

University of Nevada, Reno

Reproductive Ecology of Greater Sandhill Cranes in Nevada

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science in
Natural Resources and Environmental Science

by

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We recommend that the thesis
prepared under our supervision by

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ABSTRACT

We evaluated factors influencing survival of nests and chicks (i.e., colts) of greater sandhill cranes (*Grus canadensis tabida*) in northeastern Nevada, USA, during 2009-2010. We monitored 161 nests and 101 colts and used a maximum-likelihood based approach to test multiple competing hypotheses and estimate daily survival rates, nest success, fledging success, and covariates. Daily survival rates (DSRs) of nests were negatively related to density of crane pairs, and positively related to proximity to roads and vegetation height at nests. Low daily minimum temperatures had a negative effect on DSR, and the effect increased as incubation progressed. We found some support for a negative impact of summer grazing on DSR. Nest success in our study (32.3%, SE = 8.3%) was the lowest reported for sandhill cranes. Managers should encourage landowners to conserve wet-meadow habitat containing tall vegetation to enhance nest success of sandhill cranes. Areas with low-density nesting pairs may be particularly important for productivity, and should be given the highest conservation priority.

We found colt survival was lower on Ruby Lake National Wildlife Refuge compared to private- or state-owned lands. Colts located on the Refuge had practically no prospect of fledging ($1 \pm 6\%$ in 2009, $<1 \pm 3\%$ in 2010), whereas colts located on private and state lands had higher and more variable probability of fledging ($25 \pm 13\%$ in 2009, $15 \pm 9\%$ in 2010). Survival rates were lowest early in development and increased with age of colts. We did not detect an effect of weather or habitat use on survival. Our results support previous findings of predation as the primary cause of pre-fledging mortality in cranes. Our findings are inconsistent with sibling competition as a major source of colt mortality, but support extrinsic factors as important determinants of survival. Our results

suggest that management of predator populations may influence fledging for cranes in northeast Nevada.

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CHAPTER 1.

INTRODUCTION

The greater sandhill crane (*Grus canadensis tabida*) is one of six subspecies of sandhill crane (*Grus canadensis*) found in North America. Within the Pacific Flyway, several populations of cranes are recognized under specific management plans. Cranes breeding in southwest and south-central Idaho, northeast Nevada, northwest Utah, and likely northwest Idaho, USA (Ivey and Herzigler 2006) are assigned to the Lower Colorado River Valley (LCRV) population of greater sandhill cranes. The LCRV population is the least abundant (Drewien et al. 1976, Drewien and Lewis 1987), has the lowest reported recruitment rate (4.8%), and is the least studied of any migratory crane population in North America (Drewien et al. 1995). A small experimental hunt was initiated December 2010 in the wintering areas of the LCRV because the population estimate surpassed the population objective of 2,500 (Kruse et al. 2009), despite few data on the population dynamics of the LCRV population of greater sandhill cranes.

Population growth rate is most sensitive to adult survival in long-lived species of birds (Sæther and Bakke 2000). However, temporal variation in recruitment is often greater than variation in adult survival rate (Erikstad et al. 1998, Sæther and Bakke 2000, Weimerskirch et al. 2000). Therefore, population growth should be most influenced by recruitment for long-lived species (Sæther and Bakke 2000), such as cranes. Vital rates that have the highest temporal and spatial variation typically also have the greatest potential for management.

To better understand factors that may be limiting recruitment, and therefore population growth in the LCRV population, we monitored two important components of recruitment, nest survival and chick survival, for the segment of the LCRV population breeding in northeastern Nevada. For the second chapter, we examined several temporal, habitat, and spatial variables that may influence survival and success of nests including: nest initiation date, age of nest, year, weather (daily minimum temperature, daily maximum temperature, and daily precipitation), water depth around nests, vegetation height, land-use practice (idled, hayed, fall-grazed, or summer-grazed), density of crane pairs surrounding nests, landcover type (open water, marsh, meadow, and riparian habitats), nearest distance to roads, nearest distance to settlements, and a visitation effect. We estimated daily survival rates (DSR) and evaluated the influence of environmental variables (i.e., covariates) using maximum likelihood based approaches by implementing the nest survival model in Program MARK (White and Burnham 1999). The model constrains DSR to vary according to groups or individual attributes, while allowing irregular intervals between visits (Dinsmore et al. 2002). We compared performance of models using an information-theoretic approach by ranking models according to Akaike's Information Criterion (AIC) and by calculating AIC model weights (w_i ; Burnham and Anderson 2002).

For the third chapter, we used morphological measurements from crane chicks to estimate relative body size and estimate age of chicks from unmonitored nests. We also compared the time of death between siblings within a brood to assess the role of sibling competition on survival. Finally, we examined several temporal, habitat, and spatial variables that may influence survival of crane chicks during the pre-fledging period

including: hatching date, chick age, year, weather (daily minimum temperature, daily maximum temperature, and daily precipitation), landownership (private, state, or federal), landcover type (open water, marsh, wet meadow, and riparian habitats), nearest distance to roads, and a handling effect that was immediate or extended. We employed a procedure similar to the nest survival analysis to estimate daily survival rates and pre-fledging success of crane chicks and evaluate the effect of different environmental factors on DSR. Results from this thesis are intended to provide information to inform management decisions that may improve population growth of LCRV greater sandhill cranes. Additionally, these results should represent a comprehensive analysis of survival of nests and young of cranes using modern analytical techniques.

The following two chapters of this thesis are written in journal format in preparation for submission to *The Journal of Wildlife Management*. This thesis is single authored, although co-authors for each manuscript are referenced on the first page of each chapter. The “we” in each chapter refers to all authors referenced.

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CHAPTER 2.

Sandhill Crane Nest Survival in Nevada: effects of conspecific density, human development, and weather

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ABSTRACT

We evaluated factors influencing nest survival of greater sandhill cranes (*Grus canadensis tabida*) in northeastern Nevada, USA, during 2009-2010. We monitored 161 nests and used a maximum-likelihood based approach to test multiple competing hypotheses and estimate daily survival rates, nest success, and covariates. Daily survival rates (DSRs) were negatively related to conspecific density ($\beta = -0.27 \pm 0.11$) and positively related to proximity to roads ($\beta = -0.23 \pm 0.11$) and vegetation height at nests ($\beta = 0.23 \pm 0.13$). Low daily minimum temperatures had a negative effect on DSR ($\beta = 1.28 \pm 0.47$), and the effect increased as incubation progressed (minimum daily temperature \times nest age interaction $\beta = -0.07 \pm 0.03$). We found some support for a negative impact of summer grazing on DSR. Nest success in our study (32.3%, SE = 8.3%) was the lowest reported for sandhill cranes. Managers should encourage landowners to conserve wet-meadow habitat containing tall vegetation to enhance nest

success of sandhill cranes. Areas with low-density nesting pairs may be particularly important for productivity, and should be given the highest conservation priority.

KEY WORDS density-dependent, *Grus canadensis tabida*, human development, nest success, weather.

In birds, sensitivity of population growth rate to adult survival increases as survival increases (Sæther and Bakke 2000). Long-lived birds often live in stochastic environments, in which temporal variation in recruitment is high and variation in adult survival is low (Erikstad et al. 1998, Sæther and Bakke 2000, Weimerskirch et al. 2000). The contribution of a demographic trait to population growth rate is inversely related to its temporal variation in a wide variety of avian taxa (Horvitz et al. 1997, Ehrlén and van Groenendael 1998, Pfister 1998, Sæther and Bakke 2000). Ultimately, demographic parameters that have high temporal variation such as recruitment have the largest impact on population growth (Sæther and Bakke 2000). Fitness components that have the highest temporal and spatial variation typically also have the greatest potential for management.

Sandhill cranes (*Grus canadensis*) are among the longest lived (annual survival rates = 0.86-0.95; Tacha et al. 1992), and have the lowest recruitment rates of any game bird in North America (Drewien et al. 1995). Population growth of sandhill cranes is therefore most susceptible to changes in recruitment rate of young into the breeding population, in the absence of harvest or additional sources of adult mortality. Because sandhill cranes exhibit low fecundity, with small clutch size (1.94 ± 0.02 , Drewien 1973) and low incidence of reneating (1.5-10.5% of total nests [Austin et al. 2007]), nest success may limit recruitment and therefore population growth.

Human modification of the landscape influences nest success for birds, often by influencing predation (Stephens et al. 2003). Roads may attract nest predators by increasing abundance of carrion (Knight and Kawashima 1993). Roads have been associated with increased reproductive success of common ravens (*Corvus corax*) because of anthropogenic food sources associated with roads (Kristan 2001). Ravens are an important egg predator for sandhill cranes in the western U.S. (Walkinshaw 1949, Drewien 1973, Littlefield 1976, Littlefield and Thompson 1987). No studies have yet documented impacts of human development, including roads, on nest survival of sandhill cranes.

Previous studies on nest success of greater sandhill cranes (*Grus canadensis tabida*; hereafter cranes) focused on the importance of water depth (Austin et al. 2007, Ivey and Dugger 2008, McWethy and Austin 2009) and vegetation height surrounding nests (Littlefield and Ryder 1968, Littlefield 1995), and examined effects of land management that reduce nesting cover (Littlefield and Paullin 1990, Austin et al. 2007, Ivey and Dugger 2008). These studies did not, however, examine possible direct impacts of grazing on nest success. Because livestock often use mesic habitats in the arid west (Fleischner 1994), impacts of livestock on nest survival of cranes is possible and should be assessed. Few studies have accounted for variation in crane nest survival within a year (Austin et al. 2007, Ivey and Dugger 2008). No studies have attributed intra-seasonal variation in nest survival associated with a particular environmental factor.

Previous research has focused primarily on productivity of nesting cranes on national wildlife refuges, with limited studies on private agricultural land. Although refuges may provide important habitat, the overall contribution to population dynamics of

cranes nesting on state and federal wildlife management areas may be relatively minor, because suitable habitat may largely occur on private land.

Our objectives were to estimate daily nest survival rates and nest success of cranes nesting primarily on private lands in northeastern Nevada, and to test multiple competing hypotheses of factors affecting nest success. We hypothesized nest survival would be negatively related to human development and density of crane pairs. Among land-use practices, we hypothesized survival would be lowest for nests within summer-grazed fields, because of disturbance by livestock.

STUDY AREA

Our study area encompassed Elko, White Pine, and extreme northern Lincoln Counties in northeastern Nevada, USA (Fig. 2.1). Topography was characterized by north-south oriented mountain ranges and associated basins (Fiero 1986). Average annual precipitation and average annual snowfall in Elko, NV during this study was 24 cm and 73 cm, respectively. Average daily temperatures from April-June in Elko, NV during this study ranged from 21° C to 2° C. Elevation in the study area ranged from approximately 1,300 m at the edge of the Great Salt Lake Desert, to nearly 4,000 m at Wheeler Peak. Lower elevation areas in the study area were used primarily for cattle grazing and native hay production in pastures irrigated by geothermal springs and from intermittent mountain streams via diversion ditches. Although 86% of the land area is in public ownership in Nevada, >85% of lowland meadow habitat is privately owned (McAdoo et al. 1986). Field work was performed at a mean elevation of $1,757 \pm 6$ m and directed towards known concentrated breeding areas of cranes in northeastern Nevada (Rawlings 1992).

We divided the study area into five subareas each representing a concentrated crane breeding area (Fig. 2.1): Ruby Valley Area (composed of Ruby, Secret, Steptoe, Spring, and Lake Valleys), Huntington Valley (composed of Huntington Creek Floodplain and Mound and Newark Valleys), Lamoille Valley Area (composed of Humboldt River Floodplain and Lamoille and Starr Valleys), Independence Valley Area (composed of South Fork of the Owyhee River Floodplain and Independence Valley), and North Fork Area (composed of O'Neil Basin, Thousand Springs Valley, and floodplains of the Upper North Fork drainages of the Humboldt River, Bruneau River, Salmon Falls Creek, and Mary's River).

METHODS

Field Methods

Nesting data.—We searched for nests in hay meadows and pastures in northeastern Nevada from early April to early July in 2009 and 2010. We searched wet-meadow habitat in pastures and hay fields composed of grasses (*Poa spp.*), rushes (*Juncus spp.*), and sedges (*Carex spp.*). We also searched emergent vegetation along slow-moving streams and in beaver ponds, within natural and artificial ponds, and within marshes containing common cattail (*Typha latifolia*), hardstem bulrush (*Scirpus acutus*), and willow (*Salix spp.*). We began searches on 7 April in 2009 and 11 April in 2010 and searched for nests daily between 1 hr after sunrise and 1 hr before sunset. We focused our nest searching efforts in areas where cranes were present and signs of breeding (i.e., lone individuals or individuals agitated by our presence) were observed. We located active crane nests during searches on foot ($n = 120$ nests), helicopter ($n = 37$) and fixed-wing aircraft ($n = 28$) surveys, remote observations using spotting scopes or binoculars ($n =$

18), and canoeing ($n = 3$). We spent ≤ 2 consecutive days searching for nests at each property and rotated among four subareas (≤ 5 consecutive days per subarea) to ensure even coverage of the study area and an adequate sample of nests that spanned the entire nesting season (Fig. 2.1).

When we found a nest, we floated each egg to estimate incubation stage (6 flotation stages span 3-8 days each, Westerskov 1950, Ackerman and Eagles-Smith 2010) and hatch date (Westerskov 1950, Fisher and Swengel 1991). We assumed eggs were laid at 2-day intervals (Littlefield and Ryder 1968, Drewien 1973). To assess abandonment due to investigator disturbance, we marked an X on one side of each egg and laid the marked side facing down. We considered nests with cold, intact eggs, no rotation of marked eggs from the previous visit, and no crane present on subsequent visits as abandoned. We checked all nests classified as abandoned again after 6 days to verify abandonment. We used a handheld Global Positioning System (GPS) unit to record Universal Transverse Mercator (UTM) coordinates of nests. We revisited nests regularly (mean interval = 8 days) until fate was determined (≥ 1 egg hatched [success] or the nest was destroyed or abandoned [fail]). We also visited nests near the expected hatch date to capture and radio-tag chicks. We used presence of detached egg shell membranes or egg shell fragments, behavior of the territorial pair, or presence of young in, or near, nests to indicate a successful hatch (Nesbitt 1992). Any of these indicators subsequent to pipping eggs was also assumed to indicate a successful nest. Failed nests were represented by broken or missing eggs (Ivey and Dugger 2008). During each nest visit, we floated eggs and measured water depth (± 1 cm) 1 m from nest edges, and vegetation height (± 1 cm) 4 m from nest centers and at 1 m height in each cardinal direction using a modified Robel

pole (Toledo et al. 2008). We recorded vegetation height as the lowest one centimeter band $\geq 50\%$ obscured by vegetation. We averaged 4 measurements for each visit to obtain date-specific measurements for each nest.

We classified the land-use practice in fields containing nests into 1 of 4 categories: idled, hayed, fall-grazed, or summer-grazed. We classified natural habitats or fields managed for wildlife as idled, which primarily occurred on National Wildlife Refuge land. Fields cut for hay and subsequently fall-grazed during the previous growing season were classified as hayed. We hypothesized direct impacts of livestock (i.e., disturbance) being present during nesting would have a greater impact on nest survival than reduction in vegetation height associated with grazing during the previous or current growing season. Therefore, we classified fields as summer-grazed if livestock were present during nesting.

Pair density.—To assess density-dependent effects, we identified pair locations through the presence of nests, young, or pairs. In conjunction with ground searches of nests, we regularly monitored suitable crane habitat for occupancy and we monitored pairs for nesting activity throughout the nesting period in 2009 and 2010. Cranes have high nest-site fidelity (Drewien 1973), and adult cranes generally nest annually (Tacha et al. 1992). Therefore, a pair location for one year was assumed to represent a pair location during the entire two-year study period. Also, failed breeders generally do not abandon nesting and brood-rearing areas until after the conclusion of the nesting period (Drewien 1973). We performed fixed-wing aircraft surveys on 13 and 20 May 2009, and helicopter surveys during 19-25 May 2010, to identify crane territories and access remote and restricted areas otherwise not available for observation from the ground. We augmented

aerial sightings through ground surveys and field observations in areas not covered during the aerial surveys. Where possible, we located nests and young, and confirmed pair locations on the ground within a week after aerial surveys.

To avoid double-counting pairs in areas with high nesting densities and consequently overestimating density of pairs, we identified reneating pairs using multiple criteria. We classified nests as reneats if distance between nests was ≤ 350 m (Drewien 1973) and if both 1) the interval between failure and initiation of nests was ≥ 10 days (Gee 1983), and 2) failure of a potential preceding nest occurred before 15 days of incubation (Drewien 1973). We also assumed females produced similar egg sizes (Walkinshaw 1973), and used this as a final criteria to identify reneats. To identify the same pairs between years, we assumed a similar distance (≤ 350 m) between nests of the same pair, and we assumed similar egg sizes for the same nesting pairs in successive years. Consequently, our estimates of pair density were conservative.

Spatial Data

Landscape-scale data.—We analyzed the importance of different habitat types using land cover data derived from the Southwest Regional Gap Analysis Project. We employed the land cover types: open water, North American arid West emergent marsh (hereafter marsh), Great Basin foothill and lower montane riparian woodland and shrubland (hereafter riparian), inter-mountain basins semi-desert grassland (hereafter grassland), and agriculture (USGS National Gap Analysis Program, 2004). Open water was defined as water bodies with $< 25\%$ vegetation or soil cover. Marsh was frequently or continually inundated by water and contained $> 80\%$ vegetation cover. Riparian areas had $> 20\%$ vegetative cover of forest or shrubland and periodically saturated soil or substrate.

Grassland was sparse to moderately dense herbaceous layer dominated by medium-tall and short bunch grasses, often in a sod-forming growth, on lowland and upland areas. These areas were often flood-irrigated for hay production or pasture. Agriculture consisted of both center-pivot irrigated crops and hay fields. We observed a large proportion of hay meadows categorized as agriculture that was visually indistinguishable from grassland. Additionally, crop land composed a minor portion of the study area, and was primarily unused by nesting crane pairs. Therefore, we combined the land types agriculture and grassland to create a meadow habitat type. Because of limited vegetation cover, we hypothesized open water habitats would be negatively related to nest survival. Conversely, we hypothesized marsh and meadow habitat would have positive effects on nest survival, because increased vegetation cover should have provided increased nest concealment. Because common ravens prefer riparian areas for nest and roost sites (Engel and Young 1992), we hypothesized increased riparian habitat would result in decreased nest survival.

To assess anthropogenic impacts on nest survival, we identified sources of human development or human disturbance. We identified occupied residences during field observations and recorded locations on aerial photos using ArcMap. We extracted named roads from a Bureau of Land Management road network data layer to identify primary or regularly-traveled roads.

We employed a Geographical Information System (GIS) using ArcMap to help characterize the spatial aspects of our landscape-scale analysis. We calculated distance to nearest roads and distance to the nearest development (roads or settlements) using ArcGIS. We summed the number of 30-m pixels for each habitat type at radii within 100

m (area = 3 ha), 200 m (13 ha), 400 m (50 ha), 800 m (201 ha), and 1000 m (314 ha) of nests. These radii represent varying scales of habitat selection for nesting area, brood-rearing area, foraging area, territory, and home range, respectively (Baker et al. 1995). To identify con-specific effects on nest survival, we calculated density of territories (pair per hectare) around nests within radii of 800 m (201 ha), which approximates the upper limit of territory sizes estimated for cranes (McMillen 1988; 199 ± 51 ha, Duan et al. 1997).

Weather data.—We gathered weather data from Remote Automated Weather Stations (RAWS) and Natural Resource Conservation Service’s SNOTEL sites through MesoWest, and National Weather Service’s Cooperative weather stations through the National Climate Data Center. We collected daily minimum temperature, daily maximum temperature, and daily precipitation for each nest from the nearest low-elevation weather station with available data (distances from nests to stations = 0.8 – 42.0 km). We estimated daily weather values for 24-hr periods ending at 0800.

Data Analysis

To assess fluctuations in water levels and vegetation height throughout the incubation period, we applied a general linear regression between date-specific measurements across nest visits. We assumed linear changes in water depth and vegetation height because intervals between nest visits were relatively short (mean = 8 days). For nests with only one day of measurement ($n = 6$ nests), we calculated average change (i.e., slope) in water depth or vegetation height across all active nests for that date. For nests with missing values during one visit, but with measurements from ≥ 2 visits, we interpolated using the slope from the regression equation to estimate missing values ($n = 7$ nests). We also

averaged date-specific measurements across all visits for each nest to estimate one season-specific measurement for each nest.

We used the nest-survival model in Program MARK and an information-theoretic approach to evaluate support for competing models (Burnham and Anderson 2002). We evaluated the strength of support for each model by ranking models with Akaike's Information Criterion adjusted for small sample size (AIC_c) and by calculating AIC_c model weights (w_i ; Burnham and Anderson 2002). Prior to model building, we standardized nest-site habitat, landscape, pair density, and weather variables and we standardized nest initiation dates within years (mean = 0 ± 2 SD).

We developed univariate nest survival models to analyze temporal variation in daily nest survival associated with nest initiation date, nest age, and year. Daily nest survival rates often vary with date (Klett and Johnson 1982, Grant et al. 2005), so some models included nest initiation date as a covariate to account for this variation. We fit a linear trend on nest survival because daily survival commonly increases with nest age (Van Der Burg et al. 2010). To allow for nonlinear patterns in daily survival, we also fit a quadratic trend to nest age. To assess the role of weather variables on temporal variation in nest survival, we compared performance of models containing nest initiation date and nest age variables against models including only time-dependent weather variables (daily minimum and maximum temperatures, and daily precipitation). Annual variation in nest survival rates is often due to a variety of factors including weather conditions and fluctuations in predator and prey numbers (Bety et al. 2001, Dinsmore et al. 2002), that we did not measure. Therefore, we did not attempt to explain annual variation in nest

survival using covariates. We also considered two-factor models allowing year to be additive or interactive with continuous time-dependent variables.

We developed univariate models containing different habitat types and anthropogenic impacts to detect sources of variation in nest survival beyond the spatial scale of a nest-site. To avoid obtaining competitive models that spuriously resulted by comparing models of different habitat types at different spatial scales, we chose *a priori* to restrict model comparison to a single spatial scale. We compared the relative performance of course-scale (1000 m spatial scale) models with their equivalent fine-scale (100 m and 200 m) models. Overall, we found course-scale models performed better than fine-scale models, so we restricted our comparison of habitat models to the 1000 m spatial scale. We incorporated spatial variables into our main-effects models containing land-use practice and nest habitat variables if 85% confidence intervals did not overlap zero (Arnold 2010).

To reduce bias in daily nest survival estimates attributed to human disturbance during nest visits, we estimated observer-effects (Rotella et al. 2000). We assumed a nest visitation effect on nest survival only occurred during a short period (one day) following visits, reasonable for predators that may find nests by watching observers visit nests or by following fresh human scent to nests (Rotella et al. 2000). We added the observer-effects variable to the best approximating model lacking observer effects to assess the impact of nest visitation on nest survival.

We calculated nest exposure days as the period from initiation of incubation to hatching of the last egg. We assumed eggs hatched at 1-day intervals (Drewien 1973; Walkinshaw 1973). We calculated nest success by multiplying daily nest survival rates

over the first 30 days of incubation (mean incubation period = 30.2 ± 0.19 d, Drewien 1973).

We considered parameters important for nest survival if 85% confidence intervals did not overlap zero (Arnold 2010). To account for model selection uncertainty, we calculated parameter estimates and standard errors from models with $\Delta AIC_c \leq 4$ using AIC_c weights (Burnham and Anderson 2002). Estimates are given as mean \pm standard error.

RESULTS

We monitored 161 nests in 2009 and 2010. Of 49 nests monitored in 2009, 18 were successful. Of 112 nests monitored in 2010, 38 were successful. We monitored nests located in hayed (63%, $n = 102$), fall-grazed (21%, $n = 34$), idled (11%, $n = 17$), and summer-grazed (5%, $n = 8$) fields.

We found no support for differences in daily survival rates between years, but we found a significant interaction between year and a quadratic trend on nest age. From field observations, we suspected, a priori, weather conditions were different between years. May of 2009 was cooler (<5th percentile coldest May on record) than May 2010 (<20th percentile warmest May on record; National Climate Data Center). June of 2009 was the second wettest June on record for northeastern Nevada (National Climate Data Center). We compared the year \times quadratic nest age trend interaction model with models containing a surrogate time-dependent variable of minimum daily temperature or maximum daily temperature. We found that a model containing quadratic trend in nest age and an interaction between minimum daily temperature and nest age performed better than the year-by-trend model, so we constrained all further models to contain this

temporal variation. In addition, we found nest initiation was later in 2009 (mean Julian date = 135 ± 2.00 , mode = 138) compared to 2010 (mean Julian date = 128 ± 1.61 , mode = 122). Because we standardized initiation dates within years, we needed to account for seasonal variation in nest survival attributed to an environmental factor. Our best temporal model that accounted for seasonal variation in nest survival contained an interaction between daily precipitation and initiation date. Therefore, our final temporal model contained a quadratic trend on nest age, minimum daily temperature, interaction between minimum daily temperature and nest age, initiation date, daily precipitation, and interaction between initiation date and daily precipitation. All terms within the temporal model except initiation date and daily precipitation were important for explaining temporal variation in daily survival rates. Therefore, we constrained all further models to contain these variables accounting for temporal variation, and considered this our base model for comparison of landscape or habitat effects.

We found pair density within 800 m of nests to be an important spatial variable, so we incorporated this variable into our final model set. Within our landscape-scale analysis of univariate models, both distance to roads and distance to development were important. Models $<12 \Delta AIC_c$ performed better when distance to roads rather than distance to development was included, and these variables were highly correlated ($r = 0.84$, $P < 0.001$). Therefore, we included the distance to roads variable in our final model set to test for anthropogenic impacts on nest survival.

Variables within our base model important for nest survival included linear ($\beta = -0.24 \pm 0.11$) and quadratic trends on nest age ($\beta = 0.006 \pm 0.003$), minimum daily temperature ($\beta = 1.28 \pm 0.47$), and minimum daily temperature \times nest age interaction ($\beta =$

-0.07 ± 0.03). Among the models considered, we found strong support for an effect of pair density within 800 m [Sum of Akaike weights ($\sum w_i$) = 0.98], nest-site habitat (water depth + vegetation height, $\sum w_i = 0.91$), and distance to roads ($\sum w_i = 0.90$) on nest survival. Daily survival rates (DSR) were negatively associated with density of crane pairs ($\beta = -0.27 \pm 0.11$) and increased closer to roads ($\beta = -0.23 \pm 0.11$). Addition of nest-site habitat improved performance of models (Table 2.1). For nest-site habitat, vegetation height ($\beta = 0.23 \pm 0.13$) was important, but water depth was less so ($\beta = 0.16 \pm 0.11$).

Our best approximating nest survival model included the effects of water depth, vegetation height, distance to road, pair density within 800 m, and summer grazing (Table 2.1). The second-best model ($AIC_c w_i = 0.39$; Table 2.1) was similar to the best supported model, but without a summer grazing effect and had $\Delta AIC_c = 0.11$ with 1 less parameter. Thus, although contained within the best model, we found a general lack of support for a summer grazing effect ($\sum w_i = 0.51$, $\beta = -0.30 \pm 0.63$; Table 2.1).

Furthermore, an effect of summer grazing alone performed worse than our base model (Table 2.1). When added to the best model, we failed to find support for an observer effect on daily nest survival ($\beta = -0.75 \pm 0.80$). A model lacking covariates was not competitive, indicating environmental variables had important effects on nest survival.

Lower minimum daily temperatures had a negative effect on nest survival and the effect increased with nest age. Additionally, increasing daily precipitation had a negative effect on daily survival rates of nests initiated early, but a positive effect for nests initiated late (Fig. 2.2). Nest survival did not differ among fields that were idled, hayed, or fall-grazed. Daily survival rates for nests in summer-grazed fields were lower and

more variable than in other fields (Fig. 2.3). Survival was nonlinear across the 30 days of incubation. A negative trend in survival occurred during the first half of incubation, shifting to a positive trend thereafter (Fig. 2.3).

DISCUSSION

We found nest survival was negatively related to pair density, which was the most important variable describing variation in nest survival. This is the first study we are aware of to detect density-dependent effects on nest survival of cranes. Density-dependent predation may be caused by either a functional or numerical response to prey density (Krebs 2001). Predators with large home ranges may detect heterogeneity in local prey density and alter search image or foraging pattern (Schmidt and Whelan 1999). Effects of density-dependent predation on nest success have been mixed. Some studies found density-dependent predation varied with availability of alternate prey (Hogstad 1995, Bety et al. 2001), or local predator communities (Ackerman et al. 2004, Elmberg et al. 2009).

Inverse density-dependent success of nests caused by intraspecific competition has been demonstrated in ducks (Titman and Lowther 1975, Duebbert et al. 1983) and geese (Ewashuk and Boag 1972, Prop and Quinn 2003), but has not been demonstrated in a wild crane population, although it has been suggested in at least one instance (Leito et al. 2005). Several researchers have observed frequent skirmishes along boundaries of neighboring crane territories (Littlefield and Ryder 1968). In cranes, males engage in the majority of territorial defense and females eventually leave nests unattended after not being relieved from incubation (Walkinshaw 1973). Greater time spent during territorial bouts likely results in lower nest attendance and presumably greater predation risk

(Littlefield and Ryder 1968). Nesting cranes are also more vocal in areas with more conspecifics and often call when exchanging nest duties (Walkinshaw 1973), which may provide clues about nest site locations for auditory predators. Without intensive observation or remote nest monitoring, assessing the relationship between nest attendance, density of cranes, and nest survival is difficult.

Contrary to our initial prediction, we found higher survival for nests closer to roads. Activity patterns of predators may shift in human altered and disturbed landscapes (McClennen et al. 2001). In Illinois, coyotes and red foxes (*Vulpes vulpes*) were less common in developed areas compared to raccoons (*Procyon lotor*; Randa and Yunger 2006). We frequently observed coyotes during field observations, but rarely observed red foxes, striped skunks (*Mephitis mephitis*), or raccoons. Coyotes are known to exclude red foxes (Sargent et al. 1987). Coyotes in areas with more human disturbance decrease diurnal activity and increase nocturnal activity, presumably to avoid human disturbance, shooting or trapping mortality, and competition with domestic canids (McClennen et al. 2001). We believe higher survival of nests closer to roads was primarily related to persecution of coyotes. No crane studies have yet to assess impacts of human development on nest success. The Eastern migratory population of cranes exhibited a long-term increase (Van Horn et al. 2010), which may be explained by positive impacts of human development on nest success found in our study.

We found significant variation in nest survival associated with weather. Although Tacha et al. (1992) suggested decreased susceptibility to cold as eggs develop (Tacha et al. 1992), we found lower minimum daily temperatures had an increasingly negative effect on daily survival rates as nest age increased. Previous experiments on Mallards

(*Anas platyrhynchos*) revealed older embryos were less resistant to cold than younger embryos, causing deformities that prevented hatching (Batt and Cornwell 1972). We also found precipitation had a negative effect on daily survival rates of nests initiated early, but a positive effect on daily survival rates of nests initiated late. Water used for flood irrigation of hay meadows and pastures was primarily from mountain streams supplied by snowfall, which was abundant during early spring when cranes initiated nesting. Additional precipitation during early spring may have caused rapid changes in water levels resulting in nest desertion (Nesbitt 1988). Some early-spring precipitation was snowfall, which may also have caused nest desertion. Precipitation late in the nesting season, when water levels are low, may increase nest isolation and decrease predator activity.

Similar to other studies, we found nest-site habitat to be important for nesting cranes. Previous studies consistently found water depth (Austin et al. 2007, Ivey and Dugger 2008, McWethy and Austin 2009) to be important, but importance of vegetation was inconsistent. In contrast, we found nest-site vegetation height had a greater impact on nest survival than water depth. Differences in importance of water depth versus vegetation height may reflect differences in local predator communities. Previous studies that found importance of water depth also reported high populations of mammalian predators (Austin et al. 2007, McWethy and Austin 2009). Nest concealment was found important for ground-nesting birds when predation was predominantly by visual (i.e., avian) predators (reviewed by Clark and Nudds 1991), which may explain importance of vegetation height in our study. However, differences in field methods make comparisons difficult. To examine the relationship between nest habitat and nest predators, future

studies need to identify predators by using devices such as cameras near nests. Water is likely a factor limiting plant growth in our study area. Consequently, tall vegetation (e.g. cattails and bulrush) may largely be concentrated in areas inundated by water. We suspect vegetation height provided a simpler, more informative description of both vegetation height and water depth, and may act as a surrogate for both nest concealment and isolation. However, we found no correlation between vegetation height and water depth at nests ($r = 0.07$, $P = 0.39$). We failed to find any importance of habitat beyond the scale of the nest-site, but the resolution (0.09 ha) of available data may have limited our ability to detect fine-scale landscape features important for nest survival.

Similar to previous studies (Austin et al. 2007, Ivey and Dugger 2008), we failed to detect variation in nest survival among idled, hayed, or fall-grazed fields. We found weak to modest support for a summer-grazing effect, but inferences are limited due to small sample size and consequently large variation in survival rates for these fields. We also did not distinguish between types of livestock (e.g. horses, bulls, cow-calf pairs, yearling cattle), which could influence the effect of livestock on cranes. We compared a stocking rate covariate to our categorical covariate of livestock presence and found the categorical covariate performed better. We suggest future studies examine possible effects of livestock being present during nesting on nest survival and further distinguish among livestock types.

Nest success estimates for the Lower Colorado River Valley Population of greater cranes nesting in northeastern NV (0.32 ± 0.08 for 30-d incubation period, in fields ungrazed during summer) was lower than estimates from either the Central Valley (0.72 ± 0.04 , Ivey and Dugger 2008) or Rocky Mountain (0.41 ± 0.03 , Austin et al. 2007; 0.65

± 0.10 , McWethy and Austin 2009) populations. Comparisons are limited because only one study (McWethy and Austin 2009) occurred on private land, and previous studies report apparent nest success or variations of Mayfield estimates, which assume constant daily survival rates that can inflate nest success estimates (Jehle et al. 2004). We used a maximum-likelihood approach to test competing hypotheses that account for heterogeneity in nest survival. Additionally, our study spanned a relatively short period for such a long-lived species and importance of environmental factors may vary temporally.

Additional research is needed to estimate productivity of cranes breeding on private lands. Future research should also focus on identifying the mechanism underlying negative density-dependent nest success for cranes, which could inform future reintroduction efforts for threatened crane species. If the cause is a functional response of individual predators or intraspecific competition, reintroductions should develop populations with a more scattered breeding distribution. Finally, our findings that human development had a positive effect on crane nest success require additional work to better understand this functional relationship.

MANAGEMENT IMPLICATIONS

Our results indicate that nest success is highest for cranes nesting in low density near roads within habitats that provide good nest concealment. Managers should encourage landowners to conserve wet-meadow habitat containing tall vegetation to enhance nest success of cranes. Areas with low-density nesting pairs may be particularly important for productivity, and should be given the highest conservation priority.

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Table 2.1. Model selection results for factors affecting survival of greater sandhill crane nests in northeastern Nevada, USA, 2009-2010.

Model ^{a,b}	ΔAIC_c^c	Akaike wt	No. parameters	Likelihood
BASE + WTR + VEG + RD + PR + GRAZE	0.0	0.41	13	1.00
BASE + WTR + VEG + RD + PR	0.1	0.39	12	0.95
BASE + WTR + VEG + PR	4.2	0.05	11	0.12
BASE + RD + PR + GRAZE	4.3	0.05	11	0.11
BASE + WTR + VEG + PR + GRAZE	4.9	0.04	12	0.09
BASE + RD + PR	5.3	0.03	10	0.07
BASE + WTR + VEG + RD	7.3	0.01	11	0.03
BASE + PR	8.3	0.01	9	0.02
BASE + PR + GRAZE	8.3	0.01	10	0.02
BASE + WTR + VEG + RD + GRAZE	8.4	0.01	12	0.02
BASE + WTR + VEG	11.4	0.00	10	0.00
BASE + WTR + VEG + GRAZE	13.1	0.00	11	0.00
BASE + RD	13.3	0.00	9	0.00
BASE + RD + GRAZE	13.9	0.00	10	0.00
BASE	16.3	0.00	8	0.00
BASE + GRAZE	17.6	0.00	9	0.00

^aBASE = quadratic trend on nest age + interaction between minimum daily temperature and nest age + interaction between daily precipitation and initiation date.

^bWTR = water depth, VEG = vegetation height, RD = distance to road, PR = pair density within (800 m), GRAZE = summer graze.

^cDifference in Akaike's Information Criterion from top model.

Figure 2.1. Location of greater sandhill crane study area and five subareas in northeastern Nevada, USA, 2009-2010.

Figure 2.2. Interacting effect of daily precipitation and Julian date on daily nest survival rates of greater sandhill cranes nesting in northeastern Nevada, USA, 2009-2010.

Figure 2.3. Model-averaged ($<4 \Delta AICc$) daily nest survival rates of greater sandhill cranes nesting in fields (a.) not grazed and (b.) grazed during summer in northeastern Nevada, USA, 2009-2010.

Figure 2.1.

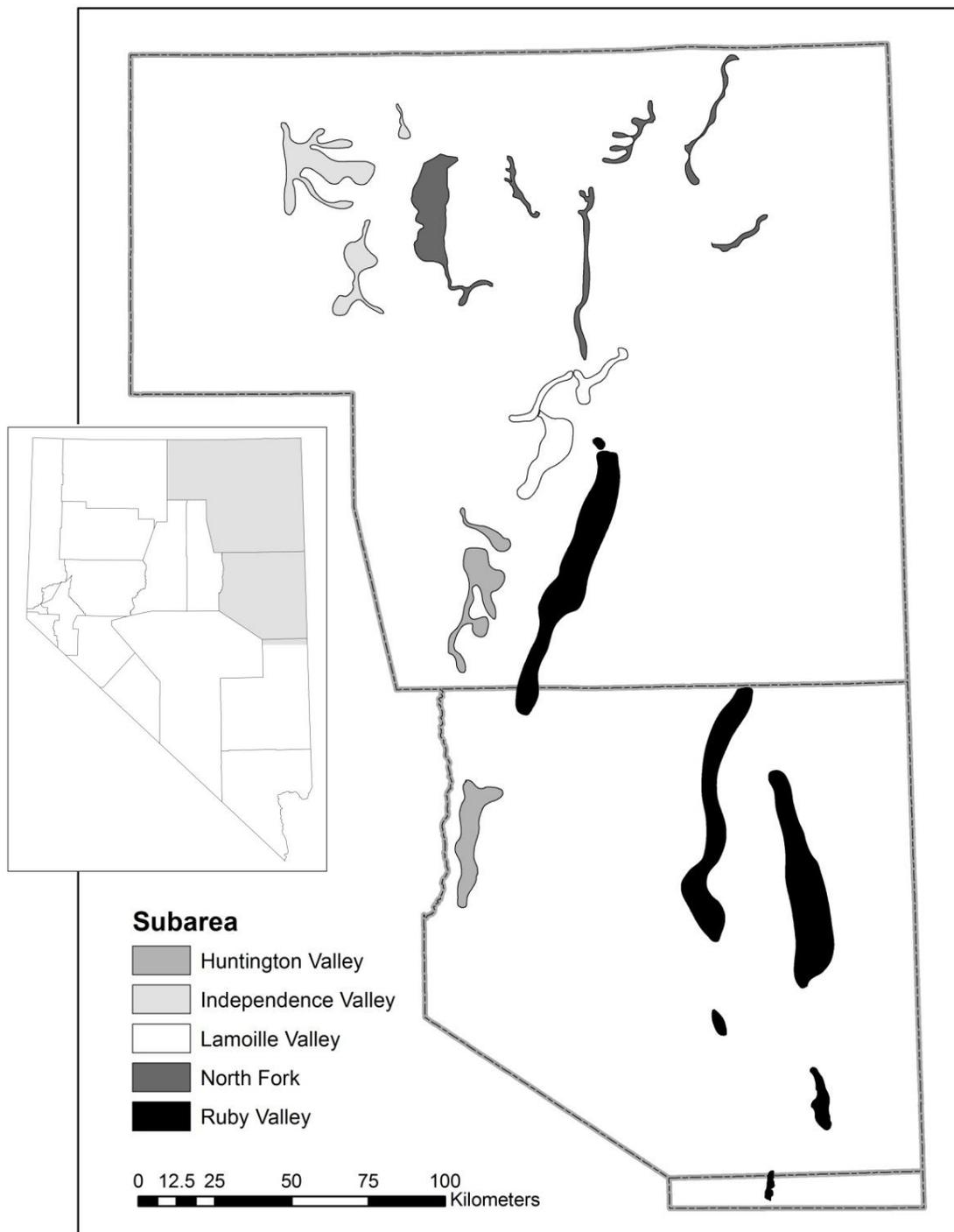
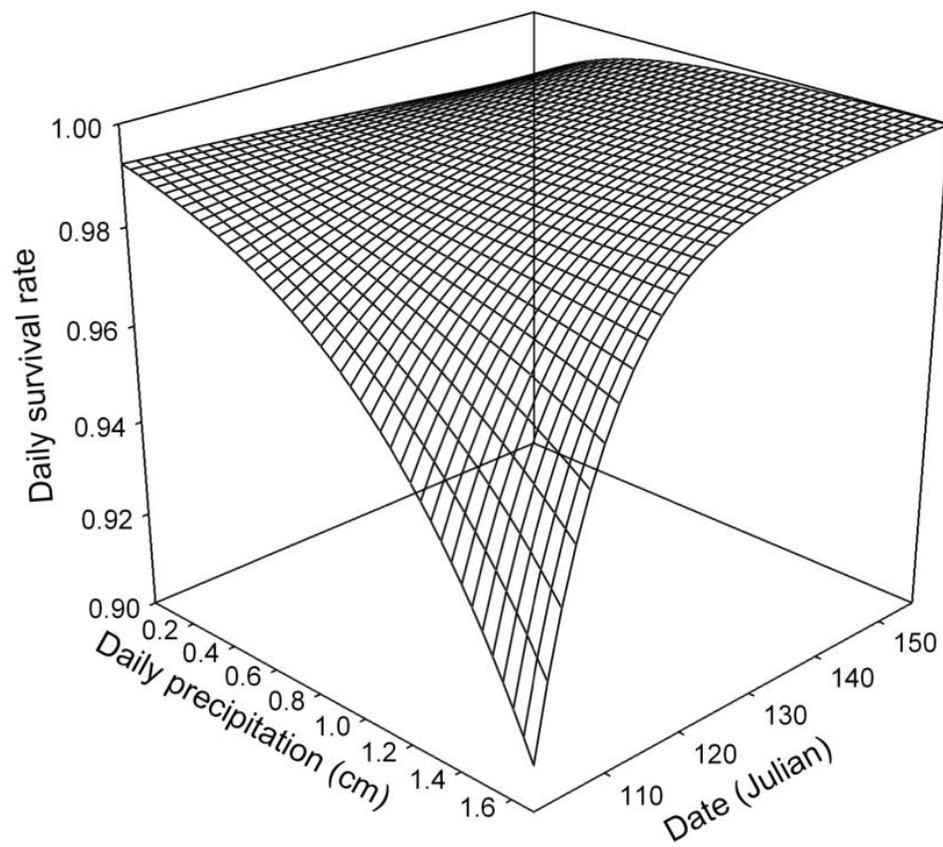


Figure 2.2.



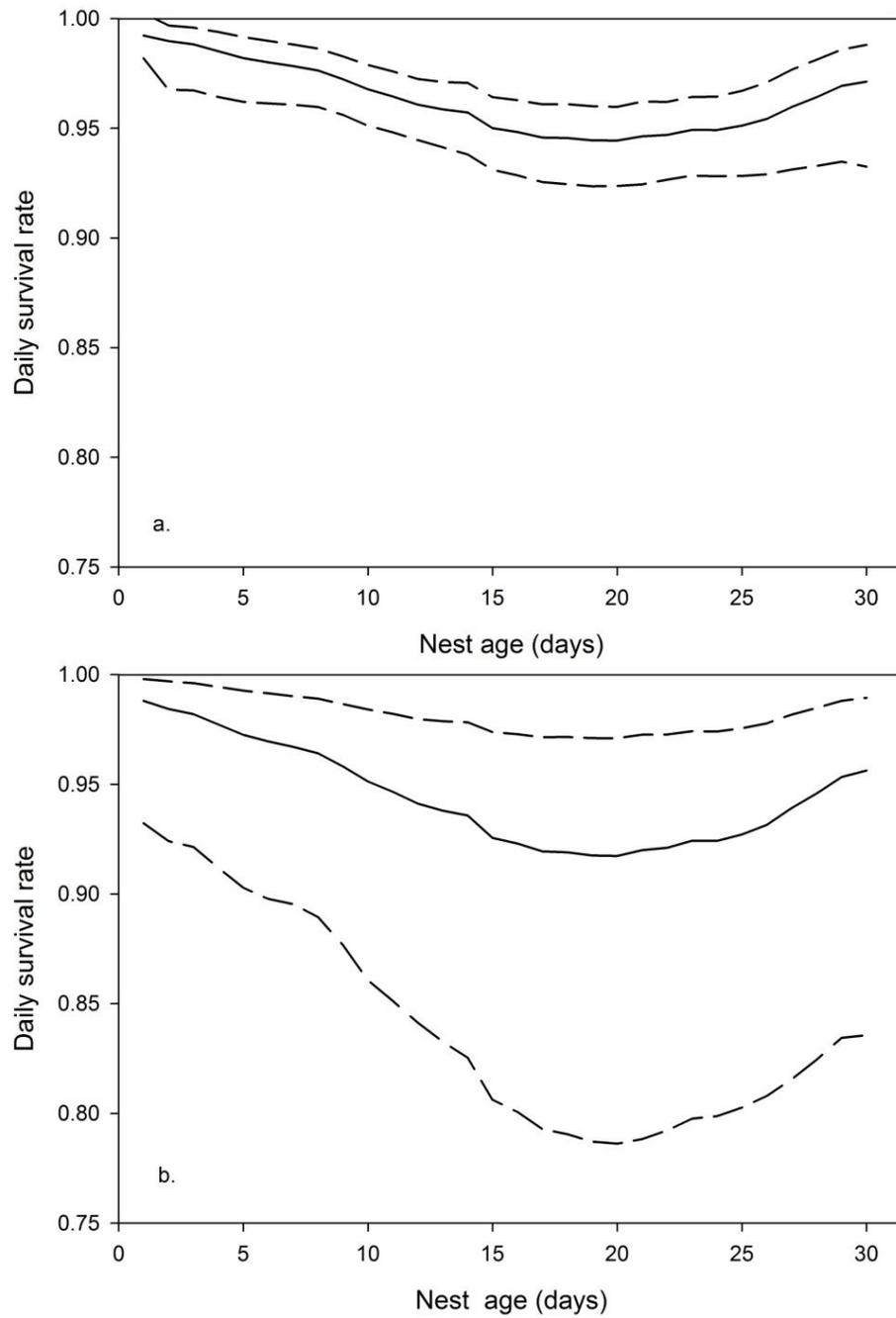


Figure 2.3.

CHAPTER 3.

Age-Specific Survival of Greater Sandhill Crane Colts in Nevada

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ABSTRACT

We estimated daily survival rates and fledging success, and evaluated factors influencing survival of greater sandhill crane (*Grus canadensis tabida*) chicks (i.e., colts) in northeastern Nevada, USA, during 2009-2010. We monitored 101 colts during 2009-2010. We found survival was lower on Ruby Lake National Wildlife Refuge compared to private- or state-owned lands. Colts located on the Refuge had practically no prospect of fledging ($1 \pm 6\%$ in 2009, $<1 \pm 3\%$ in 2010), whereas colts located on private and state lands had higher and more variable probability of fledging ($25 \pm 13\%$ in 2009, $15 \pm 9\%$ in 2010). Survival rates were lowest early in development and increased with age of colts. We did not detect an effect of weather or habitat use on survival. Our results support previous findings of predation as the primary cause of pre-fledging mortality in cranes. Our findings are inconsistent with sibling competition as a major source of mortality, but support extrinsic factors as important determinants of survival. Our results suggest that management of predator populations may influence fledging for cranes in northeast Nevada.

KEY WORDS brood reduction, chick survival, fledging success, *Grus canadensis tabida*, handling effect, predator removal, radiotelemetry, sibling rivalry.

Recruitment is an important determinant of population dynamics, despite population growth being most sensitive to adult survival in long-lived species (Sæther and Bakke 2000), because recruitment is highly variable in numerous populations (Boyce et al. 2006). Demographic components that have the greatest temporal variation, such as recruitment, have the greatest impact on population growth (Pfister 1998).

Sandhill cranes (*Grus canadensis*) have among the highest adult survivals of any game bird (annual survival rates = 0.86-0.95; Tacha et al. 1992). Greater sandhill cranes (*G. c. tabida*; hereafter cranes) wintering along the lower Colorado River Valley (LCRV) have the lowest recruitment rates (4.8% young in winter) of any crane population in North America (Drewien et al. 1995), suggesting recruitment may be a component limiting growth in this population.

Chick (hereafter colt) survival is the least understood component of recruitment in cranes. Previous studies have focused on identifying direct causes of colt mortality, including predators and disease (Littlefield and Lindstedt 1992, Desroberts 1997, Ivey and Scheuring 1997), or habitat use. Although this may be informative for selective management of causes of mortality, the relative contribution of other environmental factors is unknown. No studies have estimated colt survival relative to time-dependent factors such as weather and hatching date.

Mortality of precocial young is often high early in development, and survival probability commonly increases with age (Flint et al. 1995, Colwell et al. 2007, Stafford and Pearse 2007, Fondell et al. 2008), which has been attributed to increased ability to thermoregulate, forage, and evade predators during the growth period. Weather may have greater affect on survival at young ages, when chicks are more susceptible to cold

temperatures. Also, inherent heterogeneity in traits affecting survival of colts allows selective removal of lower-quality individuals. Although previous studies have demonstrated high mortality of young colts (Bennett and Bennett 1990, Nesbitt 1992), no studies so far have estimated daily survival rates of crane colts.

Predation is the most common cause of pre-fledging mortality in cranes (Desroberts 1997, Ivey and Scheuering 1997). Unlike most wetland birds, cranes nest in aquatic habitats, but raise young in terrestrial habitats where colts are at greater risk of predation by mammals. Coyotes (*Canis latrans*) are a major predator of crane colts in the western U. S. (Littlefield 1976, 1995). Predator reduction has been a method used to reduce livestock depredation across the western U.S. (Berger 2006). To a lesser extent, predator removal has been used to benefit game and other wildlife populations. Predator removal has been credited with increased nest success (Drewien and Bouffard 1990, Littlefield 2003) and increased recruitment of cranes (Littlefield 2003). The impact of predator removal on crane recruitment may, however, vary among years (Drewien and Bouffard 1990), presumably being influenced by weather that affects availability of food (Quale 1976) and abundance of alternate prey. Drewien and Bouffard (1990) found predator removal enhanced colt survival in years with abundant supplies of water and food, but little impact during years when these factors were limited.

Sibling competition has been suggested as an additional source of mortality of crane colts (Drewien 1973, Quale 1976). Miller (1973) hypothesized sibling competition as the primary explanation for the fact that cranes typically lay 2 eggs, but rarely fledge >1 young. Few researchers have directly observed aggressive behavior between wild sibling colts (Drewien 1973, Walkinshaw 1973). After intensive observations, Layne

(1982) failed to detect sibling competition in wild Florida sandhill cranes (*G. c. pratensis*). Quale (1976) observed aggression between crane colts that decreased with age and was mediated by food, but observations were performed in an artificial setting, which may not reflect behavior in the wild. Impacts of sibling competition on colt survival have not been rigorously evaluated in a natural setting.

Our objectives were to estimate daily survival rates and pre-fledging success of crane colts in northeastern Nevada, and evaluate factors affecting colt survival. Because of reported prevalence of sibling competition in cranes, we hypothesized survival would be negatively correlated between siblings. Similar to previous studies of precocial birds, we hypothesized survival would increase with the age of colts (Flint et al. 1995, Colwell et al. 2007, Stafford and Pearse 2007, Fondell et al. 2008). Because predation is the major cause of colt mortality, we hypothesized reduction in predator populations would increase survival. We also hypothesized survival would increase with body size of colts.

STUDY AREA

Our study area encompassed Elko, White Pine, and extreme northern Lincoln Counties in northeastern Nevada, USA (Fig. 2.1). Lands within the study area were primarily owned by the federal government (80%), and to a lesser extent by private landowners (18%) and state government (<1%). For a detailed description of the study area see Chapter 2.

Lower elevation areas in the study area were used primarily for cattle grazing and native hay production in pastures irrigated by geothermal springs and by intermittent mountain streams via diversion ditches. Fieldwork was performed primarily on private ranchlands, and to a lesser extent Ruby Lake National Wildlife Refuge (NWR) and State Wildlife Management Areas.

METHODS

Field Methods

We searched for nests of cranes in flood-irrigated hayfields and pastures containing grasses (*Poa spp.*), rushes (*Juncus spp.*), and sedges (*Carex spp.*) in northeastern Nevada from early April to early July in 2009 and 2010. We focused our search efforts for nests in areas where cranes were present and signs of breeding (i.e., lone individuals or individuals agitated by our presence) were observed. We located active crane nests during searches on foot ($n = 120$ nests), helicopter ($n = 37$) and fixed-wing aircraft ($n = 28$) surveys, remote observations using spotting scopes or binoculars ($n = 18$), and canoeing ($n = 3$). We monitored nests near the expected hatch dates to capture and radio-tag colts in conjunction with a nest survival study.

We projected hatch dates using flotation of each egg in the clutch and assuming an average incubation period of 30 days (30.2 ± 0.19 d, Drewien 1973). We floated each egg in the clutch during each nest visit to refine estimates of incubation stage and hatch dates. We captured colts when they were present during a nest visit and after all viable eggs hatched. We assumed eggs hatched at 1-day intervals (Drewien 1973, Walkinshaw 1973).

We also captured colts incidental to nest searches when crane pairs displayed parental behavior (i.e., wing display or guard call). We inspected crane pairs for colts using spotting scopes and binoculars from vehicles and elevated viewing areas from mid-May through late August. We searched similar habitats as those searched for nests, but also searched upland habitats containing sagebrush (*Artemisia spp.*), greasewood (*Sarcobatus spp.*), and rabbitbrush (*Chrysothamnus spp.*) near crane pairs known or

presumed to accompany colts. We captured flightless colts on foot using a two-member crew, with an observer monitoring colt movements and communicating locations to a pursuer via hand-held radio. After ≤ 20 minutes of unsuccessful searching, we hid in dense vegetation and waited for parents to call and release colts from hiding. To avoid abandonment, we spent < 30 minutes per pair actively searching for colts.

For each colt, we measured diagonal tarsus length and weight using dial calipers (± 0.1 mm for measurements ≤ 150 mm), cloth tapes (± 10 mm for measurements > 150 mm), electronic scales (± 1 gm for mass ≤ 2 kg), and spring scales (± 10 gm for mass > 2 kg). We recorded Universal Transverse Mercator (UTM) coordinates of the capture location using a hand-held Global Position System (GPS). We attached 3-gm (2009) or 5-gm (2010) VHF (Advanced Telemetry Systems, Isanti, MN) radio transmitters to colts' backs using 2 non-absorbable sutures. Heavier transmitters in 2010 included a mortality switch with longer battery life. We monitored colts approximately twice weekly using a handheld Yagi antenna and a receiver (ATS, Isanti, MN) by foot, vehicle, or fixed-wing aircraft. Approximately once weekly, we captured colts to record weights and measurements. When colts were ≥ 3 weeks old, we recaptured them and placed 3.2 cm tall, white, PVC leg bands with blue, 2-digit, alpha-numeric codes above the left tibio-tarsal joint and we removed sutured transmitters and epoxied transmitters to PVC leg bands. We also placed U. S. Geological Survey (USGS) aluminum bands on the right leg.

Spatial Data

Landscape-scale data.—We analyzed the importance of different habitat types for colt survival using land cover data derived from the Southwest Regional Gap Analysis Project (SWReGAP). We employed land cover types: open water, North American arid West emergent marsh (hereafter marsh), Great Basin foothill and lower montane riparian woodland and shrubland (hereafter riparian), inter-mountain basins semi-desert grassland (hereafter grassland), and agriculture (USGS National Gap Analysis Program 2004). Open water was defined as water bodies with <25% vegetation or soil cover. Marsh was frequently or continually inundated by water and contained >80% vegetation cover. Riparian areas had >20% vegetative cover of forest or shrubland and periodically saturated soil or substrate. Grassland was sparse to moderately dense herbaceous layer dominated by medium-tall and short bunch grasses, often in a sod-forming growth, on lowland and upland areas. These areas were often flood-irrigated for hay production or pasture. Agriculture consisted of center-pivot irrigated crops and some hay fields. We extracted center-pivot irrigated land cover from the agriculture data layer and combined remaining agriculture, consisting primarily of hay fields, and grassland land cover to create a meadow habitat type. To assess anthropogenic impacts on nest survival, we extracted named roads from Bureau of Land Management's road network data layer to identify primary or regularly-traveled roads.

We employed a Geographical Information System (GIS) using ArcMap to help characterize spatial aspects for our landscape-scale analysis. We calculated distance to nearest roads using ArcGIS. We analyzed habitat types at radii within 500 m (79 ha) of colt locations during capture events. Because proportion of habitat types and distance to roads varied through time, associated with colt movements, we treated habitat variables

as time-varying covariates for which we constrained values to be constant from one capture event to the day prior to the subsequent capture.

Weather data.—We gathered weather data from Remote Automated Weather Stations (RAWS) and Natural Resource Conservation Services' SNOTEL sites through MesoWest, and National Weather Service's Cooperative weather stations through the National Climate Data Center. We collected daily minimum temperature, daily maximum temperature, and daily precipitation for each colt from the nearest weather station with available data. We estimated daily weather values for 24-hr periods ending at 0800.

Data Analysis

Growth model.—To estimate age of colts with unknown hatching dates and estimate body size, we created generalized linear models to describe crane colt growth using program R (Faraway 2006). We randomly sampled one capture record for each colt to be used in model development ($n = 48$). Because growth is typically sigmoidal from hatch to fledging, we developed generalized linear models predicting colt age as a quadratic or a cubic function of tarsus length. We used the same dataset to develop a tarsus regression equation that estimated tarsus length as a function of age for known-age colts. We calculated residuals from our tarsus regression equation as a measure of relative body size for known-age colts and set values of tarsus residuals to the mean value for unknown-age colts.

Sibling fate independence.—We assigned the date of colt mortality as the midpoint between the date last known alive and the date first recorded as dead. We estimated correlation between siblings time of death using program R.

Colt survival.— To estimate the effect of predator reduction, we classified colts according to landownership status. We classified colts located on lands owned by the state government or private citizens into one group because predator control was permitted and commonly practiced on these areas. We separately classified colts located on Ruby Lake NWR because active management of predator populations was not practiced (J. Mackay, Ruby Lake NWR, personal communication).

We estimated daily survival rates of colts using the nest-survival module in Program MARK because exact date of mortality was not known for all colts (White and Burnham 1999). We censored encounter histories of colts with undetermined fate at the time when colts were last known alive. We used an information-theoretic approach to evaluate support for competing models (Burnham and Anderson 2002) by ranking models using Akaike's Information Criterion, adjusted for small sample size (AIC_c), and by calculating AIC_c model weights (Burnham and Anderson 2002).

We used the best-approximating model from our a priori model set to assess potential impacts of investigator disturbance caused by capture and handling. We initially developed three models to investigate handling effects and duration of the effect on colt survival: an effect that occurred shortly (1-day) after handling, and an extended effect that lasted either 4-days or 9-days posthandling and declined linearly with time. To the best-supported handling-effect model, we tested for dependency of a handling effect on colt age by adding an interaction term between handling effect and age of colt.

We model-averaged parameter estimates for models $< \Delta 4 AIC_c$ units from the best-supported model. We estimated importance of specific variables using AIC_c sums of model weights containing that variable ($\sum w_i$; Burnham and Anderson 2002). We

calculated fledging success by multiplying daily survival rates of colts over the first 71 days of life (mean age at midpoint of last interval for fledged colts = 71.1 ± 2.1 days, $n = 4$; C. W. August, unpublished data). Estimates are reported as mean \pm SE.

RESULTS

We monitored 101 colts in northeastern Nevada, USA during 2009-2010; 40 colts in 2009 and 61 colts in 2010. Of 32 colts with known fates in 2009, 12 fledged (38%). Of 56 colts with known fates in 2010, 10 fledged (18%). We monitored colts located on private ranches ($n = 83$), state wildlife management areas ($n = 5$), and on Ruby Lake NWR ($n = 13$).

Age of colts was best explained as a cubic function of tarsus length {adjusted $r^2 = 0.98$, $F_{3,44} = 723$, $P < 0.001$ [AGE = $-22.02 + 0.6529 \times (\text{TARSUS}) - 0.003637 \times (\text{TARSUS}^2) + 0.0000086 \times (\text{TARSUS}^3)$] Fig. 3.1}. Additionally, tarsus length was explained as a cubic function of age {adjusted $r^2 = 0.98$, $F_{3,44} = 998$, $P < 0.001$ [TARSUS = $42.56 + 2.64 \times (\text{AGE}) + 0.11 \times (\text{AGE}^2) - 0.0015 \times (\text{AGE}^3)$]}. Timing of death between siblings was positively correlated (Pearson correlation = 0.54, $P = 0.017$, $n = 19$).

The best performing model of temporal variation constrained colt survival as a quadratic function of age. Weather variables were not competitive with other time-dependent variables. We constrained further models to contain a quadratic trend on colt age. Also, land cover types did not improve our temporal model, and therefore were not incorporated into further modeling.

Within our a priori model set, we found substantial support for an effect of federal versus state or private landownership ($\sum w_i = 0.99$) and an interaction between relative

body size and age of colt ($\sum w_i = 0.98$) (Table 3.1). We found moderate support for differences in colt survival related to year ($\sum w_i = 0.65$).

Model-averaged variables important (i.e., 85% confidence intervals did not overlap zero) for colt survival included year ($\beta = 0.66 \pm 0.33$), additive effect of private and state versus federal ownership ($\beta = 1.14 \pm 0.41$), a linear trend on colt age ($\beta_{\text{AGE}} = 0.064 \pm 0.037$), an interaction between relative body size ($\beta_{\text{BODY}} = 0.92 \pm 0.39$) and colt age ($\beta_{\text{BODY} \times \text{AGE}} = -0.03 \pm 0.01$), an interaction between a handling effect ($\beta_{\text{HANDLING}} = 4.13 \pm 2.74$) and colt age ($\beta_{\text{HANDLING} \times \text{AGE}} = -0.10 \pm 0.054$), and a 4-day handling effect ($\beta_{\text{HANDLING-4d}} = 0.54 \pm 0.36$).

We found daily survival rates of colts and probability of survival through the 71-day pre-fledging period were lower on federal lands [fledging success = 1% (95% CI = <1 – 12%) in 2009, <1% (95% CI = <1 – 6%) in 2010] than private or state lands [fledging success = 25% (95% CI = 6 – 50%) in 2009, 15% (95% CI = 3 – 33%) in 2010] (Fig. 3.2).

DISCUSSION

We found colt survival was lower on Ruby Lake NWR versus state or private lands, despite high nest success (C. W. August, unpublished data) and abundance of marsh and wet meadow habitat found at Ruby Lake NWR. Therefore, we believe observed differences in survival was primarily related to differences in management of predator populations. In 1984, predator management ceased on Ruby Lake NWR. During 1986-1993, no colts fledged from an average annual population of 15 breeding pairs (J. Mackay, unpublished report). Reduction in the size of a local breeding population of cranes has been observed in areas with persistently low recruitment (Littlefield 1995, J.

Mackay, personal communication). Abundant populations of generalist predators, such as coyotes, may exhibit predation that is inverse density-dependent predation, whereby predation exceeds recruitment, which can lead to extinction of prey populations (Sinclair and Pech 1996). In the arid intermountain west, maintenance of wetland or mesic habitats that are attractive to waterbirds may create sink habitats because predators respond numerically to the increased number of nests such habitats create (Hartman and Oring 2009). Future studies that manipulate predator populations are needed to assess the role of predation in population regulation of cranes before implementing predator management programs. Additionally, we suggest caution with species-specific predator control because compensatory predation may occur (Drewien and Bouffard 1990, Littlefield 2003, Ivey and Dugger 2008).

We found time of death between siblings was not independent, but positively related. Survival decreased rather than increased after the death of a sibling. Our findings fail to support sibling competition as a major mortality factor for cranes. Alternatively, our findings suggest extrinsic factors shared by both colts in a brood such as weather, food, or predation were more important determinants of colt survival in our study. This is further supported by data showing annual variation in brood size is strongly related to annual variation in recruitment rates among several populations of cranes (Drewien et al. 1995). This is to be expected because long-lived birds often live in stochastic environments, in which reproduction during years of favorable conditions is essential for population maintenance (Erikstad et al. 1998). Strong correlation between siblings' survival is consistent with our frequent observations of either whole brood loss or whole

brood success and provides further support of predation as a major factor limiting survival for crane colts in northeast Nevada.

Consistent with previous studies, we found mortality was greatest early in development. We regularly observed nests in which two eggs hatched, but only one or no colts were found shortly after the expected hatch date. We suspect colts are particularly vulnerable to mammalian predation immediately following hatch as colts move from aquatic to terrestrial habitats. We suggest future studies examine factors that may affect predators' ability to detect younger, less mobile colts, such as vegetation cover surrounding nests. We also found body size to be important to survival, but only for young colts. This may result from 1) underweight colts being removed by selection early in development, resulting in decreased variation in size as age increased, or 2) high quality parents compensating for underweight colts by moving young into high quality habitats, resulting in body size at early ages being a poor predictor of survival at later ages.

We failed to find variation in survival within a season. Higher survival for earlier hatched young has been demonstrated for other precocial birds including ducks (Amundson and Arnold 2011), geese (Fondell et al. 2008), and sarus cranes (*Grus antigone*; Sundar 2009). A narrow range of hatch dates may have limited our ability to detect time-dependent variation in survival. Unlike many wetland birds, however, young cranes are highly mobile and may not be as impacted by changing habitat conditions. We observed crane families use upland habitats more frequently during dry periods or after disturbance from haying, handling events, or predators. Also, we did not find a relationship between habitat use and colt survival, but inferences are limited because of

the resolution of available spatial data and our assumption of constant habitat type between encounter occasions. Future studies should investigate impacts of haying on movements and survival of colts.

We found survival to be higher during 2009 than 2010. However, the brood-rearing period (May-August) was drier in 2009 [Palmer Drought Severity Index (PDSI) = -2.25] than 2010 (PDSI = -0.92). Also, radio transmitters were slightly lighter during 2009 (3 g) than 2010 (5 g), which may have contributed to observed differences in survival between years. We were unable to address this confounding relationship.

MANAGEMENT IMPLICATIONS

Our findings indicate predation was a major factor limiting colt survival during our study. For the Nevada breeding portions of the LCRV population of cranes, we suggest active management of predator populations during the brood-rearing period in areas where recruitment is below levels required for population maintenance. However, future investigations that manipulate predator populations are needed to assess the role of predation in population regulation of cranes before implementing predator management programs. Survival of colts is particularly low during early development and nutrition during this period is important for fledging success.

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Table 3.1. Model selection results for factors affecting survival of greater sandhill crane colts in northeastern Nevada, USA, 2009-2010.

Model ^a	ΔAIC_c ^b	Model wt	No. params	Deviance
Handling-effects model set				
AGE ² + YR + OWN + BODY × AGE + HANDLE × AGE + HANDLE _{4d}	0.0	0.56	11	305.9
AGE ² + YR + OWN + BODY × AGE + HANDLE × AGE + HANDLE _{4d} × AGE	1.7	0.24	12	305.7
AGE ² + YR + OWN + BODY × AGE + HANDLE × AGE	4.4	0.06	10	312.4
AGE ² + YR + OWN + BODY × AGE + HANDLE + HANDLE _{4d} × AGE	3.8	0.09	11	309.7
AGE ² + YR + OWN + BODY × AGE + HANDLE + HANDLE _{4d}	6.5	0.02	10	314.5
AGE ² + YR + OWN + BODY × AGE	7.5	0.01	8	319.5
AGE ² + YR + OWN + BODY × AGE + HANDLE	7.8	0.01	9	317.8
AGE ² + YR + OWN + BODY × AGE + HANDLE _{9d}	9.4	0.01	10	317.4
A priori model set ^c				
AGE ² + YR + OWN + BODY × AGE	0.0	0.63	7	319.5
AGE ² + OWN + BODY × AGE	1.3	0.33	6	322.8
AGE ² + YR + OWN	7.5	0.01	5	331.0
AGE ² + BODY × AGE	8.5	0.01	5	332.0
AGE ² + YR + BODY × AGE	9.5	0.01	6	331.0
AGE ² + OWN	11.0	0.00	4	336.5
AGE ² + YR	17.6	0.00	4	343.1
AGE ²	18.4	0.00	3	345.9

^aAGE² = quadratic trend on colt age, YR = 2009 versus 2010, OWN = state/private versus federal landownership, BODY × AGE = interaction between relative body size and age of colt, HANDLE = Handling effect on day of capture or extended handling effect that declines 4-d (HANDLE_{4d}) or 9-d (HANDLE_{9d}) posthandling, HANDLE_{4d} × AGE = interaction between extended 4-d posthandling effect and age of colts.

^bDifference in Akaike's Information Criterion adjusted for small sample size (AIC_c) from top model.

^cAIC_c of best a priori model = 333.5.

Figure 3.1. Length of tarsus related to age of greater sandhill crane colts in northeastern Nevada, USA, 2009-2010.

Figure 3.2. Daily survival rates of greater sandhill crane colts on non-federal and federal lands in northeastern Nevada, USA, during 2009 and 2010.

Figure 3.1.

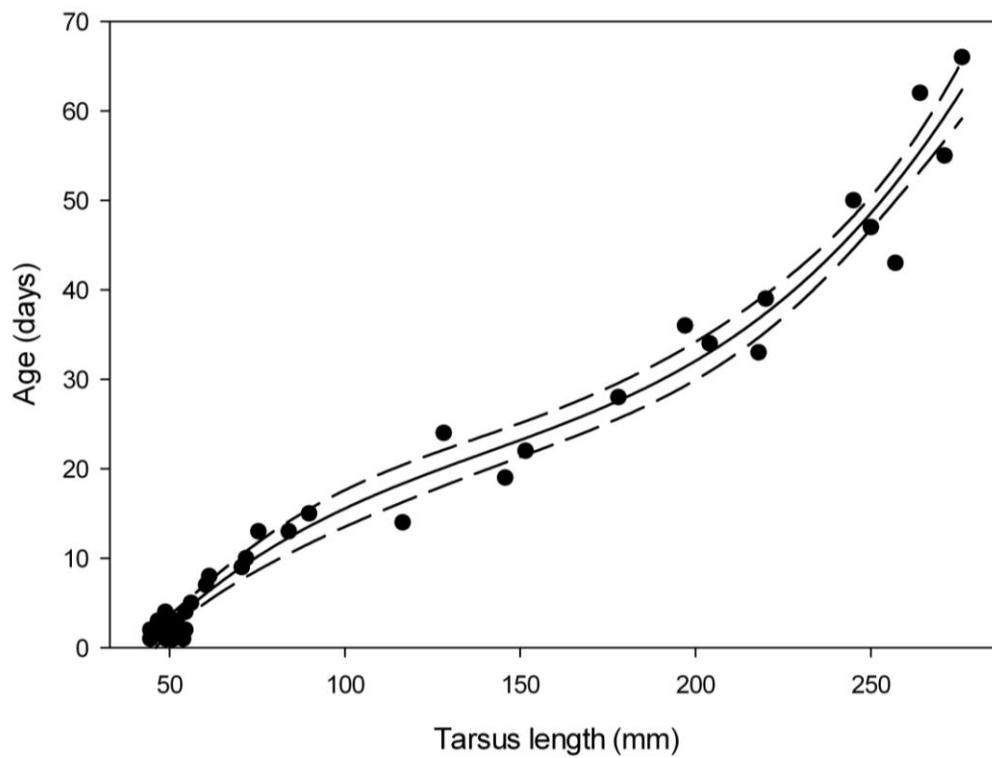
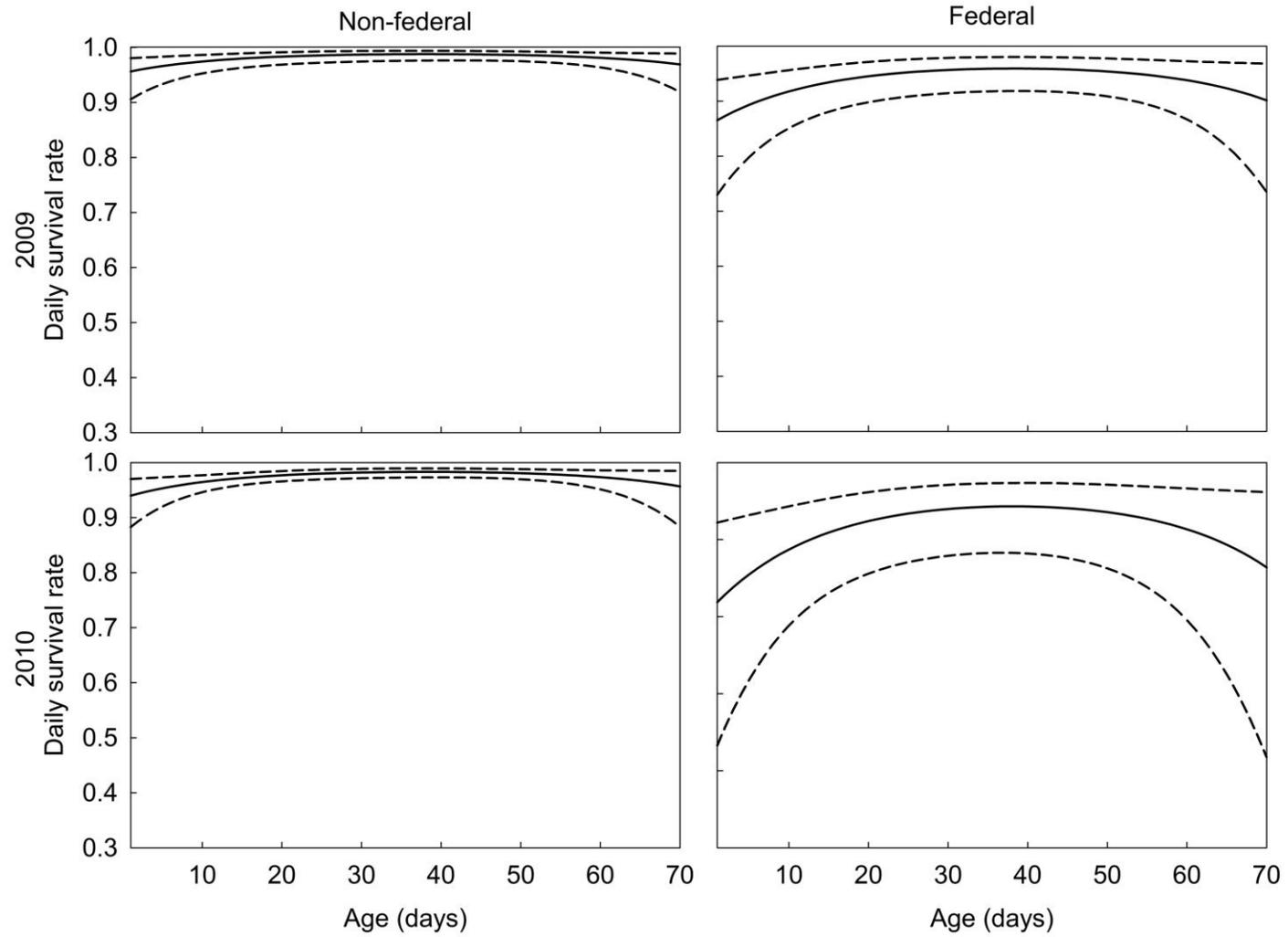


Figure 3.2.



CHAPTER 4.

CONCLUSION

We examined two components, nest survival and chick survival, that contribute to recruitment and therefore population growth for greater sandhill cranes breeding in northeastern Nevada, USA. We monitored 161 nests and 101 chicks during 2009-2010.

For the second chapter, we found higher daily survival rates (DSR) for nests located closer to roads, which we believe represents avoidance of roads by predators within the study area. Nest survival was negatively related to density of cranes, which was likely correlated with habitat productivity and abundance of predators. We also found vegetation height was more important for survival than water depth surrounding nests, indicating that visual predators such as birds may play a greater role than mammals as predators of eggs. Although we failed to find impacts of haying on nest survival we found some support for a negative impact of summer grazing on DSR. Future research is needed to examine any possible impact of grazing on nest survival of cranes. We recommend that managers encourage landowners to conserve wet-meadow habitat containing tall vegetation to enhance nest survival of cranes.

In the third chapter, DSR of crane chicks (i.e., colts) located on Ruby Lake NWR, where predator management was not practiced, was lower than those located on private or state lands, where predator management was common. Additionally, we found time of death between siblings was positively related, indicating that sibling competition was not a major mortality factor for colts. Alternatively, our findings suggest extrinsic factors

shared by both colts in a brood, such as local predators, were important sources of colt mortality in our study.

Collectively, our results indicate that predation is a major factor limiting survival of nests and colts and contributing to low recruitment for cranes in northeastern Nevada. In the arid intermountain west, predators may respond numerically to the abundant prey that mesic habitats support, resulting in high levels of predation where cranes breed. For the Nevada breeding portions of the LCRV population of cranes, we suggest active management of predator populations in areas where recruitment is below levels required for population maintenance. However, future investigations that manipulate predator populations are needed to assess the role of predation in population regulation of cranes before implementing operational predator management programs.