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Fidelity and Survival of Breeding Mallards in the Nebraska Sandhills

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ABSTRACT Assessment of demographic parameters of a population allows managers to better understand factors affecting populations and increase efficiency of conservation efforts. Few data on demographics exist for mallards (*Anas platyrhynchos*) breeding in the Nebraska Sandhills. Thus, we used banding data to estimate probabilities of fidelity, survival, band recovery, and recapture of mallards banded in the eastern Sandhills, 2005–2008. Our recapture probability estimate for mallards was 0.074 (95% CI: 0.033–0.158), and the recovery probability estimate was 0.300 (95% CI: 0.156–0.497). Mallard annual survival was 0.795 (95% CI: 0.609–0.906) with a fidelity probability of 0.618 (95% CI: 0.283–0.868). High annual survival of mallards breeding in the Sandhills appears to be the result of low nest success and mixing with other regional populations during harvest. High probabilities of fidelity compared to other breeding areas may be related to more stable habitats and potential differences in mating strategies by males. A simple population modeling exercise suggested that generally high fidelity and survival for mallards in the Sandhills may not be enough to balance low nest survival. Mallards in the Sandhills could act as a reservoir of younger females with high survival rates that are available to move to other breeding habitat in future years, but our model suggests that immigration is needed to maintain the population in the Sandhills. Small-scale dynamics, such as those observed in the Sandhills may assist in understanding the complex dynamics of the mid-continent population of mallards.

KEY WORDS *Anas platyrhynchos*, banding, breeding, fidelity, mallard, Nebraska, Sandhills, survival.

Efficient manipulation or conservation of habitat to increase population size requires the determination of factors that affect survival or recruitment (Johnson et al. 1992, Cowardin et al. 1995). For waterfowl, traditional nest searching or telemetry studies can be logistically and financially challenging to implement. However, band-recapture-recovery models may allow managers to use localized trapping and banding to estimate some population demographics such as survival, fidelity, recapture, and recovery probabilities (Burnham 1993, Doherty et al. 2002). These parameters can provide demographic information that managers can use to better target areas for habitat conservation and management for local waterfowl breeding populations.

Large tracts of intact grassland, such as the Sandhills of Nebraska, are often associated with high duck nest success, because these areas are typically thought to have fewer impacts of predators on ground-nesting birds (Cowardin et al. 1985, Dufor and Clark 2002, Hoekman et al. 2002, Stephens et al. 2005). However, the Sandhills region appears to support relatively low levels of nest survival (Glup 1986, Walker et al. 2008). Female survival during the breeding season, in contrast, appears to be relatively high (Walker et al. 2008) when compared with other studies (Blohm et al. 1987, Sargeant and Raveling 1992, Devries et al. 2003, Brasher et al. 2006). In other regions, successful females also have been shown to exhibit higher fidelity to breeding sites then unsuccessful females (Lokemoen et al. 1990). The proportion of second-year (SY) female mallards breeding in the Sandhills is higher than reported in other areas (Cunningham et al. 2016), and SY females are less successful at nesting than older or after-second-year (ASY) birds (Krapu and Doty 1979, Curio 1983, Devries et al. 2008). In addition, SY females have been shown to have a higher breeding season survival because of a lower reproductive investment (Cowardin et al. 1985, Dufour and Clark 2002, Hoekman et al. 2002).

Our goal was to extend the 2-year banding dataset of Walker et al. (2008) so that we could use methods of Doherty et al. (2002) to investigate aspects of mallard demographics in the Nebraska Sandhills. Our objectives were to (1) use mark-recapture-recovery methods to estimate probabilities of recovery, recapture, survival and fidelity for mallards banded in the Sandhills, and (2) to place our estimates in context with a simple population growth model.

STUDY AREA

The landscape of the Nebraska Sandhills is a mosaic of wetlands (404,685 ha) and sand dunes now stabilized by grass (5.2M ha; Bleed and Flowerday 1990). Most of this region consists of privately-owned ranchland used for beef production (Novacek 1989, LaGrange 2005). Despite some fragmentation due to roads and farmstead tree lines, the grasslands of the Sandhills are relatively intact (Bleed and Flowerday 1990).

Our study was conducted almost entirely on privately owned ranchland located approximately 24 km south of Bassett, Nebraska (42º 20’ N, 99º 29’ W) and encompassed 26,347 ha (Fig. 1). Land-cover of the study area was composed of 69% native grassland, 14% hayland, 11% wetlands, 1% cropland, and 5% other classes (Walker et al. 2008). The study area was typical of the eastern Sandhills in terms of its climate, land-use, and plant community. Annual precipitation

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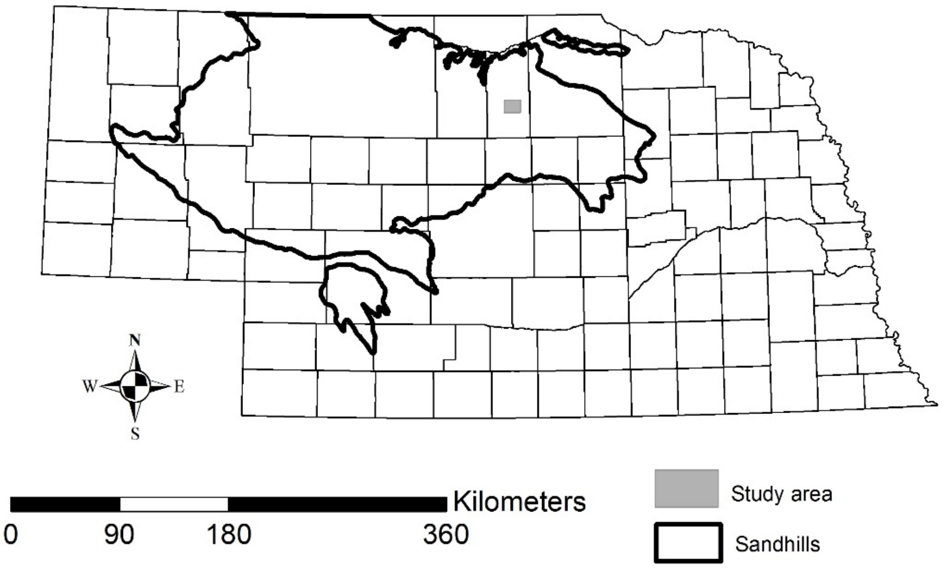

Figure 1. Location of the local-scale examination of survival and fidelity of mallards in the Nebraska Sandhills, 2007–2008 (after Walker et al. 2008).

on the study area averages 51–58cm and an average summer temperature ranged from 19.4º C to 23.9º C (Bleed and Flowerday 1990).

Duck densities at our study site were similar to, and thus representative of, other areas of the Sandhills (Vrtiska and Powell 2011). Current population trends of breeding ducks in the Sandhills appeared stable and estimates from this region have exceeded 275,000 in some years with mallards, blue-winged teal (*A. discors*), and gadwall (*A. strepera*) as the most abundant species (Vrtiska and Powell 2011).

We chose our study site based on 4 considerations: (1) it is the same study site used by Walker et al. (2008), (2) waterfowl are abundant in the area, (3) there is an intricate network of wetlands and intact grasslands in the area, and (4) most of the area is privately-owned ranchland, which is representative of land use in the area.

METHODS

Study Design

To capture female mallards prior to nesting during 2005–2008, we trapped ducks with 24 spring-loaded hen-decoy traps using live, pen-raised female mallards as bait (Ringelman 1990). Placement of decoys traps within our study site was based on several factors, including: (1) observation of mallard pairs behaving territorially the previous day (Sharp and Lokemoen 1987), (2) distance between wetlands, (3) wetland availability on the landscape, (4) accessibility from roads, and (5) landowner permission. Decoy traps were set in the morning at the exact location where the breeding pair was observed and checked every 24 hours with decoy hens being replaced with a fresh bird every 3 days. We avoided returning to the trapping location during the same 24-hour period in an attempt to reduce disturbance to the breeding pair. We removed traps from the wetland once the female had been captured or if the pair moved to another location. In some cases, we used multiple traps at a single site if mallard pairs avoided the trap. We attempted to place decoy traps across a variety of wetland types and locations on the 26,347 ha study area in an attempt to reduce potential bias and to ensure our sampling effort was well dispersed across the study site (Cunningham 2011). We set 24 traps at different locations each day, resulting in >200 total trapping locations during the study. We recorded UTM coordinates for each trap site and trapped 7 days a week from 1 April – 7 June for a total of 67 days each year.

We checked all captured ducks for United States Geological Survey (USGS) aluminum leg bands from the current or previous trapping seasons and recorded their recapture location using GPS. Those not previously marked were fitted with USGS aluminum leg bands and released. Captured pairs were released together to minimize disruption of pair bonds. Our capture, handling, and marking procedures (including the use of decoy hens) were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Nebraska (IACUC protocol #05-02-008).

Statistical Analysis

We obtained band recovery data for all normal releases of mallards banded on our study site between 1 April 2005 and 1 April 2009 from the U.S. Bird Banding Laboratory (BBL), Laurel, Maryland. We included all reported band returns within this time frame in our analysis regardless of method of recovery.

We estimated survival, fidelity, recapture, and recovery probabilities for mallards using the Burnham Live and Dead Encounters data type in program MARK (White and Burnham 1999). Our capture histories were constructed using a banding year that spanned from April 1 to the following March 31. We constructed 54 a priori models based on sample size, observations made in the field, and biologically appropriate combinations of the following parameters based on White and Burnham (1999) and Doherty et al. (2002), as defined below. The 54 models we constructed included a null model ($S_. p_. r_. F_.$), where:

p_i = probability that a bird present on the study site at the time of banding in year *i* is recaptured at that time. We hypothesized that p_i would vary by gender (potential decoy trap bias; Grand and Fondell 1994) and year.
r_i = probability that a bird dies during year *i* does so during the hunting season and is retrieved and its band reported to the BBL (Seber-type recovery probability). We hypothesized that r_i would vary by gender and year.
S_i = probability that a bird alive at the time of banding in year *i* is alive at the time of banding in year *i + 1* (annual survival). We hypothesized that S_i would vary by gender.
F_i = probability that a bird present on the study site at the time of banding in year *i* is also present on the study site at the time of banding in year *i* + 1, given that it is alive at *i* + 1 (fidelity). We hypothesized that F_i would vary by gender and year.

We expected survival estimates to be high similar to estimates for breeding season survival previously reported by Walker et al. (2008), but expected fidelity to be low (<0.4) for both male and female mallards due to low nest survival. Lokemoen et al. (1990) reported unadjusted return rates of 0.223 for unsuccessful SY females and 0.111 for unsuccessful ASY females. We used an information-theoretic approach to select models that best showed the relationships between mallard survival, fidelity, recapture, and recovery and observed nest success. We used Akaike's Information Criterion (AIC) scores to rank models and AIC weights (w_i) to determine the confidence level of each of the models (Burnham and Anderson 1998). We also used model likelihood, and the number of parameters (*k*) of each model to describe model results. We were prepared to use model averaging and to report unconditional standard errors (SE) for our model-averaged estimates if model uncertainty was high.

We anticipated that our parameter space might have some uncertainty, given 4 years of data and our small sample sizes. To explore the influence and sensitivity of nest success, annual survival, and fidelity in our system, we used a simple population model to predict population trends over time (Starfield et al. 1995). We used a deterministic model to calculate future population size of adult females, N_{t+1}, as a function of the current population (N_t), births, survival, and fidelity. We used the model to determine the probability of fidelity at which a constant population would be achieved, given a range of probabilities of nest success, *NS*, and annual adult survival, S_A. Adults remained in the population as a function of survival (S_A = 0.6, 0.7 and 0.8) and fidelity (*F*). Juveniles, *J*, were produced at time *t* as a function of nest success (*NS* = 0.03, 0.05, 0.10, 0.15, after Glup et al. 1986 and Walker et al. 2008), average number of nests per female (*n* = 1.3, Walker et al. 2008), clutch size of females (*cs* = 4, assuming 50:50 M:F ratio from total *cs* = 8, Walker et al. 2008). Walker et al. (2008) reported that fewer than 100% of adult females nested, so we used a value of 0.8 as the proportion of females that bred (*pfb*) each year. We did not estimate annual juvenile survival in our study, so we assumed that annual juvenile survival, S_J, would be less than adult survival; we chose a value of $S_J = 0.75S_A$. Thus:

$$J_t = N_t\,(pfb)(cs)(NS)(n)$$

And:

$$N_{t+1} = N_t(S_A)(F) + J_t(S_J)(F)$$

After setting the fixed values for *n*, *cs*, and *pfb*, we adjusted *NS* and S_A to create a unique scenario, and we then altered the value for *F* until the number of individuals in the population remained stable over 100 years. Thus, the output of our model was the threshold value for *F*, at which the population remained stable given scenarios of *NS* and S_A. We note that our model is based on the typical BIDE population model structure. However, our model assumes an immigration rate of 0, as our study design and the structure of our mark-recapture model for our empirical data did not allow estimation of immigration.

RESULTS

We captured 797 unique individual mallards (2005:266, 2006:266, 2007:87, 2008:178; Fig. 2). One hundred (13%) individuals were female and 697 (87%) were male. Ninety-five mallard bands (12%) were returned as hunter recoveries (direct and indirect) from 1 April 2005 through 1 April 2009, and 12 non-hunted dead returns were reported during the same time period. Of these band returns, 12 (13%) were female and 83 (87%) were male, which constituted 12% and 11.9% of all females and males banded, respectively. Mallards banded on our study site during the breeding season were recovered in 15 states and 2 Canadian provinces with the majority (76%) recovered in Nebraska and other Central Flyway states and provinces (Cunningham 2011). We recaptured 34 unique individual mallards (4.3%, 3 female, 31 male) of the 797 mallards banded between 2005 and 2008.

No single mark-recapture model captured >0.12 of AIC weights (w_i), so we selected the null model ($S_. p_. r_. F_.$; model

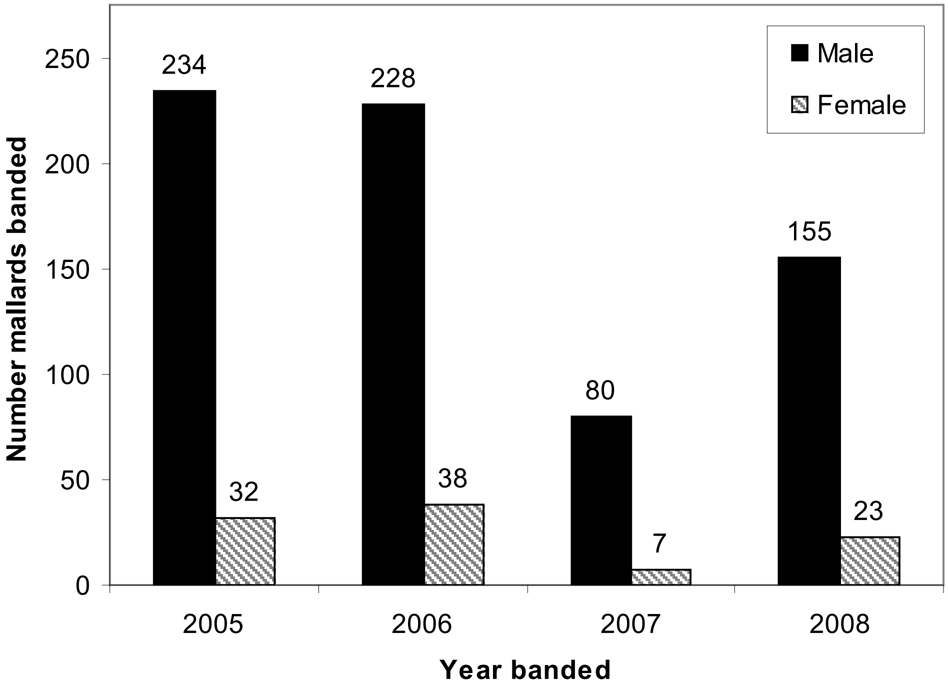

Figure 2. Number of individual male and female mallards banded during 2005–2008 in the Nebraska Sandhills.

3, Table 1) to represent mallard survival, fidelity, recapture, and recovery probabilities. We chose this model over models with larger AIC weights (w_i) and lower ΔAIC values because of the relative lack of evidence for a better model among the set, as well as the parsimony of the null model (Arnold 2010). In addition, confidence intervals indicated no difference in survival, fidelity, recapture, or recovery probabilities between genders, age, or over time in any of the models with $w_i \geq 0.03$ (Table 1).

Mallards banded in our study (male and female combined) had an annual survival probability of 0.795 (SE: 0.077; 95% CI: 0.609–0.907). We found no evidence to support gender difference in survival; none of the top four models included gender-specific survival (Table 1) and the model averaged, gender-specific annual survival probabilities were very similar (males: 0.866, SE = 0.083, 95% CI: 0.610–0.964; females: 0.862, SE = 0.101, 95% CI: 0.540–0.971). Probability of recovery from the null model was 0.300 (SE: 0.090; 95% CI: 0.157–0.497). Model averaged, gender-specific recovery probabilities were 0.308 (SE: 0.099; 95% CI: 0.152– 0.526) for males and 0.287 (SE: 0.103; 95% CI: 0.130–0.520) for females.

Recapture probability from the null model was 0.074 (SE: 0.030; 95% CI: 0.033–0.158). Model averaged, gender-specific recapture probability estimates were 0.086 (SE: 0.038; 95% CI: 0.035–0.199) for males and 0.055 (SE: 0.036; 95% CI: 0.014–0.187) for females. The top model's estimate of probability of fidelity (pooled across gender) was 0.618 (SE: 0.170; 95% CI: 0.283–0.868). The model averaged, gender-specific estimate of fidelity for males was 0.514 (SE: 0.162; 95% CI: 0.228–0.791) and 0.706 (SE: 0.253; 95% CI: 0.179–0.963) for females.

At low probabilities of nest success (e.g., NS = 0.03), the model predictions suggested that mallards in the Sandhills region were only locally sustainable at extremely high probabilities of annual survival (scenario: S = 0.9) and fidelity (F > 0.95, Fig. 3). Fidelity probability of >0.75 was required to sustain populations in the best scenario of high survival (S = 0.9) and high nest success (NS = 0.15, Fig. 3). The highest survival scenario in our model (S = 0.9) did not intersect the parameter space created by the range of our empirical nest success and fidelity estimates (Fig. 3), suggesting that significant immigration of birds was necessary to maintain breeding mallards in the Sandhills region.

DISCUSSION

Mallards banded in the Sandhills exhibited high annual survival. Our estimate of annual survival for males was higher than annual survival estimates from other sites in North America (Smith and Reynolds 1992, Doherty et al. 2002, Lake et al. 2006). Male mallards banded in this study were recovered across the Central and Mississippi Flyways (Cunningham 2011). Thus, as males from the Sandhills mix with

Table 1. Top ten models that estimated probabilities of mallard survival (S), fidelity (F), recapture (p), and recovery (r) from individuals marked in the Nebraska Sandhills during 2005-2008. Models are listed in order of support and include estimates of parameters that were constant (.), gender-specific (g), or time-specific (t). Models with larger AIC weights (w_i) and lower ΔAIC values have more support. Models shown have $w_i > 0.030$, and k is the number of parameters in each model.

Model[1]	AICc	ΔAIC	w_i	Model Likelihood	k	Deviance
1 $S_{.}\,p_{g}\,r_{t}\,F_{g}$	1149.32	0.00	0.124	1.000	9	50.88
2 $S_{.}\,p_{.}\,r_{t}\,F_{.}$	1149.58	0.26	0.109	0.879	7	55.22
3 $S_{.}\,p_{.}\,r_{.}\,F_{.}$	1151.02	1.70	0.053	0.427	4	62.75
4 $S_{.}\,p_{g}\,r_{t}\,F_{.}$	1151.13	1.81	0.050	0.404	8	54.74
5 $S_{g}\,p_{g}\,r_{t}\,F_{g}$	1151.28	1.95	0.047	0.377	10	50.79
6 $S_{.}\,p_{g}\,r_{.}\,F_{g}$	1151.30	1.98	0.046	0.372	6	58.97
7 $S_{.}\,p_{.}\,r_{t}\,F_{g}$	1151.45	2.13	0.043	0.345	8	55.05
8 $S_{g}\,p_{.}\,r_{t}\,F$	1151.53	2.21	0.041	0.332	8	55.13
9 $S_{.}\,p_{.}\,r_{t}\,F_{t}$	1151.79	2.47	0.036	0.290	9	53.35
10 $S_{.}\,p_{t}\,r_{t}\,F$	1152.04	2.72	0.032	0.257	9	53.60

[1] Lower-ranked models ($w_i < 0.030$) with details not shown: $S_{.}p_{g}r_{.}F_{.}$; $S_{.}p_{t}r_{t}F_{t}$; $S_{.}p_{.}r_{g}F_{.}$; $S_{.}p_{.}r_{.}F_{g}$; $S_{g}p_{.}r_{.}F_{.}$; $S_{g}p_{g}r_{t}F_{.}$; $S_{.}p_{g}r_{g}F_{g}$; $S_{g}p_{g}r_{.}F_{g}$; $S_{.}p_{g}r_{t}F_{t}$; $S_{g}p_{.}r_{t}F_{g}$; $S_{.}p_{.}r_{.}F_{t}$; $S_{.}p_{t}r_{.}F_{.}$; $S_{g}p_{.}r_{t}F_{t}$; $S_{.}p_{t}r_{t}F_{g}$; $S_{g}p_{t}r_{t}F_{.}$; $S_{g}p_{.}r_{g}F_{.}$; $S_{.}p_{t}r_{.}F_{t}$; $S_{.}p_{g}r_{g}F_{.}$; $S_{g}p_{g}r_{.}F_{.}$; $S_{.}p_{.}r_{g}F_{g}$; $S_{g}p_{t}r_{t}F_{t}$; $S_{g}p_{g}r_{g}F_{g}$; $S_{g}p_{.}r_{.}F_{g}$; $S_{g}p_{.}r_{g}F_{g}$; $S_{.}p_{g}r_{.}F_{t}$; $S_{.}p_{.}r_{g}F_{t}$; $S_{g}p_{g}r_{t}F_{t}$; $S_{.}p_{t}r_{.}F_{g}$; $S_{.}p_{t}r_{g}F_{.}$; $S_{g}p_{.}r_{.}F_{t}$; $S_{g}p_{t}r_{.}F_{.}$; $S_{g}p_{t}r_{t}F_{g}$; $S_{.}p_{t}r_{g}F_{t}$; $S_{g}p_{g}r_{g}F_{.}$; $S_{g}p_{t}r_{.}F_{t}$; $S_{g}p_{.}r_{g}F_{t}$; $S_{.}p_{g}r_{g}F_{t}$; $S_{g}p_{g}r_{.}F_{t}$; $S_{g}p_{t}r_{g}F_{.}$; $S_{.}p_{t}r_{g}F_{g}$; $S_{g}p_{t}r_{.}F_{g}$; $S_{g}p_{t}r_{g}F_{g}$; $S_{g}p_{t}r_{g}F_{t}$; $S_{g}p_{g}r_{g}F_{t}$

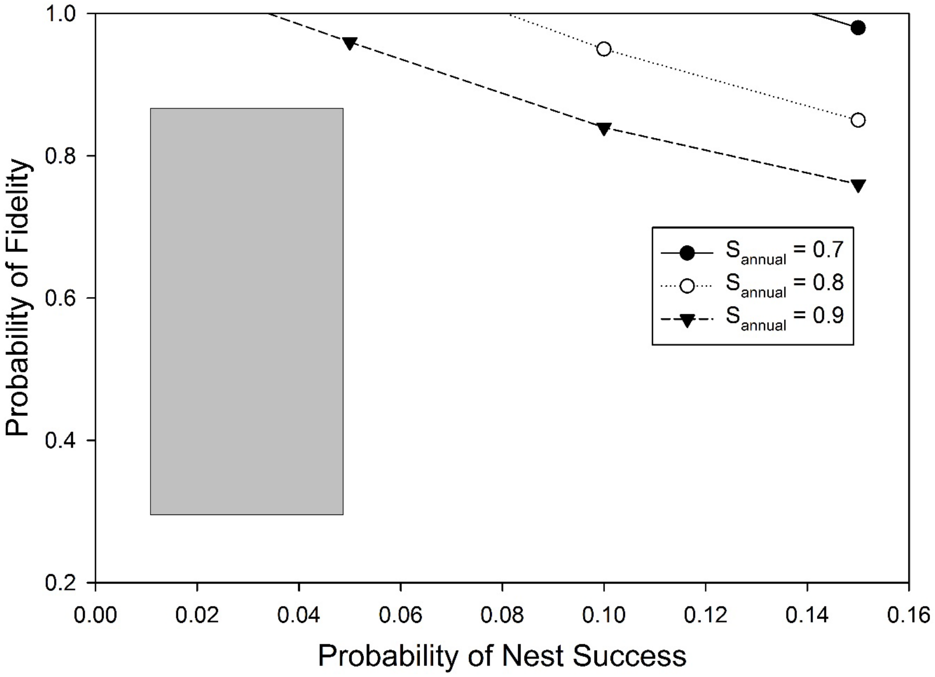

Figure 3. Threshold levels of probability of fidelity needed to maintain a stable population of female mallards in the Nebraska Sandhills under four nest success scenarios (0.03, 0.05, 0.10, and 0.15) and three annual female survival (0.7, 0.8, and 0.9) scenarios. Scenarios are not shown in necessary fidelity exceeded 1.0 (100%). The parameter space for our study's empirical estimates (95% confidence intervals) of nest success (0.3, 95% CI: 0.01–0.05; Walker et al. 2008) and fidelity (0.618, 95% CI: 0.283–0.868) is shown in as a shaded area to emphasize, despite considerable uncertainty in our estimate of fidelity, the need for extremely high survival probabilities (>>0.90) to intercept our parameter space for nest success and fidelity to maintain a stable population in the Sandhills.

birds from larger populations from the Prairie Pothole Region and other areas of North America, the level of harvest may be diluted for Sandhills birds and distributed evenly across the larger pool of mallards. Our model selection and the gender-specific estimate of annual survival provide no evidence of male:female differences in survival probability in the Sandhills; had recapture and recovery rates of females been higher, our power to detect such a difference would have improved.

Our study also provides further evidence of high survival during the breeding season in the Sandhills. Walker et al. (2008) reported high levels of 22-week survival ($\hat{S}$ = 0.84) for radio-marked females during the breeding season on our study site. Assuming constant survival throughout the year, our annual survival would translate to a 22-week, breeding season survival probability of 0.91. High survival for females may be linked to the low nesting success in the Sandhills (Glup 1986, Walker et al. (2008). Young (SY) female mallards have been shown to be less successful at nesting than older (ASY) birds (Krapu and Doty 1979, Curio 1983) and have been shown to have a higher breeding season survival because of a lower reproductive investment (Cowardin et al. 1985, Dufor and Clark 2002, Hoekman et al. 2002). We suspect that predators are driving this system, but in ways beyond simple productivity (Amundson et al. 2013), as high nest predation in contiguous grasslands may affect age ratios of breeding females, which may affect average survival of locally breeding females. The nest predator community in the semi-arid Sandhills appears to be dominated by snakes (Walker et al. 2008, Powell et al. 2012), and females may not encounter much risk during the breeding season from meso-predators (e.g., coyotes [*Canis latrans*], raccoons [*Procyon lotor*]). Our population model (Fig. 3) also suggests that low nest success necessitates immigration of new breeding individuals to maintain the Sandhills population, even with the high annual survival we observed.

Successful females in other regions are known to exhibit higher fidelity to a breeding area than unsuccessful younger females (Lokemoen et al. 1990, Majewski and Beszterda 1990). We anticipated lower fidelity given low nest success in the Sandhills (Glup 1986 and Walker et al. 2008) and the high proportion of SY females (Cunningham et al 2016). Our data set did not allow us to compare probabilities of fidelity between age groups in our sample, and our estimate of fidelity had a high level of uncertainty. Our point estimate for fidelity of females, F = 0.71, was higher than return rates (unadjusted for survival) of 0.13–0.58 reported in Anderson et al. (1992). Wetland conditions may affect homing (Majewski and Beszterda 1990, Dufour and Clark 2002). Sandhills wetlands are sourced by on-surface ground water, and wetland conditions in the Sandhills may be relatively stable (e.g., less effect of annual drought cycles) as compared to the precipitation-fed potholes further north in the mallard breeding region. Thus, wetland stability in the Sandhills may result in high fidelity of breeding mallards.

There are few comparisons for male mallard fidelity to breeding areas. Our results provided limited evidence for higher philopatry among male mallards than previous studies (Titman 1983, Evrard 1990) but were similar to those of Doherty et al. (2002). However, unlike Doherty et al. (2002), we banded mallards in spring on a local-scaled breeding area rather than late summer across a regional-scaled breeding area. High fidelity to a local breeding site supports the notion that some male mallards engage in resource-defense rather than the widely-held notion that males engage strictly in a mate-defense breeding strategy (i.e., following females to any breeding site; Anderson et al. 1992). We concur with Anderson et al. (1992) and Doherty et al. (2002) that further investigation of male mallard philopatry is needed to better understand waterfowl mating and dispersal strategies. Our data and our system model provide a framework for investigations that may provide critical information about these complex relationships. Such evidence of demographic trade-offs is rare and the Sandhills may provide insight that would be useful in other breeding areas.

Our demographic analyses suggest that mallards using the Sandhills region have unique characteristics, which are not typically expected of waterfowl breeding in large, contiguous grasslands. Mallards in our sample had a high proportion of first-year breeders, high survival, and high fidelity (Cunningham et al. 2016). Walker et al. (2008) reported that mallards in the first two years of our study had low levels of nest survival. Mallards in the Sandhills are part of the continental population of mallards, and we suspect that large-scale dynamics contribute to the demographic characteristics that we observed. Nebraska is south of the Prairie Pothole Region, and migratory position, breeding site fidelity, and relative quality of breeding habitat most likely affect the structure of Nebraska's breeding mallards. Our model suggests that the probability of fidelity and high probability of survival of mallards at our study site are not high enough to provide a stable population with the extremely low nest survival rates reported by Walker et al. (2008). Thus, the connection to the continental population appears to be critical to maintaining stable populations in the Sandhills region.

For the population of mallards using the Sandhills, strategies and actions that maintain this ecosystem are critical. The Sandhills population could act as a reservoir of younger females with high survival rates of which a portion are available to move to other breeding habitat in future years. Thus maintaining habitat quality in the Sandhills could benefit continental populations. On a regional level, better understanding and implementation of management actions that increase recruitment but do not jeopardize survival of mallards and other ducks would be beneficial. Finally, the Sandhills ecosystem provides a unique landscape for future research that could lead to a better understanding of regional variation in duck nesting ecology, predator community dynamics, and effectiveness of grassland management techniques.

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LITERATURE CITED

Alisauskas, R. T., T. W. Arnold, J. O. Leafloor, D. L. Otis, and J. S. Sedinger. 2014. Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. Ecology and Evolution 4:132–143.

Amundson, C. L., M. R. Pieron, T. W. Arnold, and L. A. Beaudoin. 2013. The effects of predator removal on mallard production and population change in northeastern North Dakota. Journal of Wildlife Management 77:143–152.

Anderson, M. G., J. M. Rhymer, and F. C. Rohwer. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 *in* B. D. J. Bratt, A. D. Afton, M. G Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bellrose, F. C. 1980. Ducks, geese, and swans of North America. Stackpole Books. Harrisburg, Pennsylvania, USA.

Bleed, A. S., and C. A. Flowerday. 1990. An atlas of the Sand Hills. Conservation and Survey Division, Institute of Agriculture and Natural Resources, University of Nebraska. Lincoln, USA.

Blohm, R. J., R. E. Reynolds, J. P. Bladen, J. D. Nichols, J. E. Hines, K. H. Pollock, and R. T. Eberhardt. 1987. Mallard mortality rates on key breeding and wintering areas. Transactions of the North American Wildlife and Natural Resources Conference 52:246–257.

Brasher, M. G., T. W. Arnold, J. H. DeVries, and R. M. Kaminski. 2006. Breeding season survival of male and female mallards in Canada's prairie-parklands. Journal of Wildlife Management 70:805–811.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhäuser Verlag, Basel, Switzerland.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carney, S. M. 1992. Species, age and sex identification of ducks using wing plumage. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C., USA.

Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. Wildlife Society Bulletin 19:534–543.

Coluccy, J. M., T. Yerkes, R. Simpson, J. W. Simpson, L. Armstrong, and J. Davis. 2008. Population dynamics of breeding mallards in the Great Lakes states. Journal of Wildlife Management 72:1181–1187.

Cowardin, L. M., D. S. Gilmer and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92:1–37.

Cowardin, L. M., T. L. Schaffer, and K. M. Kraft. 1995. How much habitat management is needed to meet mallard production objectives? Wildlife Society Bulletin 23:48–55.

Cunningham, Z. J. 2011. Breeding fidelity and landscape effects on distribution of mallards and duck broods in the Nebraska Sandhills. Thesis. University of Nebraska-Lincoln, Lincoln, USA.

Cunningham, Z. J., L. A. Powell, M. P. Vrtiska, S. E. Stephens, and J. A. Walker. 2016. Skewed age ratios of breeding mallards in the Nebraska Sandhills. American Midland Naturalist 175:280–285.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125:400–404.

Dahl, A. L., K. L. Baer, T. L. Shaffer, G. A. Sargeant, M. A. Johnson, and R. E. Reynolds. 1999. The relation of mallard nest numbers on constructed islands to upland habitat and mallard breeding pairs in North Dakota. North Dakota Game and Fish Department, Bismarck, North Dakota, USA.

Devries, J. H., J. J. Citta, M. S. Lindberg, D. W. Howerter, and M. G. Anderson. 2003. Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. Journal of Wildlife Management 67:551–563.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618–628.

Doherty, P. F., Jr., J. D. Nichols, J. Tautin, J. V. Voelzer, G. W. Smith, D. S. Benning, J. K. Bidwell, K. Bollinger, A. R. Brazda, E. K. Buelna, C. F. Ferguson, J. R. Goldsberry, F. H. Roetker, J. W. Solberg, P. P. Thorpe, and J. S. Wortham. 2002. Sources of variation in breeding-ground fidelity of mallard ducks. Behavioral Ecology 13:543–550.

Dufour, K. W., and R. G. Clark. 2002. Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. Condor 104:297–308.

Dzubin, A. 1969. Comments on carrying capacity of small ponds for ducks and possible effects of density on mallard production. Pages 138–160 *in* Saskatoon Wetland Seminar. Canadian Wildlife Service Report Series 6.

Evrard, J. O. 1990. Male philopatry in mallards. Condor 92:247–248.

Glup, S. S. 1986. Effect of land use and predation on waterfowl production on Valentine National Wildlife Refuge, Nebraska. Thesis. University of Nebraska-Lincoln. Lincoln, USA.

Grand, J. B. and T. F. Fondell. 1994. Decoy trapping and rocket-netting for northern pintails in spring. Journal of Field Ornithology 65:402–405.

Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. Wildlife Monographs 128:3–57.

Henebry, G. M, B. C. Putz, L. R. Vaitkus, and J. W. Merchant. 2006. Nebraska Gap Analysis Project. Final Project Reports. Gap Analysis Bulletin No. 14.

Higgins, K. F. 1986. A comparison of burn season effects on nesting birds in North Dakota mixed-grass prairie. The Prairie Naturalist 18:219–228.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883–900.

Johnson, J. D., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446–485 *in* B. D. J. Bratt, A. D. Afton, M G Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Klett, A. T., H. F. Duebbert, and A. D. Kruse. 1986. Techniques for studying nest success of ducks in the Prairie Pothole Region. U.S. Fish and Wildlife Service Resource Publication 158. Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA.

Klett, A. T., T. L. Shaffer, and D. H. Johnson. 1988. Duck nest success in the Prairie

Pothole Region. Journal of Wildlife Management 52:431–440.

Krapu, G. L., and H. A. Doty. 1979. Age related aspects of mallard reproduction. Wildfowl 30:35–39.

Kruse, A. D., and B. S. Bowen. 1996. Effects of grazing and burning on densities and habitats of breeding ducks in North Dakota. Journal of Wildlife Management 60:238–246.

LaGrange, T. 2005. Guide to Nebraska's wetlands and their conservation needs. Second Edition. Nebraska Game and Parks Commission, Lincoln, Nebraska, USA.

Lake, B. C., J. Walker, and M. S. Lindberg. 2006. Survival of ducks banded in the Boreal Forest of Alaska. Journal of Wildlife Management 70:443–449.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67:413–418.

Lokemoen, J. T., H. F. Duebbert, and D. E. Sharp. 1990. Homing and reproductive habits of mallards, gadwall, and blue-winged teal. Wildlife Monographs 106:1–28.

Majewski, P., and P. Beszterda. 1990. Influence of nesting success on female homing in the mallard. Journal of Wildlife Management 54:459–462.

Nebraska Game and Parks Commission. 1999. Nebraska Sandhills breeding duck population estimates. Unit Report, Lincoln, Nebraska, USA.

Novacek, J. M. 1989. The water and wetland resources of the Nebraska Sandhills. Pages 340–384 *in* A. van der Valk, editor. Northern Prairie Wetlands. Iowa State University Press. Ames, USA.

Powell, L. A., M. D. Giovanni, S. Groepper, M. L. Reineke, and W. H. Schacht. 2012. Attendance patterns and survival of Western Meadowlark nests. Studies in Avian Biology 43:61–66.

Reynolds, R. E., R. J. Blohm, J. D. Nichols, and J. E. Hines. 1995. Spring-summer survival rates of yearling versus adult mallard females. Journal of Wildlife Management 59:691–696.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. Journal of Wildlife Management 65:765–780.

Ringelman, J. K. 1990. Decoy traps for ducks. Leaflet 13.2.10 *in* D. H. Cross, compiler. Waterfowl management handbook. U.S. Fish and Wildlife Service, Fish and Wildlife Leaflet 13.

Sargeant, A. B., S. H. Allen, and R. T. Eberhardt. 1984. Red fox predation on breeding ducks in the midcontinent North America. Wildlife Monograph 89:1–41.

Sargeant, A. B., and D. G. Raveling. 1992. Mortality during the breeding season. Pages 396–422 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

SAS Institute Inc. 2008. SAS/STAT 9.2 User's Guide. Cary, North Carolina, USA.

Sharp, D. E., and J. T. Lokemoen. 1987. A decoy trap for breeding-season mallards in North Dakota. Journal of Wildlife Management 51:711–715.

Smith, G. W., and R. E. Reynolds. 1992. Hunting and mallard survival, 1979-88. Journal of Wildlife Management 56:306–316.

Starfield, A. M., F. S. Chapin III, and P. Duffy. 2002. Modeling the impact of black spruce on the fire regime of Alaskan boreal forest. Climatic Change 55:213–233.

Stephens, S. E., J. J. Rotella, M. S. Lindberg, M. L. Taper, and J. K. Ringelman. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. Ecological Applications 15:2137–2149.

Titman, R. D. 1983. Spacing and three-bird flights of mallards breeding in pothole habitat. Canadian Journal of Zoology 61:839–847.

Vrtiska, M. P., and L. A. Powell. 2011. Estimates of duck breeding populations in the Nebraska Sandhills using double observer methodology. Waterbirds 34:96–101.

Walker, J. A., Z. J. Cunningham, M. P. Vrtiska, S. E. Stephens, and L. A. Powell. 2008. Low reproductive success of mallards in a grassland-dominated landscape in the Sandhills of Nebraska. The Prairie Naturalist 40:1–13.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. vBird Study 46: Supplement:120–138.

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