >50% of black ducks in the state, or ~22% of black ducks in the Mississippi Flyway (Fronczak 2012, R. M. Wheat personal communication). However, black ducks wintering in the TNWR have declined as well, from ~20,000 birds in 1964 to 2,913 in 2015 (R. M. Wheat personal communication).

Listed as a "Species of Greatest Conservation Need" by 74% of the states in the Mississippi and Atlantic flyways (Devers and Collins 2011), conservation and research initiatives to increase black duck populations are priorities for government agencies, conservation organizations, and hunters, because of the economic, ecological, and cultural significance of the species. Given concerns over declining black duck populations in the Mississippi Flyway and specifically in the TNWR, a major wintering area for mid-continent Mississippi Flyway black ducks, our objectives were to: (1) determine contemporary winter survival estimates of black ducks, and (2) evaluate biotic and abiotic factors that may be affecting black duck survival in the TNWR.

## METHODS

### Study Area

Our primary study area was the Duck River Unit (DRU; 35°57'30N, 87°57'00W) of the TNWR in western Tennessee (Figure 1). The DRU is the largest (10,820 ha) of 3 wetland complexes comprising the TNWR (20,784 ha). Primary resources in the DRU include: (1) seasonally flooded, emergent herbaceous (i.e. moist-soil) wetlands (594 ha); (2) cooperatively farmed row crop agriculture (673 ha); (3) impounded open water areas (537 ha); (4) woody sloughs, scrub-shrub, and bottomland hardwoods (2,016 ha); (5) uplands dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.; 2,468 ha); and (6) portions of the Kentucky Reservoir (3,458 ha) and Duck River (777 ha). Crops grown in the TNWR include corn, millet, grain sorghum, winter wheat, soybean, and clover. Interior levees



**FIGURE 1.** Land cover map of Tennessee National Wildlife Refuge's Duck River Unit in Humphreys County in western Tennessee, USA, winter 2010–2011.

divide the DRU into 14 managed impoundments, and an outer perimeter levee helps protect impoundments from flooding by the Kentucky Reservoir and Duck River. Waterfowl hunting is not permitted in the TNWR, but hunting occurs on surrounding private and public lands. Most roads within the DRU are closed to foot and vehicular traffic from November 15 to March 15 annually.

### Trapping and Transmitter Attachment

We baited and deployed swim-in traps and rocket nets in the DRU from November through early February of 2010–2012 in areas where black ducks were consistently observed. Swim-in traps were constructed of 1.5 m tall,  $2.5 \times 5.0$  cm welded wire, and roofed with  $5 \times 5$  cm plastic mesh. We baited areas around swim-in traps and rocket nets with a combination of whole kernel corn, wild bird seed mix, chufa tubers, and milo, beginning November 15

each year. All captured male and female black ducks were transported to DRU headquarters to be banded, but only females were radio-tagged.

We banded all black ducks with U.S. Geological Survey standard aluminum tarsus bands and aged birds by wing plumage characteristics (Carney 1992, Ashley et al. 2006). Females were weighed with a 2.5-kg Pesola spring scale (Pesola AG, Baar, Switzerland) and only instrumented if a 23-g, harness-type, VHF transmitter (Model A1820, Advanced Telemetry Systems, Isanti, Minnesota, USA) was  $<3\%$  of an individual's body mass ( $\sim 900$  g; Dwyer 1972, Gustafson et al. 1997). Only one captured female was released without a transmitter because she did not meet the weight requirement. Transmitters were equipped with mortality sensors that doubled the signal pulse rate after 8 hr of inactivity. After marking females, we placed them in crates and left them undisturbed for  $\sim 1$  hr before releasing females and males at trap sites (Cox and Afton 1998). We commenced data collection on the third day postrelease to avoid possible biases associated with acclimation to transmitters (Conroy et al. 1989, Davis et al. 2009). All transmitters were deployed by February 3 in both winters.

### Telemetry Data Collection

We determined the survival status and locations of a subsample (i.e. randomly selected without replacement) of radio-tagged female black ducks daily, 6 days per week (Davis and Afton 2010). The subsample of radio-tagged ducks was tracked diurnally and nocturnally within a 24-hr cycle using vehicles equipped with roof-mounted, 4-element, null-peak antenna systems (Advanced Telemetry Systems, Isanti, Minnesota, USA; Cox et al. 2002, Pearse et al. 2011). We also equipped vehicles with Global Positioning System units (Trimble GeoXM handheld, Trimble Navigation Ltd, Sunnyvale, California, USA), laptops with Location of a Signal software (LOAS 4.0.3.8, Ecological Software Solutions, Hegymagas, Hungary), and electronic compasses (Azimuth 1000R, KVH Industries, Middletown, Rhode Island, USA; Cox et al. 2002, Davis and Afton 2010). Electronic compasses were calibrated to within  $\pm 0.5^\circ$  of known locations of beacon transmitters, and crew members were trained to use the tracking system and triangulate beacon transmitters until they were able to maintain a standard deviation  $\leq 3^\circ$  (Davis et al. 2009, Davis and Afton 2010, Pearse et al. 2011).

Upon detecting radio-tagged ducks, we recorded Universal Transverse Mercator (UTM) coordinates of the tracking vehicle and  $\geq 3$  azimuths in LOAS to estimate locations and 95% confidence ellipses, based on a maximum-likelihood estimator (Lenth 1981) and a bearing standard deviation of  $3^\circ$  (Davis et al. 2009, Davis and Afton 2010, Pearse et al. 2011). If necessary, we obtained additional azimuths until confidence ellipses were within 1 habitat type or detection vantage points were exhausted



(Davis et al. 2009). If  $>3$  azimuths were recorded, the combination of bearings that resulted in the smallest confidence ellipse was used for analyses. Additionally, we conducted aerial surveys in a Cessna 172 equipped with strut-mounted, 4-element antennas when radio-tagged ducks were not detected via ground reconnaissance (Gilmer et al. 1981). When a mortality signal was detected, we immediately located the transmitter, recorded the location, and determined cause of death if possible (Cox and Afton 1998).

### Explanatory Variables

We used the following explanatory variables in our known-fate survival models: year (winter 2010–2011 or 2011–2012); female age (hatch and second year [HY] or after hatch and after second year [AHY]); regression residuals of body mass at capture on the date of capture (see below); hunting period (during hunting or posthunting season); and weather (minimum temperature [°C], rainfall [mm], snowfall [mm], and a weather severity index [WSI]).

**Body mass.** Waterfowl experience endogenous changes in body mass throughout winter (Hepp 1986, Loesch et al. 1992). Because we captured and measured the body mass of females from December to February each winter, we accounted for endogenous changes in mass by evaluating linear and polynomial regression models of body mass at capture on the date of capture and used the residuals from the best model in our survival analyses (Lancaster 2013, Newcomb 2014). We used  $F$ -tests to compare null (i.e. intercept only), linear, and polynomial regression models relating body mass at capture to the date of capture for each year. When evaluating regression models of body mass at capture ( $m$ ) on the date of capture ( $d$ ), we detected an interaction between date and year of capture on body mass by analysis of covariance ( $F_{3,109} = 7.3$ ,  $P < 0.001$ ). Therefore, we determined the best model for each year separately. We detected neither an effect of age ( $P = 0.77$ ) nor an interaction of age by date of capture ( $P = 0.84$ ) on body mass, so we did not include models incorporating age in subsequent comparisons of regression models.

For the winter of 2010–2011, neither linear ( $P = 0.87$ ) nor polynomial ( $P = 0.48$ ) regression models explained variation in body mass better than the null model ( $m = 1201 - 0.1d$ ). For winter 2011–2012, a second-order polynomial regression model ( $m = 1426 - 19.6d + 0.3d^2$ ) fit better than null ( $P < 0.001$ ) or linear ( $P < 0.002$ ) models; however, a third-order polynomial regression model did not fit better than the second-order model ( $P = 0.33$ ). Based on these analyses, we used residuals from the null model for the 2010–2011 winter and residuals from the second-order polynomial regression model for the winter of 2011–2012. After the most appropriate model was identified, we used Fligner-Killeen and Shapiro-Wilk tests

to test for homogeneity of variances and normality of residuals, respectively (Crawley 2013).

Body condition indices of waterfowl can vary by season, species, sex, and among populations (Miller 1989, Sparling et al. 1992). Schamber et al. (2009) recommended using body mass alone instead of unvalidated indices because adjustment with a structural measurement often provides little improvement for prediction of body fat than body mass alone, and White (1994) concluded that body mass adjusted by structural measurements was of little value for predicting body fat of black ducks in the TNWR. Thus, we did not adjust body mass by any structural measurements. We also did not adjust body mass to account for esophageal contents, which may have introduced additional variation that was unaccounted for in our analysis. However, because all traps and rocket nets were baited similarly, we assumed that the presence and amount of esophageal contents were random among birds and that body mass at capture was an adequate index of relative condition (Blomberg et al. 2014).

**Weather.** We modeled the effects of weather on survival by including covariates for rainfall (RAIN), minimum temperature (TMIN), snowfall (SNOW), and the weather severity index (WSI; Schummer et al. 2010). The WSI incorporates mean daily temperature, snowfall, and snow depth into a single index value, and Schummer et al. (2010) demonstrated its usefulness in examining the effects of temperature on energy expenditure of waterfowl and resource availability. We acquired weather data from the National Oceanic and Atmospheric Administration's National Climatic Data Center (<http://gis.ncdc.noaa.gov/map/viewer/#app=cdo>) and the Southern Regional Climate Center (Louisiana State University, Baton Rouge, LA) for the Global Historical Climatology Network–Daily (GHCND) weather station in Camden, Tennessee (14.5 km west-northwest of the DRU). We retrieved any data missing from the Camden weather station from the GHCND weather station in Mt. Moriah, Tennessee (7.2 km west of the DRU). Despite the Mt. Moriah station being closer to the DRU than the Camden station, we did not use the Mt. Moriah data because that station had more missing observations than the Camden station. Missing mean daily temperature values ( $n = 2$  of 200 days) were calculated by using the median between 2 dates for which data existed. Because each interval over which survival was estimated represented multiple days, we used the mean value of daily weather covariates for each interval. We calculated WSI for each day and subsequently calculated the mean WSI value for each interval. We standardized all covariates to facilitate maximum-likelihood estimation (Franklin 2001, Cooch and White 2013), and looked for correlation amongst covariates using Pearson's product-moment correlation test. The covariates TMIN and SNOW were correlated ( $r = -0.31$ ,  $P = 0.013$ ,  $n = 62$ ), so

we did not include them together in any models. We did not detect a correlation between WSI and RAIN ( $r = -0.12$ ,  $P = 0.36$ ), and thus we included them together in models.

**Hunting.** We created a binary covariate to represent whether hunting occurred during a monitoring interval ( $HUNT = 1$ ) or not ( $HUNT = 0$ ). Hunting occurred daily outside the TNWR from December 4, 2010, to January 30, 2011, and from December 3, 2011, to January 29, 2012, so we coded each interval during those periods as hunted. Youth hunts occurred on February 5–6, 2010, and February 4–5, 2011; we coded February 4–6 as hunted in both years. We did not divide the intervals to more accurately reflect hunting occurrence because it took 4 days to record locations for all radio-tagged ducks at that time.

### Statistical Analysis

We used the R 3.0.1 (R Development Core Team 2014) package RMark 2.1.5 (Laake and Rexstad 2013) to construct known-fate models in program MARK 7.1 (White and Burnham 1999) to estimate survival rates of radio-tagged female black ducks and to explain variation in rates relative to explanatory variables. We modeled winter survival from December 11, 2010 to March 17, 2011 (30 encounter occasions), and from December 19, 2011 to April 1, 2012 (32 encounter occasions). Survival was estimated over uneven intervals (i.e. 2–4 days) instead of daily intervals because we were only able to locate all females and determine their status (i.e. alive or dead) every 2–4 days. Mortalities that occurred  $\leq 4$  days after radio-tagging were excluded from survival analyses to avoid mortality bias associated with capture and radio-tagging ( $n = 2$ ; Cox and Afton 1998, Dooley et al. 2010a).

**Model selection.** We used an exploratory, sequential modeling approach to avoid overfitting the data while evaluating models incorporating covariates of interest (Fleskes et al. 2007, Amundson and Arnold 2011). Additionally, we avoided using a comprehensive, global model as the basis for model selection because only 12 mortalities were included in analyses, which did not support heavily parameterized models (e.g., global or fully time-dependent models). In the first step of model selection, we compared the constant (i.e. null) survival model and additive and interaction models incorporating year (YEAR), female age (AGE), and regression residuals of body mass at capture on the date of capture (MASS). We included AGE and MASS in the first step of model selection because these covariates often influence individual survival of waterfowl in winter (Conroy et al. 1989, Krementz et al. 1997, Anderson 2008). We also included YEAR in the first step because of the interaction that we found between body mass residuals and year. The constant survival model and models with informative parameters that ranked above the constant survival model were

included in subsequent steps of model selection (Fondell et al. 2008, Arnold 2010). We tested for the effects of HUNT and weather covariates in subsequent steps to account for additional variation in survival rates of black ducks. We included models with HUNT in the second step and models with RAIN, TMIN, SNOW, and WSI in the third step of model selection, in addition to the constant survival model and those models supported from previous steps. Estimates of dispersion in the model set ranged from 0.4 to 1.2, so we used  $\hat{c} = 1$  (Burnham and Anderson 2002, Zuur et al. 2009).

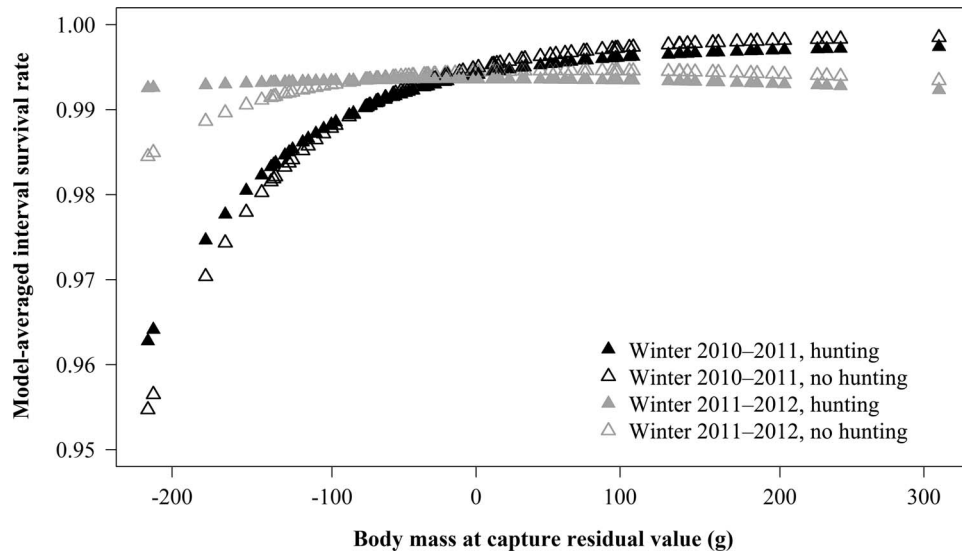
To evaluate models, we used Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ), Akaike weights ( $w_i$ ), and the difference from the top model in  $AIC_c$  ( $\Delta AIC_c$ ; Akaike 1973, Burnham and Anderson 2002). We used RMark to model-average parameter estimates from models with  $\Delta AIC_c \leq 2$  in the final step of model selection to account for model selection uncertainty in survival estimates (Burnham and Anderson 2002). Seasonal survival estimates were calculated as the product of all interval survival estimates for the period of interest, and the variance of the product was calculated using the Delta method in RMark (Cooch and White 2013, Laake and Rexstad 2013). We present 85% confidence limits for survival and  $\beta$  estimates because variables that exclude zero with 85% confidence intervals are supported by model selection with AIC (Arnold 2010).

### RESULTS

We radio-tagged 113 female black ducks (43 AHY and 70 HY birds) in the DRU during the winters of 2010–2012. Females were radio-tagged during December ( $n = 27$ , 16), January ( $n = 20$ , 31), and February ( $n = 17$ , 2) in the 2010–2011 and 2011–2012 winter, respectively. Though we began catching male black ducks in November, we did not capture any females until mid-December each winter. The mean body masses of radio-tagged adult ( $1,211 \pm 124$  g [mean  $\pm$  SD]) and juvenile ( $1,210 \pm 123$  g) black ducks were similar across winters. However, mean body mass was greater in the 2011–2012 winter than the 2010–2011 winter for adults ( $1,236 \pm 145$  g vs.  $1,199 \pm 102$  g, respectively) and juveniles ( $1,226 \pm 147$  g vs.  $1,198 \pm 101$  g, respectively).

### Mortalities

We documented 14 (12%) black duck mortalities during the study period, including 9 deaths in the winter of 2010–2011 and 5 in 2011–2012. Mortalities occurred in December ( $n = 1$ ), January ( $n = 2$ ), February ( $n = 1$ ), and March ( $n = 1$ ) in the 2010–2011 winter, and in January ( $n = 5$ ) in the winter of 2011–2012. In the 2010–2011 winter, 1 black duck was depredated by a raptor, but the cause of mortality for the other 8 black ducks could not be



**FIGURE 2.** Survival rates of female American Black Ducks in western Tennessee, USA, during the winters of 2010–2012 determined by model-averaging 3-day interval survival estimates from the models YEAR\*MASS, HUNT\*MASS, MASS, and the constant survival model. YEAR = Winters 2010–2011, 2011–2012; MASS = Residual values from the best regression model of body mass of female black ducks at capture on date of capture, and HUNT = Dummy variable for each day, coded as 0 = not hunted and 1 = hunted.

determined because we were unable to inspect carcasses before they were scavenged. In the winter of 2011–2012, all 5 mortalities were harvests, from 10 Mile Pond Conservation Area, Missouri, USA ( $n = 2$ ); Camden WMA, Tennessee ( $n = 2$ ); and private land adjacent to the Duck River, Tennessee ( $n = 1$ ). Through reports of band recoveries, we also discovered the fates of 10 black ducks that survived the winter during which they were radio-tagged, but were later harvested. These birds, which were harvested in Ohio, Michigan, Ontario, New York, Pennsylvania, West Virginia, and Tennessee, were not included as mortalities in our analysis because they survived through the study period.

### Survival of Female Black Ducks

**Model-averaged survival estimates.** We estimated winter survival for 111 radio-tagged female black ducks ( $n = 62$  in 2010–2011 and  $n = 49$  in 2011–2012). We incorporated model selection uncertainty into survival estimates by model-averaging estimates from the models YEAR\*MASS, MASS, HUNT\*MASS, and the null model, all of which had  $\Delta AIC_c \leq 2$ . Estimated survival rates for radio-tagged female black ducks during the hunting season were 0.90 (85% CL = 0.84, 0.97; 17 intervals) for the winter of 2010–2011 and 0.91 (85% CL = 0.86, 0.96; 15 intervals) for the winter of 2011–2012 (Figure 2). During the nonhunting season, estimated survival rates were 0.94 (85% CL = 0.89, 0.99; 13 intervals) for the 2010–2011 winter and 0.91 (85% CL = 0.85, 0.97; 17 intervals) for the 2011–2012 winter (Figure 2). Overall, survival rates for the winters of 2010–2011 and 2011–2012 were 0.85 (85% CL =

0.75, 0.95; 17 intervals) and 0.83 (85% CL = 0.73, 0.92; 15 intervals), respectively.

**Model selection.** In the first step of model selection, the best-supported model among 12 candidate models was YEAR\*MASS (Table 1). The univariate MASS model also ranked above the constant survival model. Models with AGE were not supported and were thus excluded from subsequent steps of model selection. For step 2 of model selection, we retained models from step 1 with a  $\Delta AIC_c \leq 2$ , which included YEAR\*MASS and MASS, and we incorporated HUNT into a set of 8 candidate models. The YEAR\*MASS model again was the most supported in step 2, and models retained from step 1 and HUNT\*MASS

**TABLE 1.** Top models from analysis of year, age, and body mass covariates in relation to survival of radio-tagged female American Black Ducks in western Tennessee, USA, winters 2010–2012. Only models that ranked above the constant survival model are shown.  $K$  is the number of parameters,  $\Delta AIC_c$  is the difference from the top model in Akaike's Information Criteria adjusted for small sample sizes,  $w_i$  is the relative likelihood of model ( $i$ ) based on the  $AIC_c$  value, and Dev is model deviance.

Model description	$K$	$\Delta AIC_c$	$w_i$	Dev
Year <sup>a</sup> * Mass <sup>b</sup>	4	0.00 <sup>c</sup>	0.36	132.60
Mass	2	2.02	0.13	138.64
Constant <sup>d</sup>	1	2.26	0.12	54.38

<sup>a</sup> Winters 2010–2011, 2011–2012.

<sup>b</sup> Residual values from the best regression model of body mass of female black ducks at capture on date of capture.

<sup>c</sup> Lowest  $AIC_c = 140.62$ .

<sup>d</sup> Null model (intercept only).

**TABLE 2.** Top models from analysis of a daily hunting covariate and selected covariates from the first step of model selection (Table 1) in relation to survival of radio-tagged female American Black Ducks in western Tennessee, USA, winters 2010–2012. Only models that ranked above the constant survival model are shown.  $K$  is the number of parameters,  $\Delta AIC_c$  is the difference from the top model in Akaike's Information Criteria adjusted for small sample sizes,  $w_i$  is the relative likelihood of model ( $i$ ) based on the  $AIC_c$  value, and Dev is model deviance.

Model description	$K$	$\Delta AIC_c$	$w_i$	Dev
Year <sup>a</sup> * Mass <sup>b</sup>	4	0.00 <sup>c</sup>	0.36	132.60
Year * Mass + Hunt <sup>d</sup>	5	1.98	0.14	132.57
Mass	2	2.02	0.13	138.64
Hunt * Mass	4	2.14	0.13	134.74
Constant <sup>e</sup>	1	2.26	0.12	54.38

<sup>a</sup> Winters 2010–2011, 2011–2012.

<sup>b</sup> Residual values from the best regression model of body mass of female black ducks at capture on date of capture.

<sup>c</sup> Lowest  $AIC_c = 140.62$ .

<sup>d</sup> Dummy variable for each day, coded as 0 = not hunted and 1 = hunted.

<sup>e</sup> Null model (intercept only).

received some support (Table 2). The YEAR\*MASS + HUNT model also ranked above the constant survival model; however, we did not retain YEAR\*MASS + HUNT in the subsequent step of model selection because it included an uninformative parameter (i.e. HUNT; Table 2). In the final step of model selection, we retained the YEAR\*MASS, MASS, and HUNT\*MASS models from step 2 and incorporated weather covariates into a set of 44 candidate models. Models with weather covariates were not supported, and weather parameters neither improved the rankings of models nor knowledge derived from them (Table 3). The best-supported model was YEAR\*MASS, yet uncertainty persisted among competitive models (i.e.  $\Delta AIC_c \leq 2$ ). The YEAR\*MASS model had only 14% of the total Akaike weight (Table 3). Evidence ratios indicated that YEAR\*MASS was 2.7 times more likely than MASS, 2.9 times more likely than HUNT\*MASS, and 3.1 times more likely than the constant model to be the actual best model (Table 3).

**Model interpretation.** Results from the YEAR\*MASS model indicated that the effect of body mass at capture on survival of female black ducks varied by year. Although there was no statistical difference in survival between years ( $\beta_{YR2} = -0.20$ , 85% CL =  $-1.27, 0.88$ ), there was a positive effect of body mass on survival in the winter of 2010–2011 ( $\beta_{MASS} = 1.30$ , 85% CL =  $0.55, 2.05$ ) and a negative effect of body mass on survival in the 2011–2012 winter ( $\beta_{YR2:MASS} = -1.51$ , 85% CL =  $-2.45, -0.57$ ; Figure 2). Weather conditions in the winter of 2010–2011 generally were more severe (e.g., colder temperatures, less precipitation in early and mid-winter, and greater snowfall) than in the

**TABLE 3.** Top models from analysis of weather and selected covariates from previous model selection steps (Tables 1, 2) in relation to survival of radio-tagged female American Black Ducks in western Tennessee, USA, winters 2010–2012. Only models that ranked above the constant survival model are shown.  $K$  is the number of parameters,  $\Delta AIC_c$  is the difference from the top model in Akaike's Information Criteria adjusted for small sample sizes,  $w_i$  is the relative likelihood of model ( $i$ ) based on the  $AIC_c$  value, and Dev is model deviance.

Model description	$K$	$\Delta AIC_c$	$w_i$	Dev
Year <sup>a</sup> * Mass <sup>b</sup>	4	0.00 <sup>c</sup>	0.14	132.60
Year * Mass + Rain <sup>d</sup>	5	1.15	0.08	131.74
Year * Mass + WSI <sup>e</sup>	5	1.75	0.06	132.33
Year * Mass + Tmin <sup>f</sup>	5	1.87	0.05	132.45
Year * Mass + Snow <sup>g</sup>	5	2.00	0.05	132.58
Mass	2	2.02	0.05	138.64
Hunt * Mass	4	2.14	0.05	134.74
Constant <sup>h</sup>	1	2.26	0.04	54.38

<sup>a</sup> Winters 2010–2011, 2011–2012.

<sup>b</sup> Residual values from the best regression model of body mass of female black ducks at capture on date of capture.

<sup>c</sup> Lowest  $AIC_c = 140.62$ .

<sup>d</sup> Average precipitation value (mm) over 3-day interval.

<sup>e</sup> Average weather severity index value over 3-day interval; index developed by Schummer et al. (2010), and incorporates mean daily temperature, snowfall, and snow depth into a single index value.

<sup>f</sup> Average minimum temperature (°C) over 3-day interval.

<sup>g</sup> Average snowfall value (mm) over 3-day interval.

<sup>h</sup> Null model (intercept only).

winter of 2011–2012 (Table 4), which could explain why the effect of body mass on survival was greater in the 2010–2011 winter (Figure 2), despite not detecting any effects of weather or year on survival of black ducks overall. We also did not detect an effect of age on survival. Results from the MASS model indicated a positive effect of body mass on survival overall ( $\beta_{MASS} = 0.47$ , 85% CL =  $0.00, 0.95$ ). Additionally, results from the HUNT\*MASS model indicated that the effect of body mass on survival varied between hunting and nonhunting periods. Although there was not a statistical difference in survival between hunting and nonhunting periods ( $\beta_{HUNT} = -1.02$ , 85% CL =  $-2.27, 0.24$ ), there was a positive effect of body mass on survival following the closure of the hunting season ( $\beta_{MASS} = 1.49$ , 85% CL =  $0.52, 2.45$ ) and a negative interaction between period and body mass ( $\beta_{HUNT:MASS} = -1.43$ , 85% CL =  $-2.43, -0.33$ ; Figure 2).

## DISCUSSION

### Winter Survival Estimates

Overall winter survival estimates for female black ducks in our study (0.83–0.85 over 3 mo) were greater than or comparable with estimates from other recent studies of radio-tagged dabbling ducks, which ranged from 0.54 to



**TABLE 4.** Monthly summaries of Global Historical Climatology Network–Daily (<http://gis.ncdc.noaa.gov/map/viewer/#app=cdo>) weather data recorded at Camden, Tennessee, USA, for the period November 2010–March 2012.

	November		December		January		February		March	
	2010	2011	2010	2011	2011	2012	2011	2012	2011	2012
Days >1.3 cm Rain <sup>a</sup>	4	6	1	6	2	3	5	0	5	3
Days >2.5 cm Rain	3	4	1	2	0	1	3	0	3	1
Days Tmin <sup>b</sup> ≤ 0°C	7	7	26	18	28	18	16	12	6	5 <sup>c</sup>
Days Tmax <sup>d</sup> ≤ 0°C	0	0	3	0	5	0	5	0	0	0 <sup>c</sup>
Total Rain (mm)	150	230	46	167	54	101	148	38	137	114
Total Snow <sup>e</sup>	0	0	66	0	168	0	88	0	0	0 <sup>c</sup>
Extreme Tmin <sup>b</sup>	−4	−4	−14	−7	−13	−8	−16	−9	−1	−1 <sup>c</sup>
Extreme Tmax <sup>d</sup>	6	6	16	19	19	21	23	27	28	29 <sup>c</sup>
Mean Tmin	3	5	−4	0	−4	0	0	1	5	9 <sup>c</sup>
Mean Tmax	17	17	6	11	6	13	12	13	16	24 <sup>c</sup>
Mean Temp <sup>f</sup>	10	11	1	6	1	6	6	7	10	16 <sup>c</sup>

<sup>a</sup> Rainfall (mm).<sup>b</sup> Minimum temperature (°C).<sup>c</sup> Two days of data missing.<sup>d</sup> Maximum temperature (°C).<sup>e</sup> Snowfall (mm).<sup>f</sup> Mean monthly temperature (°C).

0.70 for Mallards (4–6 mo; Dooley et al. 2010a, Davis et al. 2011, Lancaster 2013), 0.81 to 0.96 for Florida Mottled Ducks (*A. fulvigula fulvigula*; 2 mo during the hunting season; Varner et al. 2014), and 0.31 to 0.93 for Northern Pintails (*A. acuta*; 4–6 mo; Cox et al. 1998, Moon and Haukos 2006, Anderson 2008). Additionally, our survival estimates exceeded most reported rates for other black duck populations in the Mississippi (0.49–0.66, 2–3 mo; Robb 1997) and Atlantic flyways (0.37–0.77, 2–4 mo; Conroy et al. 1989, Longcore et al. 1991, 2000) during the postfledging, fall migration, and winter periods. Our survival estimates were somewhat lower than those reported by Chipley (1995; 0.94–1.00, 3 mo), who also radio-tagged female black ducks in the TNWR. However, Chipley (1995) estimated survival rates for females that were radio-tagged after exposure to a 30-day hunting season, whereas we calculated survival rates for ducks during the hunting (60 days) and posthunting seasons. Although we did not assess food acquisition by or body nutrient composition of black ducks, White (1994) suggested that female black ducks may have greater winter survival in western Tennessee because of increased energy reserves compared with black ducks wintering farther north in the Mississippi and Atlantic flyways.

### Body Mass and Survival

Body mass is often used as an index of an individual's energy reserves and overall condition, and maintaining sufficient reserves is essential for winter survival of birds (Johnson et al. 1985, Labocha and Hayes 2012). We found that survival generally increased as body mass at capture increased; a bird of average body mass had ~18% lower

interval survival than a bird 100 g heavier on the same date of capture. These results corroborate the findings of several studies of black ducks and Mallards in different wintering regions (Conroy et al. 1989, Longcore et al. 1991, Bergan and Smith 1993, Davis et al. 2011). However, for wintering birds a tradeoff exists between minimizing predation and starvation risks (Lima 1986, Rogers 1987, 2015). While lean birds spend less time and energy foraging to maintain fat reserves than heavier birds, the former may have lower fat reserves available to sustain them through fluctuations in food availability, weather, and disturbance (Lima 1986, Rogers 1987, 2015). Conversely, heavy birds may have greater reserves to endure environmental fluctuations than lean birds, but also may have greater exposure to or decreased capability to escape from predators (Lima 1986, Rogers 1987, 2015, Zimmer et al. 2010, 2011). Thus, an optimal body mass for overwintering birds is an intermediate body mass that minimizes predation and starvation risks while maintaining some fat reserves and escape capabilities (Lima 1986, Rogers 1987, 2015).

The effect of body mass on female black duck survival differed between winters in our study, which may be related to the concept of optimal body mass (Lima 1986, Rogers 1987, 2015, Conroy et al. 2002b, Zimmer et al. 2010, 2011). For example, a duck with a body mass 100 g above average had 9% greater interval survival than a duck with average body mass on the same date of capture during the winter of 2010–2011, but a heavier bird had slightly lower survival than an average one during the following winter. Optimal body mass in waterfowl may decrease in response to predation risk, likely to facilitate escape from



and reduce exposure to predators (Zimmer et al. 2010, 2011), or if resources are predictable (Rogers 1987, 2015). A decrease in optimal body mass and thus lower survival for heavier ducks, such as during the hunting season of 2011–2012, may have been related to greater resource predictability in the winter of 2011–2012 because of milder temperatures and greater precipitation than in the winter of 2010–2011. Robb (1997) speculated that radio-tagged black ducks in Ohio with greater body mass had lower survival because they ventured more frequently from sanctuaries into areas with increased hunting risk. However, movement data from our study did not appear to support Robb's (1997) hypothesis (Newcomb 2014).

Alternatively, contrasting effects of body mass on survival may have been related to food availability within the sanctuary of the DRU during winter (McClanahan 2015). Hunting pressure surrounding the DRU contributes to reduced use of habitat outside the DRU during the hunting season (Newcomb 2014), which may increase demand for available resources in the DRU as winter progresses. One hypothesis is that black ducks with below-average body mass may be able to sustain themselves until hunting-related risks have passed, as it is less energetically costly to maintain a lower body mass, whereas depleting and dynamic food resources in the DRU and other exploited habitats may induce ducks with above-average body mass to seek food or other resources outside the DRU, despite risks to survival (Loesch et al. 1992, Keller et al. 2009, McClanahan 2015). Food resources during the posthunting season in late winter have been diminished greatly by foraging and natural decomposition (Foster et al. 2010, Hagy and Kaminski 2012, McClanahan 2015), and decreased survival for ducks of below-average body mass could be related to these within-winter changes in resource availability (Newcomb 2014, McClanahan 2015, Rogers 2015). Studies refining estimates of available resources in the TNWR are needed to determine the actual availability of food resources throughout winter, especially within emergent and scrub–shrub wetlands, which were strongly selected by black ducks radio-tagged in the TNWR (Newcomb 2014, McClanahan 2015).

### Weather

Weather may affect habitat use, movements, food availability, and behavior, and thus, indirectly, the survival of birds (Bennett and Bolen 1978, Nichols et al. 1983, Whyte and Bolen 1984, Lovvorn 1989, Robinson et al. 2007, Sauter et al. 2010, Salewski et al. 2013, García-Pérez et al. 2014). A direct link between survival and weather has been difficult to demonstrate empirically for wintering ducks because of complicated indirect effects (Conroy et al. 1989, Longcore et al. 1991, Dooley et al. 2010a, Gunnarsson et al. 2012; cf. Robb 1997). Despite not detecting an effect of weather covariates on the survival of black ducks, which

may be partially explained by few mortalities during our study, we observed almost twice as many mortalities during the winter of 2010–2011, which was more severe than the winter of 2011–2012 (see Table 4). For example, in the winter of 2011–2012, compared with the winter of 2010–2011, we observed higher temperatures and more rainfall, which can create additional wetlands and provide more food resources, increasing accessibility to those resources because of less snow or ice cover, and thereby potentially reducing mortalities. Colder temperatures and increased snow and ice in the winter of 2010–2011 may have restricted access to critical resources for black ducks, thus resulting in our observations of more mortalities and birds with below-average body mass having lower survival than during the following milder winter (Albright et al. 1983, Conroy et al. 1989). Furthermore, indirect effects of weather conditions (e.g., poor body condition due to decreased food availability) could increase the vulnerability of black ducks to predation or other sources of mortality (Todd et al. 1982, Albright et al. 1983). Harsh weather conditions also may exacerbate stress on birds related to carrying radio-transmitters, and increased weight loss during already stressful conditions may lead to more mortalities, such as in the 2010–2011 winter (Pietz et al. 1993, Robb 1997).

### Hunting and Age

Both additive and compensatory hunting mortality have been demonstrated for black ducks, and different populations and sex and age groups are at differential risk of hunting (Krementz et al. 1987, 1988, Longcore et al. 2000). Krementz et al. (1988) found no evidence to support compensatory hunting mortality in black duck populations in the Mississippi Flyway, and their results for female black ducks in the Tennessee River region indicated additive hunting mortality for this population. While previous research has linked black duck survival to exposure to hunting (Krementz et al. 1987, 1988, Longcore et al. 1991), we did not detect a difference in survival between hunting and nonhunting periods, which may have been due to the small number of mortalities that occurred during this study. However, hunting was a source of mortality for female black ducks in our study (winter 2011–2012,  $n = 5$ ; seasons after radio-tagging,  $n = 10$ ). Similarly, despite not finding a statistical effect of age on survival of female black ducks, 10 of 14 mortalities recorded during our study were juvenile females; indeed, several studies have demonstrated lower survival of postfledging, juvenile black ducks (Krementz et al. 1987, 1988, Longcore et al. 1991).

### Conclusion

Our results suggest that the TNWR is an important wintering area for black ducks in the Mississippi Flyway, and we speculate that winter mortality is not a primary

factor contributing to declining abundance of this species in the refuge. While fewer black ducks wintering in the TNWR may be related to a shift in the species' range (Link et al. 2006, Brook et al. 2009, National Audubon Society 2013), it is unclear what factors might be influencing this shift (e.g., climate change, habitat quantity and quality, competition with Mallards). Newcomb (2014) reported potential differences in habitat use between surviving and dying black ducks, but this comparison was limited by a paucity of mortalities. Thus, we recommend determining habitat-specific survival during winter to identify "suitable" habitats (i.e. those promoting survival; sensu Fretwell 1972, Kaminski and Elmberg 2014) for black ducks, as well as identifying any possible resource limitations that could be inducing competition with Mallards or increased exposure to hunting. Additionally, although survival did not differ between hunting and posthunting periods in our study, black ducks were exposed to hunting pressure at more northerly latitudes before arriving on their wintering grounds. Mortality rates during other periods of the annual cycle, such as migration, can influence annual survival rates and population dynamics (Klaassen et al. 2014). Therefore, we suggest that potential carryover effects from migration into winter and subsequent breeding periods be investigated (Sedinger et al. 2011, García-Pérez et al. 2014, Sedinger and Alisauskas 2014, Hostetler et al. 2015) for black duck populations in both flyways, which may be increasingly important as this species' range continues to shift to the northeast (Link et al. 2006, Brook et al. 2009, National Audubon Society 2013).

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