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ABSTRACT -- The Sandhills of Nebraska comprise approximately 5,000,000 ha of native grassland interspersed with numerous groundwater-fed wetlands. A substantial population of the mallard (*Anas platyrhynchos*) nests in this region. Previous investigations of nest survival probability of ducks in the Sandhills have estimated surprisingly low rates of nest survival for a grassland-dominated landscape. These investigations were conducted on public lands and most nest searching took place near wetlands where activity of nest predators might be highest. We predicted that mallards would nest at varying distances from wetlands and that survival probability of a representative sample of duck nests would increase with distance from wetlands. We decoy-trapped and radio-marked 71 female mallards, 32 during the 2005 nesting season and 39 during the 2006 nesting season, and monitored their individual choice of nest habitats, their survival during the nesting season, and survival of their nests. Mallards nested in various habitats, both near and far from wetlands. Nest survival probability ($\hat{S} = 0.03$, SE = 0.02) was low relative to other studies regardless of distance to wetlands. Survival of females during the nesting season ($\hat{S} = 0.84$, SE = 0.08), however, was high relative to other studies. This pattern could have resulted from the combination of a diverse community of nest predators, few predators of nesting females, and a population of largely second year females that put little effort into nesting.

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The Sandhills of Nebraska comprise the largest continuous expanse of native grassland remaining in North America: an area of approximately 5,000,000 ha (Bleed and Flowerday 1990). The grasslands of the Sandhills are interspersed with more than 394,000 ha of wetlands, including permanent lakes, seasonally-flooded meadows and, less frequently, fens (LaGrange 2005). These wetlands are influenced strongly by groundwater dynamics (Novacek 1989). Most of the region is in private ownership, and the dominant land-use practice is cattle (*Bos taurus*) grazing for beef production (Novacek 1989).

Substantial numbers of the mallard (*Anas platyrhynchos*) nest in the Sandhills. Nebraska Game and Parks Commission (NGPC) biologists have counted up to 250,000 breeding ducks in the region during annual spring surveys conducted from the air (Nebraska Game and Parks Commission, unpublished data). The mallard was the most common species in this survey composing 35% of the total pair count on average. Nonetheless, the few previous investigations of nest survival of upland-nesting ducks (mallard, gadwall (*Anas strepera*), and blue-winged teal (*Anas discors*) in the Sandhills have indicated that nest survival in this region is low (Glup 1987). These observations conflict with the higher nest survival observed in landscapes that are dominated by grassland in the Prairie Pothole Region (PPR; Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005) where researchers have concluded that grassland-dominated landscapes are associated with lower rates of nest predation (Sargeant et al. 1993). Much of the research on nest survival of ducks in the Sandhills, however, was conducted on public lands (e. g., National Wildlife Refuges) and nest searching largely was limited to areas near wetlands. We suspected that these samples might not have been representative of the fates of nests located in the majority of privately-owned grassland habitat in the Sandhills. Nests located near wetlands might have been in areas where predator activity was highest and nest survival was lowest given that increased foraging activity near wetlands by nest predators has been observed in the PPR (Phillips et al. 2003).

We predicted that mallards would nest at various distances from wetlands and that survival probability of mallard nests located in grassland habitats in the Sandhills would increase with distance from wetlands. We initiated an investigation of the nesting ecology of mallards on private land in the Sandhills to evaluate the validity of this prediction. We marked female mallards with radio-transmitters prior to breeding and observed them through the nesting season so that the resulting nest sample would be representative of the range of selected habitats. This design also allowed us to estimate other vital rate parameters such as female survival during the breeding season, hen success, clutch size, and the proportion of nests initiated in different habitat types. To our knowledge, this study was the first effort to quantify these parameters for breeding ducks in the Sandhills.

METHODS

We investigated the reproductive success of mallards on a single study area in the Sandhills during April to July 2005 and 2006. The study area was located approximately 24 km south of Bassett, Nebraska (42° 20' N, 99° 29' W) and encompassed 26,347 ha (Fig. 1). Land-cover of the study area derived from a classification of 20-m SPOT imagery was composed of 69% native grassland, 14% hayland, 11% wetlands, 1% cropland, and 5% other classes (e.g., bare soil; Ducks Unlimited, unpublished data).

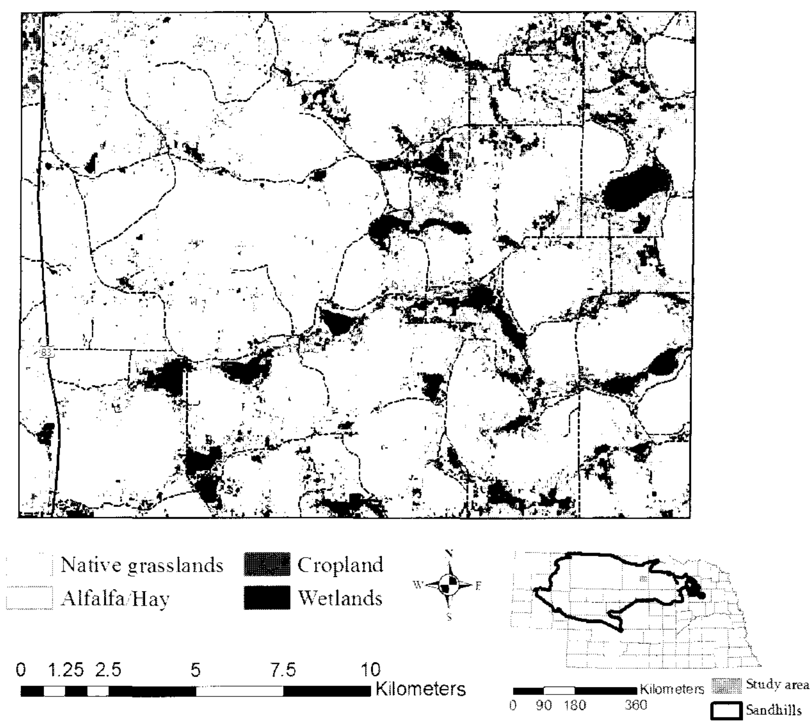

Figure 1. Location, extent, and dominant land cover of the study area where we studied mallard reproduction in the Sandhills of Nebraska during 2005 and 2006.

Our study area was typical of the eastern Sandhills in terms of climate, land-use, and plant community. Annual precipitation averaged 51 cm to 58 cm. Average summer temperature ranged from 19.4° C to 23.9° C. Dominant land-use practices were cattle grazing and forage cultivation. A detailed description of the native plant community of the Sandhills is given by Bleed and Flowerday (1990).

To capture females prior to nesting, we used decoy traps placed on wetlands where we observed mallard pairs behaving territorially (Sharp and Lokemoen 1987). When we captured a female we recorded her mass (± 5 g) and structural size (head length, tarsus length, and keel length; ± 0.1 mm) and fitted her with a United States Geological Survey (USGS) aluminum leg band. We attached a 5-gram radio transmitter (Model A4370; Advanced Telemetry Systems, Isanti, Minnesota) between her wings on the dorsal side and released her on the same wetland where she was captured (Pietz et al. 1995). Captured males were fitted with a USGS aluminum leg band and released. When we captured both members of a pair, we released them together to minimize disruption of pair bonds. The capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Nebraska (IACUC protocol #05-02-008).

We located radio-marked females 1 to 2 times daily by using truck-mounted and hand-held radio antennas and receivers. Females that left the study area were censored from the sample at the time of their last positive location. If a radio-marked female was observed in an upland location for two consecutive days, then we assumed she had initiated a nest. We attempted to locate the nest by triangulating on the location of the marked female and returning when she was absent. When we were unable to locate the nest by this method we waited 5 to 7 days (to minimize abandonment) and located the nest by flushing the female.

We recorded habitat type, number of eggs, stage of incubation (Weller 1956), and a measurement of horizontal vegetation density (Robel et al. 1970) at each nest, and we recorded the Universal Transverse Mercator (UTM) coordinates of the nest by using a handheld Global Positioning Systems (GPS) receiver. We revisited nests every 1 to 3 days until they were abandoned, destroyed, or the eggs hatched. We estimated the distance from each nest to the nearest wetland (±1 m) by using a landcover classification developed from satellite imagery of the study area taken in 2005. We also periodically located females during the brood-rearing period and attempted to count their ducklings. All marked females that remained on the study area were monitored for the duration of the study.

Predation rate on nests was very high in 2005. We deployed baited track plates (Kuehl and Clark 2002) in 2006 in an attempt to derive a preliminary assessment of the composition of the predator community on the study area. Track plates (2.5 m^2) composed of a sand and mineral oil mixture, scented plaster wafer, and plaster cast faux eggs were dispersed systematically throughout the study site. We placed track plates every 30 m radiating out from an active nest in the four cardinal directions in an attempt to identify potential predators at marked nests. Track plates were set in this same pattern in locations without active marked nests to determine potential predators searching the remaining habitat types.

We observed that many of the females captured in 2006 had feather characteristics consistent with those of Second Year (SY; i.e., approximately one-year-old) individuals. We removed greater secondary coverts from one wing of these females and compared the feathers to those in Carney (1992) to estimate the proportion of SY and After-Second-Year (ASY) birds in the 2006 sample.

We used the nest survival module in Program MARK 4.3 (White and Burnham 1999, Dinsmore et al. 2002) to estimate Daily Nest Survival (DNS) and Daily Survival Rate (DSR) of radio-marked females. We developed models of nest survival by using year, calendar date, horizontal vegetation density (ROBEL), and distance to water (DW) as predictors. Models of female survival included year and mass at capture as predictors. We evaluated relative support for competing models by using AICc differences and AICc weights (Burnham and Anderson 1998).

We estimated clutch size and number of nesting attempts per female by using Program R 2.3.1 (Ihaka and Gentleman 1996, R Development Core Team 2006). We estimated hen success as the product of nest survival probability and the number of nesting attempts per female, and we estimated the sampling variance of hen success by the delta method (Seber 1982). We estimated the proportion of nests in three habitat classes (grassland, hayland, and cropland) by assuming that these proportions followed a multinomial distribution. We also calculated survival probability of radio-marked females over a 22-week breeding season (i.e., DSR^{154}) to facilitate comparisons with other studies (Brasher et al. 2006).

RESULTS

We captured and radio-marked 32 female mallards in 2005, four of which were never detected again after capture and marking. We detected nests for 20 of the remaining 28 (71%). We radio-marked 39 female mallards in 2006, three of which were never detected again after capture and marking. We detected nests for 18 of the remaining 36 (50%). In total, we detected 28 nest initiations for 20 females in 2005 and 18 nest initiations for 36 females in 2006. Only one radio-marked female produced a brood in 2005. In 2006, there were zero broods produced. Therefore, we did not attempt to monitor or estimate brood survival.

Our best-approximating model indicated that DNS varied between years. Nonetheless, there was considerable model selection uncertainty, and the null model was a more parsimonious approximation (Table 1). Estimated, logit-scale slope coefficients from competing models for date (0.01; SE = 0.01), ROBEL (-0.04; SE = 0.12), and DW (0.001; SE = 0.01) were indistinguishable from zero. Estimated nest survival probability (i.e., DNS36; Klett et al. 1986) from the null model was 0.03

Table 1. Models of daily survival probability of mallard nests in the Sandhills of Nebraska during 2005 and 2006.

Model	Delta AICc	AICc Weight	Number of Parameters
Year	0.000	0.330	2
Null	0.276	0.287	1
Date	2.037	0.119	2
ROBEL[1]	2.218	0.109	2
DW[2]	2.290	0.105	2
Year*Date	3.788	0.050	4

[1]ROBEL is a measure of horizontal vegetation density.
[2]DW is the estimated distance from the nest to water.

(SE = 0.02). Estimated year-specific nest survival probability was 0.01 (SE = 0.01) in 2005 and 0.06 (SE = 0.05) in 2006.

We also estimated number of nesting attempts per nesting female, clutch size, female success, and the proportion of nests located in each habitat class. Average number of nesting attempts per nesting female during 2005 and 2006 was 1.31 (SE = 0.21); year-specific number of nesting attempts was 1.37 (SE = 0.27) in 2005 and 1.23 (SE = 0.32) in 2006. Estimated clutch size of radio marked mallards averaged 8.70 (SD = 1.84) in 2005 and 7.27 (SD = 1.77) in 2006. Estimated female success for both years combined was 0.04 (SE = 0.04) and was 0.01 (SE = 0.03) in 2005 and 0.07 (SE = 0.10) in 2006. Most nests were located in grassland habitat in both years (Fig. 2).

Daily survival rate of radio-marked females during the 2005 and 2006 nesting seasons was best described by a constant model, but there was some support for a positive relationship between DSR and mass at capture and variation between years (Table 2). Year-specific estimates were terms indistinguishable from each other. The estimated coefficient for mass (0.01; SE = 0.01) was not different from zero. Thus, the null model was most parsimonious of these competing models.

Daily probability of survival for a female mallard captured and radio marked on our study area was 0.999 (SE = 0.006). Estimated 22-week survival probability of radio-marked females on our study area was 0.84 (SE = 0.08). The age distribution of marked females in 2006 was highly skewed. Twenty of 23 (87%) of mallard females aged in 2006 were SY birds.

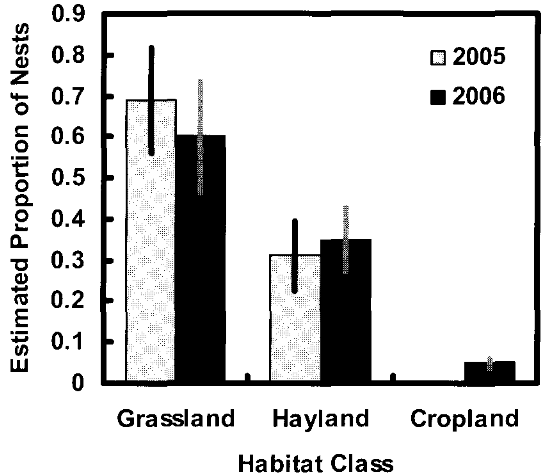

Figure 2. Estimated proportion of mallard nests (±SE) in major habitat types on the Sandhills study site during 2005 and 2006.

We detected at least eight species of potential nest predators with the track plates we deployed in 2006: coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), ground squirrel (*Spermophilus* spp.), Virginia opossum (*Didelphis virginiana*), American badger (*Taxidea taxus*), long-tailed weasel (*Mustela frenata*), and weasel (*Mustela* spp.). In addition to the detections of mammals, we also detected raptors and snakes at track stations.

DISCUSSION

We accrued no support for our hypothesis that nest survival would increase with distance to wetlands. We also observed no relationship between nest survival and ROBEL although most nests were located in grassland habitat with an average lateral density of 3.18 dm (SD = 1.50 dm) and on average were located 376 m (SD = 396 m) from water. Thus, we were doubtful that a strong relationship existed between nest survival and any of these variables.

Survival of nests was surprisingly low on our study area during 2005 and 2006. We had expected nest survival probability in a large area of intact grassland like our study area to be higher. The average nest survival probability that we observed over two-years was lower than average nest survival estimates from many intensively-cultivated sites in the PPR (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005). Most failed nests were destroyed by predators, and we

Table 2. Models of daily survival probability of female mallards in the Sandhills of Nebraska during 2005 and 2006.

Model	Delta AICc	AICc Weight	Number of Parameters
Null	0.000	0.357	1
Mass	0.120	0.335	2
Year	0.289	0.308	2

observed evidence in 2006 from track plates that the predator community on the study area was as diverse as any in the PPR (Sargeant et al. 1993). Thus, our observations provided little support for the idea that predator communities were less diverse (Sovada et al. 1995) on our grassland-dominated study area.

Most other parameters related to nesting were comparable to estimates of the same parameters from the PPR. Average clutch size of mallards on our study area was similar to that reported in Bellrose (1976) in 2005 and might have been one egg lower in 2006. Similarly, number of nests per nesting female was similar to the unadjusted estimate (1.41 nests/female) reported by McPhereson et al. (2003). These estimates indicated to us that clutch size or renesting propensity probably were not limiting production on this study area. We concluded that success of nesting females was extremely low on our study area largely as a result of low nest survival (high nest predation).

Estimated 22-week survival probability of radio-marked females on our study area ($\hat{S}$ = 0.84, SE = 0.08) was generally high relative to that observed by other researchers. Cowardin et al. (1985) reported survival of female mallards of 0.81 (SE = not reported) but suspected that their estimate was biased high because of transmitter loss (right-censoring) related to predation. A lower estimate from the prairie parklands of Canada ($\hat{S}$ = 0.60, SE = not reported) was reported by Blohm et al. (1987). Also in the Canadian prairie-parklands, Brasher et al. (2006) estimated breeding season survival of 0.78 (SE = 0.025).

Breeding season survival of females commonly is thought to be negatively related to nesting effort because most mortality of female mallards during the breeding season occurs on nests (Sargeant and Raveling 1992, DeVries et al. 2003). We observed nesting effort comparable to that of prairie mallards on the part of females for which we detected nests. Nevertheless, we did not detect any nests for many radio-marked females.

We found nests for only 71% of females in 2005 and 50% of females in 2006. This is an extremely low proportion of nesting birds in a sample of mallards marked with prong-and-suture mount radio transmitters. The low proportion of nesting birds in our sample could be an artifact of our methods. For example, transmitter effect might have caused females to put less effort into nesting or we might have failed to detect a substantial proportion of nests because many nests were destroyed early in incubation. Alternatively, the proportion of nesting females on our study area might have been low for an unknown ecological reason.

Nevertheless, we doubt that a transmitter effect produced the results that we observed. There is little evidence to support the idea of a strong relative effect of prong-and-suture mount transmitters on the probability of initiating a nest although females marked with prong-and-suture mount radios initiate fewer total nests and spend fewer days laying and incubating eggs (Paquette et al. 1997). During a study of mallard breeding ecology in North Dakota that was concurrent with our study in the Sandhills, researchers detected nests for 85% of radio-marked female mallards (Mark Sherfy, United States Geological Survey, Northern Prairie Wildlife Research Center, unpublished data). These mallards were marked with transmitters identical to the transmitters we used to mark mallards in the Sandhills and were tracked by using similar protocols. Furthermore, we tracked all of the marked females in the sample daily, and although it is almost certain that we missed some nests (see McPherson et al. 2003), it is doubtful that we missed enough nests to cause such great disparities between our study and other studies that used nearly identical methods (Paquette et al. 1997, M. Sherfy, United States Geological Survey, unpublished data). Thus, we think that a low proportion of females on our study area nested.

We suspect that the relatively low proportion of nesting females and relatively high survival probability that we observed was related to the age of the birds we marked. Our sample consisted of 87% SY females in 2006. In contrast, Devries et al. (2003) reported about 48% SY females in their sample collected over 19 site-years in the Canadian prairie parklands; the highest proportion of SY females observed in an individual site-year was about 60%. Second Year female mallards tend to invest less energy in nesting and brood-rearing (Reynolds et al. 1995, Dufour and Clark 2002). Thus, a population of SY mallards breeding in an environment with low potential for reproductive success might exhibit reduced breeding effort and higher survival. Further, the predator community on our study area might have favored higher survival of breeding females. Although we detected a diverse group of nest predators on our study area we did not detect red fox (*Vulpes vulpes*): possibly the major predator of nesting female ducks in the PPR (Sargeant and Raveling 1992, Sovada et al. 1995).

Mallard production on our study area was very low during 2005 and 2006. However, additional information would be required to make inference to the breeding mallard population in the Sandhills. We might have selected a site where reproductive success is consistently low, or we might have observed two very poor years for reproductive success. Reproductive success of the mallard is quite variable in space and time across its breeding range (Johnson et al. 1992, Hoekman et al. 2002) and it is probably variable in the Sandhills as well.

Nonetheless, our study raised some interesting questions about duck production in the Sandhills. For example, what is the level of spatial and temporal variation in predator communities and reproductive success of the mallard across the Sandhills region? Is the mallard population nesting in the Sandhills composed primarily of females in their first breeding season? Are predator communities consistently more diverse in the grassland-dominated landscape of the Sandhills than similar landscapes in the PPR? These questions could be answered with data collected during multiple (at least two) breeding seasons from a probability sample of sites across the Sandhills. The results of such an effort would be useful to waterfowl managers given the size of the population of mallards counted during the breeding season and the potential threats to groundwater resources and wetland habitat in this region.

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