



Research Article

Population Dynamics of Mallards Breeding in Eastern Washington

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ABSTRACT Variation in regional population trends for mallards breeding in the western United States indicates that additional research into factors that influence demographics could contribute to management and understanding the population demographics of mallards across North America. We estimated breeding incidence and adult female, nest, and brood survival in eastern Washington in 2006 and 2007 by monitoring female mallards with radio telemetry and tested how those parameters were influenced by study year (2006 vs. 2007), landscape type (agricultural vs. natural), and age (second year [SY] vs. after second year [ASY]). We also investigated the effects of female body condition and capture date on breeding incidence, and nest initiation date and hatch date on nest and brood survival, respectively. We included population parameters in a stage-based demographic model and conducted a perturbation analysis to identify which vital rates were most influential on population growth rate (λ). Adult female survival was best modeled with a constant weekly survival rate (0.994, SE = 0.003). Breeding incidence differed between years and was higher for birds in better body condition. Nest survival was higher for ASY females (0.276, SE = 0.118) than SY females (0.066, SE = 0.052), and higher on publicly managed lands (0.383, SE = 0.212) than agricultural (0.114, SE = 0.058) landscapes. Brood survival was best modeled with a constant rate for the 7-week monitoring period (0.50, SE = 0.155). The single variable having the greatest influence on λ was non-breeding season survival, but the combination of parameters from the breeding grounds explained a greater percent of the variance in λ . Mallard population growth rate was most sensitive to changes in non-breeding survival, nest success, brood survival, and breeding incidence. Future management decisions should focus on activities that improve these vital rates if managers want to increase the production of mallards in eastern Washington. © 2016 The Wildlife Society.

KEY WORDS *Anas platyrhynchos*, breeding demographics, mallard, nest success, survival, Washington.

For harvest management purposes, the continental mallard (*Anas platyrhynchos*) population is broken into 3 subpopulations: the mid-continent population, the western population, and the eastern population (U.S. Fish and Wildlife Service [USFWS] 2014). The Western population includes those birds breeding in Alaska, California, and Oregon (USFWS 2014); however, birds from those states comprise only a fraction of the mallards that are managed under that framework (Alisauskas et al. 2013). The applicability of the harvest model for the western population depends on the assumption that productivity and the processes that influence productivity are similar between surveyed areas in Alaska,

California, Oregon, and other regions of the West such as Washington. During the 1990s, the mallard population breeding in the defined survey area of the western subpopulation increased by 100% (USFWS 2014), whereas the mallard population breeding in eastern Washington declined 70–75% (Giudice 2003), suggesting that may not be the case.

Population models provide a tool for understanding variation in population trajectories because they link individual vital rates to the population growth rate (λ ; Caswell 2001; Hoekman et al. 2002, 2006a, b). In conjunction with perturbation analyses that identify vital rates that have the strongest influence on λ (Caswell 2001), these demographic tools can serve as a basis for developing biologically sound and targeted management plans. Robust modeling requires accurate estimates of key population metrics (e.g., nest success, female survival, brood survival)

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and an approach that allows for modeling the tradeoffs among such estimates simultaneously (Nicolai et al. 2014). The mallard is among the most well-studied birds in North America (Drilling et al. 2002) and many studies have estimated vital rates for breeding mallards (Simpson et al. 2005, Devries et al. 2008, Arnold et al. 2012, Howerter et al. 2014). Results of these studies indicate that vital rates and the relative importance of each metric to mallard population growth can vary among regions of North America (Hoekman et al. 2002, 2006b; Coluccy et al. 2008). Such variability indicates that research on breeding mallards in other portions of their range would generally improve our understanding of variability inherent in the demographic processes experienced by species with large geographic ranges. Specifically, work in other western states and provinces would improve our understanding of demographic characteristics that define the western mallard subpopulation, and improve conservation strategies targeting that subpopulation.

Previous research in eastern Washington concluded nest success was insufficient to sustain the mallard population in the region (Giudice et al. 2000). Although informative, that study was conducted on 1 wildlife management area and did not account for mallards nesting in agricultural landscapes that comprise the majority of land use in the region. Landscape composition influences clutch size, nest success, and duckling and female survival in mallards (Devries et al. 2003, Simpson et al. 2005, Stephens et al. 2005); thus, we might expect reproductive success to vary between agricultural lands and publicly managed lands. Additionally, Giudice et al. (2000) located nests using nest dragging techniques, which can bias estimates of nest success (Arnold et al. 1993). Work on population demographics from a broader segment of the Columbia Basin would inform future management decisions in the region.

Our project goal was to gain a better understanding of mallard population dynamics on publicly managed and agricultural areas in eastern Washington and, more generally, a broader understanding of mallard population dynamics throughout their breeding range. Our objectives were to estimate and compare the reproductive vital rates of mallards in publicly managed and agricultural lands in eastern Washington and use the estimated vital rates (i.e., breeding incidence, clutch size, nest success, brood survival, adult female survival during the breeding season) to conduct sensitivity and elasticity analyses to identify demographic parameters that most limit population growth in this region.

STUDY AREA

We conducted our study within the Columbia Basin Irrigation Project, a multi-purpose project, run by the United States Bureau of Reclamation. The northern boundary was the Grand Coulee Dam and the area extended to Richland, Kennewick, and Pasco to the south. The project provides 304,550 ha of irrigated land in central Washington. Dominant vegetation in non-cultivated areas included sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), bitterbrush (*Purshia tridentata*), cheatgrass (*Bromus*

tectorum), bluebunch wheatgrass (*Pseudoroegneria spicata*), and basin wild-rye (*Elymus cinereus*).

Agricultural wetlands within this region consisted of, or were associated with, canals, laterals, and drains used to transport irrigation water throughout the project area. Canals were relatively large (bottom width 12–15 m and 3–5 m deep) and used to move water along the edges of the irrigation project. Laterals were intermediate to small watercourses (bottom widths of 0.6–10 m) that carried water from canals to individual farms. Drains collected irrigation water and drained it into wasteways and reservoirs. The bottom width of drains ranged 0.6–6.1 m, with a water depth of 1–2 m and a channel depth of 1–6 m (Hoag 1980). Publicly managed lands included Frenchman Hills and Winchester Wasteways (including the Desert Wildlife Area) and Pothole Reservoir Wildlife Management Area.

Our study focused on public and agricultural landscapes located south and east of I-90, north of Highway 262 and Frenchman Hills Road, and west of Potholes Reservoir in Grant County. The crop mix for Grant County was approximately 28% alfalfa hay, 19% spring and winter wheat, 13% vegetables (e.g., asparagus, carrot, sweet corn, onion, and pea), 10% potatoes, 9% orchards (e.g., apple, pear, sweet cherry, and wine grape), and 21% other crops (e.g., hops, dry beans, grain and silage corn, peppermint, and spearmint; Huppert et al. 2004).

METHODS

We captured 50 females between 29 March and 22 April in 2006 and 30 females between 29 March and 6 May in 2007 using decoy traps (Sharp and Lokemoen 1987). Trapping effort on private land was focused on laterals and drains associated with irrigation activities located south (between I-90 and Frenchman Hills Road) and east (between Beverly Burk Road and Adams Road) of George, Washington. We implanted 50 females with transmitters in 2006; 2 disappeared because of migratory movements or radio failure within 1 week after release. An additional 9 birds in 2006 moved into areas with poor vehicle access and because we were able to locate them only intermittently during aerial surveys, we excluded them from this study. Thus, our sample size was 69 mallard females.

We checked traps each morning between 0800 hours and 1200 hours. We aged captured females as second year (SY) or after second year (ASY) by wing characteristics (Krapu et al. 1979). We weighed each bird to the nearest 10 g, and measured wing chord and head length to the nearest mm (Devries et al. 2008). We banded birds with a metal United States Geological Survey (USGS) leg band (under a USGS banding permit issued to B. Dugger) and implanted an intra-abdominal radio transmitter (Telonics model IMP/150/L, Telonics, Mesa, AZ). Transmitters weighed less than 3% of each bird's body mass. We performed all surgeries in a veterinary clinic under the supervision of a veterinarian and followed established protocols (Korshgen et al. 1984, Olsen et al. 1992, Paquette et al. 1997). After a 1-hour recovery period, we returned birds to their original trap location and released them. We held all male mallards trapped with a

female and released the male with the female to minimize pair-bond disturbance. All procedures were approved by Oregon State University Institutional Animal Care and Use Committee.

We used radio telemetry to monitor females starting the morning after capture and release until the end of brood rearing, loss of transmitter signal, death, or until we confirmed a female was associated with a flock. Females confirmed to be in a flock (determined using triangulation) were no longer considered nesting or rearing a brood. We used vehicle-mounted, null-peak, yagi antenna systems (Simpson et al. 2005) to locate females and then used triangulation (program LOCATE III; Pacer Computing, Tatamagouche, Nova Scotia, Canada) to plot the location of each observation. We attempted to locate each female once/day between sunrise and 1300 hours when females were most likely on their nests (Coulter and Miller 1968, Gloutney et al. 1993). When necessary, we searched for missing females using aerial telemetry (Gilmer et al. 1981).

We walked in to determine nesting status of females when telemetry indicated a female was in the same upland location for 3 consecutive days (McPherson et al. 2003, Devries et al. 2008). To minimize nest abandonment, we marked approximate locations with plastic flagging and visited nests only when the female was absent (between 1300 hours and sundown). Walking in and searching for nests can increase desertion rates in mallard (McPherson et al. (2003) but does not expose nests to greater predation risk (Thorn et al. 2005). During nest-site visits, we recorded the date, clutch size, incubation stage of eggs (Weller 1956), and landscape type (agriculture or public). We estimated nest initiation dates with a combination of clutch size and incubation stage (Devries et al. 2008). We monitored the status of each nest daily using radio telemetry to confirm female presence at the nest. We considered nests successful if ≥ 1 egg hatched (Klett et al. 1986). After eggs hatched, we tracked females with broods ≥ 1 time/week for up to 7 weeks (Simpson et al. 2005). We located marked females and attempted to count all ducklings in her brood.

Data Analysis

We estimated adult female survival during the breeding season, nest survival, and brood survival using known-fate models in Program MARK (White and Burnham 1999, Devries et al. 2003, McPherson et al. 2003). We used an information-theoretic approach (Burnham and Anderson 2002) to compare competing models in each analysis. Our a priori model set for each analysis included the null model, a fully time-dependent model, all single-variable models, and select multi-factor additive or interactive models based on previous research or our perceptions of how multiple factors might be important for explaining breeding demographics. We generally selected the model with the lowest Akaike's Information Criterion adjusted for small sample size (AIC_c) value and highest Akaike weights (AIC_c weights) as our best model and evaluated beta values and their confidence limits to determine the direction and strength of effects. We considered models within 2 AIC_c units ($\Delta AIC_c \leq 2.0$) of the

best model to be competitive (Burnham and Anderson 2002). For all competitive models, we also examined -2 natural log likelihood or deviance values to ensure that ΔAIC_c values were not solely a result of adding an additional, uninformative covariate (Arnold 2010).

Adult female survival.—We estimated weekly survival of adult females (39 SY and 30 ASY) during an 18-week interval from 29 March to 27 July in 2006 and 2007. We created a list of a priori candidate models to test for differences among each main effect and select interactions. We predicted that ASY females would survive better than SY females (Dufour and Clark 2002) and females that did not attempt to breed would survive better than nesting females (Cowardin et al. 1985, Dufour and Clark 2002, Devries et al. 2003). Consequently, we expected SY birds (least experienced) that nested (exposed to greater risk) would have the lowest survival rates and ASY birds that did not nest would have the highest survival. We also predicted that females using public lands would survive better than those using agricultural landscapes. We tested for the interaction between year and landscape type because the timing of alfalfa cutting varied between years and this may have influenced survival on agricultural lands in ways that would not influence public lands. Therefore, we predicted that survival would be higher on agricultural lands in 2006 than in 2007 (alfalfa was cut later in 2006), but this annual pattern may not hold on publicly managed landscapes. We included the model with no effects on survival (i.e., intercept-only or constant survival model [$S(\cdot)$]) and a general time-dependent survival model, $S(t)$, in the model set for comparison with reduced parameter models of interest.

Nest success.—We estimated a general daily nest survival rate by standardizing all nests in both years by nest stage (D1 = day first egg was laid). We monitored nests for a maximum of 38 days, representing a maximum clutch size plus a 26-day incubation period for some nests found on the day the first egg was laid. We considered a nest successful if ≥ 1 egg hatched. We developed known-fate encounter histories based on daily telemetry location data from the nest searching and monitoring period (12 Apr to 8 Jul). We developed a set of single-factor a priori candidate models to look for differences in nest survival between landscapes (agricultural and public lands), age of nesting female (SY and ASY), year (2006 and 2007), and nest initiation date. We also included select additive models a posteriori, depending on ranking of univariate models. We included a model with no effects, a general time-dependent survival model, and a general model including all 4 covariates as additive effects for comparison to reduced parameter models of interest.

Brood survival.—We could not identify individual ducklings within a brood, so we estimated weekly brood survival and considered our mean estimate of brood survival over the entire 7-week brood-rearing period as analogous to an estimate for mean maximum duckling survival to fledging. We considered a brood alive for each weekly monitoring period if ≥ 1 duckling was observed alive at the end of the interval. We estimated brood survival (likelihood that ≥ 1 duckling survives to fledge; Simpson et al. 2005, Smith et al.

2005) for the 7-week period after hatching and used this estimate to reflect mean maximum duckling survival to fledging. We developed known-fate encounter histories by monitoring broods ≥ 1 time/week for 7 weeks post-hatch. The a priori candidate models used in this analysis included a constant survival model and single-factor models including female age, landscape type, hatch date, and year. The small sample size restricted us from including interactions between covariates. We included the intercept-only model for comparison.

Breeding incidence.—An initial summarization of the data indicated that nest initiation rate (i.e., the proportion of females initiating ≥ 1 nest; Coluccy et al. 2008) was $<100\%$. Consequently, we conducted an analysis to determine what factors influenced the probability of a female initiating a nest (Oldenburger 2008). Explanatory variables for this analysis included female age, date, year, and body condition. For body condition, we were most interested in lipid reserves, which are known to influence breeding in mallards, and we wanted to control for body size; thus, we used an index calculated as the residuals from an ordinary least-squares regression of the log body mass and body size, which was the first principle component of wing chord and head length (Schulte-Hostedde et al. 2005, Devries et al. 2008). The first principle component explained 87% of the overall variation. The model set included all additive combinations of the 4 covariates. We used R (R Foundation for Statistical Computing, Vienna, Austria) to run a set of a priori logistic regression models (Venables and Smith 2008). We predicted that female age and body condition at capture would have the most influence on the probability of nest initiation, with ASY females and those in better condition more likely to nest than SY females and birds in poorer condition (Devries et al. 2008, Oldenburger 2008). We reported all means (\pm SE).

Demographic Model and Perturbation Analysis

We conducted a perturbation analysis to assess the relative impact of various vital rates on the mallard population growth rate. The vital rates used in the analysis included our estimates of breeding incidence; clutch size; nest, brood, and adult female breeding season survival; hatch success; and reneating intensity. We calculated per capita fertility (F) for females in age class i as

$$F_i = 0.5 \times BI_i \times BS_i \times (CS_i \times HS_i \times NS_i + (1 - NS_i) \times RP_i \times CS_i \times HS_i \times NS_i) \times DS_i$$

where BI_i = breeding incidence for age class i , BS_i = breeding survival for age class i , CS_i = clutch size for age class i , HS_i = hatch success for age class i , NS_i = nest success for age class i , RP_i = reneating probability for age class i , DS_i = duckling survival for age class i , and 0.5 accounts for only female offspring assuming a 50:50 sex ratio at hatch. We calculated reneating intensity following Hoekman et al. (2002), so the value for reneating intensity is a regression slope that describes the proportion of females who initiate a first nest that will initiate a second, third, or additional nest. As a consequence, the value for that parameter is always negative. We estimated non-breeding survival as the

quotient of mean annual survival rate (SY 0.660 ± 0.056 and ASY 0.606 ± 0.016 ; Giudice 2003) and our estimates of mean breeding survival (Hoekman et al. 2002). We estimated the standard deviation of empirical variation for non-breeding survival following Hoekman et al. (2002) and Seber (1982).

We used the graphical programming language STELLA and STELLA Research (2000) to develop a stage-based model with 2 age classes (SY and ASY) and a yearly projection interval (Coluccy et al. 2008). A priori, we decided to use an age-structured model to be consistent with all previous perturbation analyses of mallards (Hoekman et al. 2002, 2006a, b; Coluccy et al. 2008). Thus, even if our analysis did not support age as an important factor influencing demographic parameters (i.e., female survival), we included age-specific estimates for each parameter in our model. We assigned the initial spring female breeding population as 57:43, SY:ASY, based on the age ratio from females captured in decoy traps. Females entered the SY and ASY stage classes at the start of their first and second breeding seasons, respectively (Hoekman et al. 2002). Our model did not include information for male mallards because we assumed that females limit production (Johnson and Sargeant 1977, Johnson et al. 1987). We assumed a 50:50 sex ratio for eggs. We assumed that females must survive the breeding season to fledge young (Hoekman et al. 2002). Thus, we accounted for breeding season mortality at the beginning of the breeding season. To separate nest loss associated with mortality of nesting females (10%) from nest loss due to predation and abandonment, we corrected nest success using the following:

$$\text{Corrected nestsuccess} = p/[p = 0.9 \times (1 - p)],$$

where p = nest success. Finally, we assumed successful females forwent further nest attempts that year because female mallards that hatch nests rarely reneat (Olsen et al. 2003).

Each time step in the model began at the start of the breeding season (Mar 29). We calculated annual population growth (λ) assuming no emigration or immigration, a stable age distribution, density independence, and invariant vital rates (Caswell 2001, Coluccy et al. 2008). Probability distributions for each parameter were defined by estimated mean and empirical variation (Hoekman et al. 2002, Coluccy et al. 2008). All parameters were bound by 0 and 1, except for clutch size and reneating intensity, and we assumed all parameters had a normal distribution.

We predicted how λ was affected by changes in mean values of parameters by calculating the sensitivity and elasticity of each parameter from the model. We defined sensitivity and elasticity as

$$\text{Sensitivity} = \lambda_{\text{changed}} - \lambda_{\text{unchanged}},$$

$$\text{Elasticity} = [\text{Sensitivity}/\lambda_{\text{unchanged}}]/[(P_{\text{changed}} - P_{\text{unchanged}})/P_{\text{unchanged}}],$$

where λ_{changed} and $\lambda_{\text{unchanged}}$ are the population growth rates using new and original input values for a given parameter, and P_{changed} and $P_{\text{unchanged}}$ are the new and original input values for a given parameter (Schmutz et al. 1997); these

Table 1. Model selection results for models within 5 Akaike's Information Criterion adjusted for small sample size (AIC_c) values of the top model to identify factors that influenced probability of initiating nests (breeding incidence [BI]) by female mallards breeding in eastern Washington, 2006 and 2007. Model covariates included body condition, age (second year or after second year), capture date, and year. We considered models ≤ 2.0 ΔAIC_c values from the best model to be competitive. We included the intercept-only model (.) for comparison. We present the model deviance, number of parameters (K), ΔAIC_c , and AIC_c weights (w_i) for all models.

Model	ΔAIC_c	w_i	K	Deviance
$BI(\text{year} + \text{body condition}^a)$	0.00 ^b	0.42	3	80.31
$BI(\text{year} + \text{body condition} + \text{age})$	1.11	0.24	4	79.16
$BI(\text{year} + \text{body Condition} + \text{age} + \text{capture})$	2.77	0.10	5	78.49
$BI(\text{year})$	3.84	0.06	2	86.34
$BI(\text{body condition} + \text{age})$	4.15	0.05	3	84.45
$BI(\text{year} + \text{age})$	4.20	0.05	3	84.50
$BI(.)$	10.68	0.00	1	95.29

^a Body condition index as described in Devries et al. (2008).

^b AIC_c value of top model was 86.67.

parameters are homologous to lower-level elasticities calculated from matrix population models (Caswell 2001). We simulated 5,000 replicate sets of parameters and calculated sensitivity and elasticity for each replicate to evaluate values across empirical variation in parameters. We decomposed the variance of λ for each replicate on each parameter (Wisdom et al. 2000). Variation in, and interaction among, parameters explained all of the variation in λ because it was determined by input parameters. We determined the proportion of variation in λ explained by each parameter by the coefficient of determination for each regression.

RESULTS

Vital Rate Estimation

Nest initiation dates ranged from 7 April to 3 June and hatch dates ranged from 10 May to 1 July. Overall breeding incidence was 0.536 ± 0.060 . The best model explaining breeding incidence included year and body condition. The additive model with year, body condition, and age was competitive (< 2.0 AIC_c values from best model); however, a comparison of model deviance and 95% confidence limits that overlapped 0 on the covariate coefficient suggested age was an uninformative parameter (Arnold 2010; Table 1). Breeding incidence was higher in 2006 (0.69 ± 0.08) than 2007 (0.33 ± 0.09). Overall mean female body mass was 976 ± 72 g. Mean body mass of females that nested ($1,002 \pm 70$ g) was higher than females that did not nest (946 ± 60 g), and the probability of initiating a nest increased with increased body condition (Fig. 1). Estimates for breeding incidence were 0.41 ± 0.09 for SY females and 0.70 ± 0.09 for ASY females.

Our sample included 33 nests, 20 in 2006 and 13 in 2007, and 15 SY and 18 ASY females. Mean clutch size was 8.9 ± 0.4 eggs, and 0.83 ± 0.02 of eggs hatched in successful nests. More nests were located in agricultural areas ($n = 25$) than publicly managed landscapes ($n = 8$). Of the 4 single-factor models we examined, female age and landscape type performed best, so a posteriori, we combined these 2 covariates into an additive model that ranked highest (Table 2). Together, those 3 models received 69% of the total model weight. Although the null model was competitive

(< 2 AIC_c values from the best model), changes in deviance values supported the models including female age and landscape type. The estimate for constant daily nest survival was higher for ASY females than SY females (0.965 ± 0.012 vs. 0.927 ± 0.020) and higher for public areas than agricultural areas (0.974 ± 0.015 vs. 0.941 ± 0.013). Overall, nest success across both years and age classes throughout a hypothetical 36-day nesting period (10 egg clutch + 26 day incubation) was 0.16 ± 0.06 . Nest survival was higher for ASY females (0.28 ± 0.12) than SY females (0.07 ± 0.05) and lower on agricultural lands (0.11 ± 0.06) than publicly managed lands (0.38 ± 0.21). We detected 6 renests (2 in 2006, 4 in 2007), and reneesting intensity for all females was -0.28 ± 0.11 .

We developed encounter histories for 14 broods: 9 in 2006 and 5 in 2007. Brood survival declined with hatch date ($\beta = -0.08 \pm 0.05$, 95% CI = -0.16 to 0.01) and the single variable model with hatch date was the only model that performed better than the intercept-only model (i.e., constant survival), which was also competitive (Table 3). In addition, based on AIC_c weights, the model including hatch date

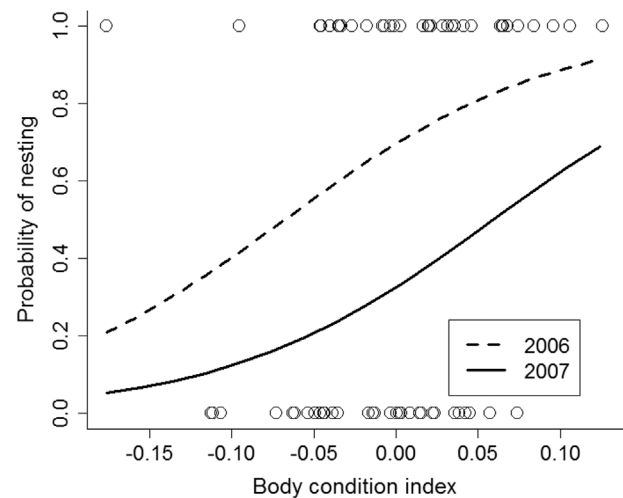


Figure 1. Predicted probability of nesting (breeding incidence) in relation to the body condition index of adult female mallards in eastern Washington, 2006 and 2007.

Table 2. Model selection results for all models in our a priori model set to estimate daily nest survival (S) of mallards and identify factors that affect nest survival in eastern Washington, 2006 and 2007. We considered nests successful if ≥ 1 egg hatched. Model covariates included landscape (agricultural lands or publicly owned lands), female age (second year or after second year), nest initiation date, and year. We ranked models according to Akaike's Information Criterion adjusted for small sample size (AIC_c). We also ranked the intercept-only model (.) and the fully time-dependent model (t). We present the model deviance, number of parameters (K), ΔAIC_c , and AIC_c weights (w_i) for all models.

Model	ΔAIC_c	w_i	K	Deviance
$S(\text{age} + \text{landscape})$	0.00 ^a	0.29	3	161.58
$S(\text{age})$	0.35	0.24	2	163.95
$S(\text{landscape})$	1.18	0.16	2	164.78
$S(.)$	1.23	0.16	1	166.86
$S(\text{initiation date})$	2.37	0.09	2	165.98
$S(\text{year})$	3.23	0.06	2	166.83
$S(\text{year} + \text{age} + \text{landscape} + \text{initiation date})$	9.13	0.00	8	160.41
$S(t)$	43.61	0.00	38	127.48

^a AIC_c value of top model was 167.64.

received almost twice the support of the intercept-only model ($0.42/0.23 = 1.83$). Although 95% confidence limits for the hatch date coefficient slightly overlapped 0, differences in model deviance supported a negative association between hatch date and brood success. The single variable model that included age was within 2 AIC_c values of the best model, but it did not perform better than the intercept-only model, so we did not consider age an important effect on brood survival in this study. Given our sample of broods was small and our sampling of hatch dates within the nesting season was limited, we used the estimate of brood survival generated from the constant survival model in our sensitivity and elasticity analyses. Brood survival was $0.91 \pm 0.04/\text{week}$ and 0.50 ± 0.16 for survival to week 7.

Five females died during the study: 3 in 2006 and 2 in 2007. Two females were killed by a predator while on the nest, 1 was killed by agricultural machinery when the alfalfa field she was nesting in was harvested, and 2 died of unknown causes away from the nest. Weekly survival of adult females was best modeled by the constant survival model (Table 4). All single-variable models were within 2 AIC_c values of the best model; however, the confidence intervals around parameter estimates and comparisons between model deviance values indicated that none of the covariates we investigated were strongly associated with female survival. Constant weekly survival for the breeding season for all females was 0.994 ± 0.003 (95% CI 0.985–0.998), and the probability

of an adult female surviving to week 18 was 0.897 ± 0.044 . The probabilities of SY and ASY females surviving to week 18 in the breeding season were 0.881 ± 0.070 and 0.912 ± 0.060 , respectively. We estimated the non-breeding season survival as 0.71 ± 0.07 for all adult females, with estimates of 0.75 ± 0.12 for SY, and 0.67 ± 0.06 for ASY females.

Demographic Model and Perturbation Analysis

Population change (λ) for our population was 0.877 and per capita F was 0.042 for SY females and 0.444 for ASY females. Sensitivity of λ at mean parameter values was greatest for non-breeding survival (0.18), nest success (0.15), and brood survival (0.11), intermediate for breeding incidence (0.09) and breeding survival (0.09), and low (<0.04) for the remaining parameters (Fig. 2). Elasticity was greatest for non-breeding season survival (1.02) and breeding survival (0.72; Fig. 3). Elasticity was low (<0.28) for the remaining parameters (Fig. 3). Variation in sensitivities and elasticities ranged from <0.01 to 0.13 (Fig. 4).

Non-breeding survival accounted for 36% of the variation in λ (Fig. 5). Brood survival, breeding incidence, nest success, and breeding survival accounted for 46% of the variation in λ , whereas clutch size, hatch success, and re-nesting intensity accounted for only 5% of the variation in λ (Fig. 5). In total, all main parameter effects accounted for 87% of the variation in λ .

Table 3. Model selection results for all models in our a priori model set designed to estimate weekly brood survival (S) and identify the factors affecting survival of mallard broods in eastern Washington, 2006 and 2007. We considered broods successful if ≥ 1 duckling survived. Model covariate included landscape (agricultural lands or publicly owned lands), age (second year or after second year), hatch date, and year. We ranked models according to Akaike's Information Criterion adjusted for small sample size (AIC_c). We also ranked the intercept-only model (.) and the fully time-dependent model (t). We present the model deviance, number of parameters (K), ΔAIC_c , and AIC_c weights (w_i) for all models.

Model	ΔAIC_c	w_i	K	Deviance
$S(\text{hatch date})$	0.00 ^a	0.42	2	29.81
$S(.)$	1.15	0.23	1	33.12
$S(\text{age})$	1.96	0.16	2	31.77
$S(\text{landscape})$	3.22	0.08	2	33.03
$S(\text{year})$	3.30	0.08	2	33.11
$S(\text{year} + \text{age} + \text{landscape} + \text{hatch date})$	5.77	0.02	5	28.55
$S(t)$	7.62	0.01	7	25.18

^a AIC_c value of top model was 34.05.

Table 4. Model selection results for all models in our a priori model set designed to estimate weekly survival (S) and identify the factors affecting survival of female mallards during the breeding season (Mar–Jul) in eastern Washington during 2006 and 2007. Model covariates were landscape (agricultural lands or publicly owned lands), female reproductive status (repro status; nesting or non-nesting), female age (second year or after second year), and year. We ranked models according to Akaike’s Information Criterion adjusted for small sample size (AIC_c). We also ranked the intercept-only model (.) and the fully time-dependent model (t). We present the model deviance, number of parameters (K), ΔAIC_c , and AIC_c weights (w_i) for all models.

Model	ΔAIC_c	w_i	K	Deviance
$S(.)$	0.00 ^a	0.31	1	38.23
$S(\text{landscape})$	0.55	0.24	2	36.77
$S(\text{repro status})$	1.36	0.16	2	37.58
$S(\text{age})$	1.89	0.12	2	38.10
$S(\text{year})$	2.00	0.11	2	38.22
$S(\text{year} \times \text{landscape})$	3.21	0.06	4	35.40
$S(t)$	18.64	0.00	18	22.02

^a AIC_c value of top model was 62.94.

DISCUSSION

Our estimate of breeding incidence (53%) in eastern Washington is considerably lower than values from the Prairie Parkland region of Canada (89%; Devries et al. 2008); Ontario, Canada (96%; Hoekman et al. 2006a); and the Great Lakes Region of the United States (84%; Coluccy et al. 2008). Our overall estimate of breeding incidence is lower than that for first-year females characterized as being in poor condition in the Prairie Parkland Region (60%; Devries et al. 2008). Breeding incidence was exceptionally low in 2007 when only 33% of our females attempted to nest. Breeding incidence is influenced by body condition (Devries et al. 2008) and the average body mass of females in our study (976 g) was lower than the Prairie Parkland (1,095 ± 77 g, $n = 3,553$) and Great Lakes studies (1,097 ± 82 g, $n = 529$). Furthermore, females in better body condition did attempt to nest at a higher rate in our study, which suggests female mallards in eastern Washington were in poor body condition compared to females in the prairies or Great Lakes regions.

Body condition during early spring may be influenced by habitat conditions on wintering or migration areas (Heitmeyer and Fredrickson 1981, Devries et al. 2008) or habitat conditions during early spring on the breeding grounds. Our

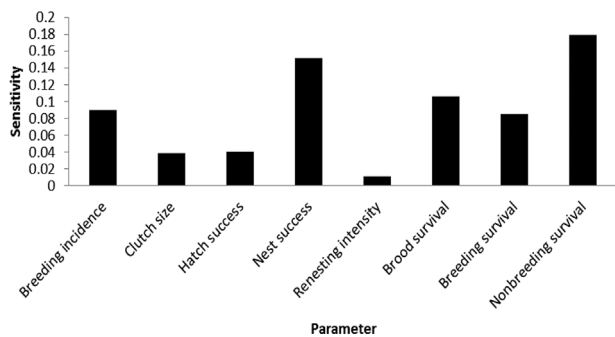


Figure 2. Sensitivities of parameters at mean values for a demographic model of female mallards in agriculture and state-managed lands in eastern Washington, 2006 and 2007.

study was not designed to differentiate between these 2 explanations, but very low breeding effort in 2007 corresponded with comparatively poor habitat conditions on our study area in spring. Specifically, irrigation was delayed for several weeks, leaving many water courses dry during the period that coincided with early nest initiation. Coinciding with delayed irrigation (i.e., poor wetland conditions) in 2007, we captured fewer females, those captured were of lower body mass (\bar{x} in 2007 = 954 g; 2006 = 989 g), and they initiated fewer nests relatively later in the nesting season. Additionally, our renest rate was lower than reported for the Prairie Pothole and Great Lakes Regions (Coluccy et al. 2008, Arnold et al. 2010). Renesting is most influenced by date of first nest attempt, which is related to body condition (Devries et al. 2008, Arnold et al. 2010). Collectively, the results suggest that spring habitat conditions on our study area had a strong effect on mallard productivity.

Our estimate of overall nest success (0.16) was within the range of values reported for other regions throughout the breeding range of mallards (McLandress et al. 1996; Stephens et al. 2005; Hoekman et al. 2006a, b; Davis 2008; Howerter et al. 2014). As we predicted, we found landscape type influenced success, with the survival rate of nests on publicly managed lands >5 times higher than on agricultural lands (0.392 vs. 0.075). One significant cause of nest failure in agricultural landscapes was haying of alfalfa crops. Under normal haying practices, the scheduled first cutting date occurs before many first nests were scheduled to hatch and the interval between first and subsequent cuttings is shorter than the time needed to establish and incubate renests. Consequently, during many years, alfalfa represents an ecological trap for nesting mallards in eastern Washington (Dwernychuk and Boag 1972, Battin 2004). Similar to a study in Saskatchewan (McMaster et al. 2005), a delay in the first cuttings in 2006 because of rainfall did allow successful hatches in alfalfa fields in our study, but all nests in alfalfa failed in 2007, when drier conditions resulted in earlier haying. Nest failure because of haying operations has also been documented for mallards nesting in the Great Lakes Region (Davis 2008) and mottled ducks (*Anas fulvigula*) nesting in Florida (Dugger et al. 2010) suggesting this association between haying practices and duck nesting success may be a general pattern in agricultural landscapes across North America.

We also observed large differences in nest success between SY and ASY females, with nest success rates >6 times higher for ASY than SY females (0.224 vs. 0.037). Our results were similar to results from the Great Lakes Region (Coluccy et al. 2008) but differed from those on the Prairies where age-related differences were slight or non-existent (Cowardin et al. 1985, Devries et al. 2008, Howerter et al. 2014). Age-related differences in reproductive success in *Anseriformes* are well documented (Rohwer 1992) and generally attributed to 2 general explanations: the restraint and constraint hypotheses. The restraint hypothesis does not seem applicable when considering nest success because females that initiate a nest should attempt to maximize the probability of hatching.

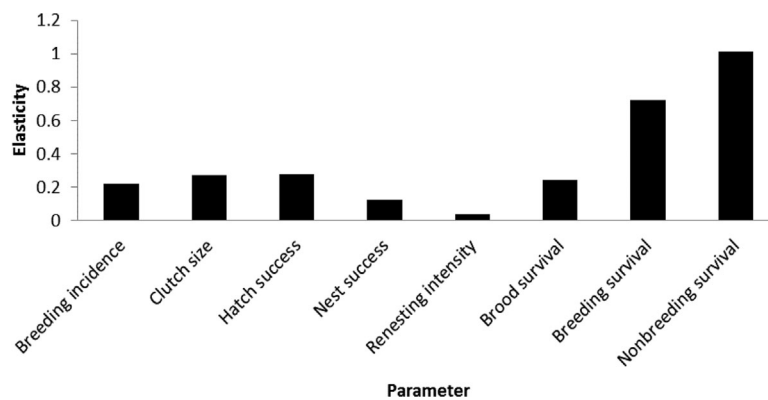


Figure 3. Elasticities of parameters at mean values for a demographic model of female mallards in agricultural and state-managed lands in eastern Washington, 2006 and 2007.

Applying the constraint hypothesis, we could hypothesize that experienced females are in better condition and, therefore, possibly less prone to abandon nests. Devries et al. (2008) did not report evidence that body condition influenced nest success for mallards on the Prairies, although that study did not specifically look at nest abandonment rates. Alternately, older females may place nests in locations less prone to being depredated, but empirical data supporting this assertion are lacking. The sample sizes were relatively small for our analysis; thus, we would caution against making broad inferences from our results, but discrepancies among studies on mallards suggest that additional testing of mechanisms that might lead to age-related differences in nest success in ducks would be informative (Afton 1984).

Our overall survival rate of adult female mallards during the breeding season (0.895) was higher than estimates from the Prairie Pothole Region (0.65–0.87; Devries et al. 2003, Brasher et al. 2006, Arnold et al. 2012, Howerter et al. 2014); Southern Ontario (0.65–0.84; Hoekman et al. 2006a); Great Lakes Region (0.74; Colucy et al. 2008); New Brunswick, Canada (0.80; Petrie et al. 2000); and northeast California (0.59; Mauser et al. 1994). On the prairies, female mortality is highest during incubation when females are exposed to a range of terrestrial predators and breeding season survival is most influential on annual survival (Arnold et al. 2012). However, female survival in our study was similar between

nesting and non-nesting birds. Our results indicate that conclusions by Arnold et al. (2012) do not extend to all regions where mallards breed. The difference between our results and those of other studies is likely due to differences in the terrestrial predator abundance and community composition in eastern Washington. One specific factor contributing to our results might be that red fox (*Vulpes vulpes*), a common predator of female dabbling ducks during the breeding season (Sargeant et al. 1984, Cowardin et al. 1985), do not occur in eastern Washington.

Non-breeding season survival was the highest rank order metric explaining variance in λ (36%), but the majority of variation in λ was associated with the breeding grounds (46%), similar to other studies of mallard demographics (Hoekman et al. 2002, Colucy et al. 2008). Among vital rates associated with the breeding season, brood survival explained the most variation in λ followed by breeding incidence, and nest success. Brood and duckling survival is often associated with wetland conditions (Rotella and Ratti 1992, Krapu et al. 2000, Hoekman et al. 2004, Amundson and Arnold 2011), particularly on the prairies where brood use of seasonal wetlands is high. Although our data on brood habitat use were limited, we found many using irrigation

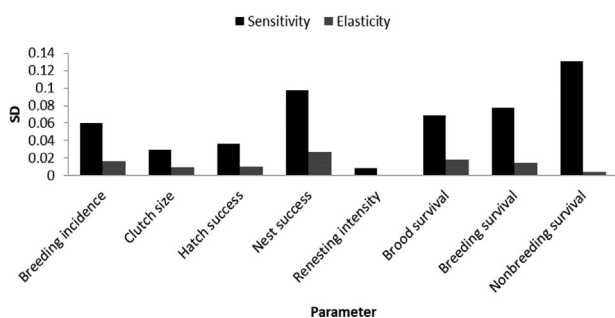


Figure 4. Variation in sensitivities and elasticities across parameters for a demographic model of female mallards in agricultural and state-managed lands in eastern Washington, 2006 and 2007.

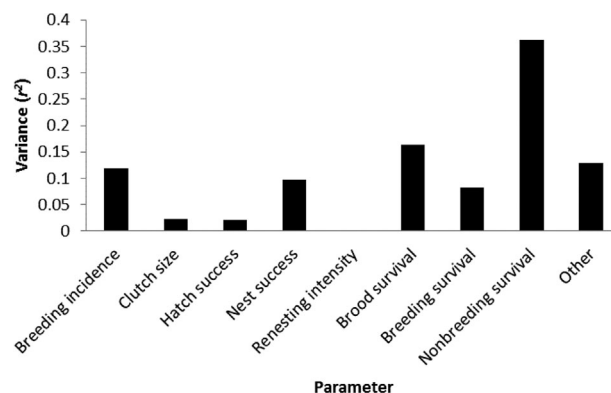


Figure 5. Proportion of variation in the population growth rate (λ) explained by variation in each parameter for a demographic model of female mallards in agricultural and state-managed lands in eastern Washington, 2006 and 2007.

ditches, which may not be productive foraging habitats (B. D. Dugger, Oregon State University, personal observation). Additionally, the linear nature of ditches and relatively low vegetation cover may have exposed broods to greater predation risk.

Perturbation analyses indicated λ was most sensitive to non-breeding adult survival similar to mallards in the Great Lakes Region (Colucy et al. 2008), the Central Valley of California (Oldenburger 2008), and mallards in New Brunswick (Hoekman et al. 2006b). However, mid-continent (Hoekman et al. 2002) and California (Oldenburger 2008) mallard populations were also sensitive to adult breeding season survival, which is contrary to our study. Nest success, which was ranked most sensitive on the prairies (Hoekman et al. 2002, Howerter et al. 2014), ranked second in eastern Washington. Of several perturbation analyses of mallard populations, ours is the first to suggest that breeding incidence had an important influence on λ , but this result is consistent with breeding incidence being lower in eastern Washington than any other region reported on to date for mallards.

MANAGEMENT IMPLICATIONS

Our estimates of vital rates and perturbation analyses can provide guidance for considering management actions to increase the population size of mallards breeding in eastern Washington. Population change was most sensitive to non-breeding survival followed by nest success, brood survival, and breeding incidence. Cause-specific estimates of winter mortality are lacking for the population of mallards in eastern Washington, but if harvest by recreational hunters is a major mortality source then an examination of harvest derivations might suggest opportunities to structure season timing to protect locally produced mallards. Most birds placed nests in agricultural fields and nest survival was lower on agricultural lands compared to publicly managed lands. Thus, creating incentives to delay the initial cutting of hay on lands farmed for alfalfa or finding ways to encourage mallards to nest away from agriculture fields, which might involve increasing wetland quality and abundance in the region, could increase abundance in the region. Increasing wetlands in the region would have the added benefit of improving habitat quality for early nesting females by increasing food, which might increase body condition leading to higher breeding incidence, earlier nest initiation, greater re-nesting potential, and higher brood survival.

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