Factors Influencing Nest Success of Greater Sandhill Cranes at Malheur National Wildlife Refuge, Oregon

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Abstract.—We used logistic regression to model the effects of weather, habitat, and management variables on Greater Sandhill Crane (*Grus canadensis tabida*) nest success at Malheur National Wildlife Refuge in southeast Oregon. We monitored 506 nests over 9 breeding seasons. Mean apparent nest success was 72% ± 4% and varied from 51 to 87%. Nest success was lower one year after a field was burned and declined with nest initiation date. Nest success was higher during warmer springs, in deeper water, and in years with moderate precipitation. Haying, livestock grazing, and predator control did not influence nest success. We suggest the short-term consequence of burning on nest success is outweighed by its long term importance and that water level management is the most important tool for managing crane nest success. Finally, studies of brood ecology are needed to develop a more complete picture of crane nesting ecology. *Received 18 March 2007, accepted 20 August 2007.*

Key words.—breeding ecology, *Grus canadensis tabida*, land management, Oregon, predator control, Sandhill Crane, weather.

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The Greater Sandhill Crane (*Grus canadensis tabida*) is one of six subspecies of Sandhill Crane in North America (Tacha *et al.* 1992). Historically this subspecies bred in suitable wetland sites throughout the Intermountain West. However, populations declined and the breeding distribution became contracted and fragmented due to the pressures of human settlement (Walkinshaw 1949). Because of these historic declines, the Greater Sandhill Crane was listed as endangered in Washington in 1981, threatened in California in 1983, sensitive in Oregon in 1989, and a British Columbia Blue List species in 1998.

The breeding biology of all cranes is characterized by delayed maturity, long-term monogamy, annual breeding, small clutch size, and extensive pre- and post-fledging parental care (Tacha *et al.* 1989; Drewien *et al.* 1995). These demographic factors result in naturally low recruitment that limits the species' ability to recover from declines (Tacha *et al.* 1992). Recruitment rates of the three populations of Greater Sandhill Cranes that breed in the Intermountain West (Central Valley, Lower Colorado River Valley and Rocky Mountain) are among the lowest for North American cranes and are believed to be the major factor limiting population growth (Drewien *et al.* 1995). Low recruitment has primarily been attributed to predation of nests and prefledged young (Littlefield 2003). Thus, there is a need to identify factors that contribute to variation in these vital rates (Tacha *et al.* 1994).

Factors reported to influence nest success include, water depth at the nest (Littlefield 1995a; Littlefield 2001), vegetation type around the nest (Littlefield and Ryder 1968; Drewien 1973; Littlefield 1995b), nest concealment (Littlefield 1995a) and, to a lesser extent, land use practices (Littlefield and Paullin 1990; Littlefield *et al.* 2001). A few studies have suggested that weather influences reproductive success (Littlefield 1976; Drewien *et al.* 1995); however, an analysis of weather factors has not been conducted. Presumably, weather features influence nest detection and access by predators and nest attentiveness by adults. The relative importance of factors may vary regionally. For example, land use practices were reported to affect nest success in Oregon (Littlefield and Paullin 1990) but not in Idaho (Austin *et al.* 2007). Differences may reflect regional or temporal variation in the relative importance of each factor; however, differences in methodologies and analytical technique make direct comparison between studies difficult.

The effect of land use practices is particularly important as a large percentage of intermountain west Sandhill Cranes nest on private lands in flood-irrigated hay meadows that are hayed and grazed by livestock (Littlefield *et al.* 1994). Spring grazing can contribute directly to nest losses due to trampling of nests by cattle and by disturbance from cattle that can cause abandonment (GLI, pers. obs.). Indirectly, grazing, burning and haying may lower nest success by reducing nest cover thereby making nests easier for predators to detect (Littlefield and Paullin 1990). Predation is the most common source of nest loss, while predator control is a controversial management tool that has been used in efforts to increase reproductive success of cranes (Drewien *et al.* 1985; Littlefield and Cornely 1997; Littlefield 2003). Predator control has been credited with increasing Sandhill Cranes nest success (percentage of nests in which at least on egg hatches; Littlefield 2003); however, the importance of predator control relative to habitat characteristics and management practices remains unclear because no study has simultaneously included these factors in the same analysis.

Malheur National Wildlife Refuge (NWR) is the most important breeding site for the Central Valley Population of Greater Sandhill Cranes (Littlefield *et al.* 1994), supporting 245 pairs in 2000 (GLI, unpubl. data). Similar to private ranchlands in the intermountain west, wetland habitat management at Malheur NWR includes the use of haying, grazing and controlled burning. In this paper, we use data from nine breeding seasons to estimate Greater Sandhill Crane nest success, determine the relative importance of the effects of weather, nest site, landuse and predator control and compare trends in success from earlier studies at Malheur NWR (Littlefield 2003).

METHODS

Study Site

Malheur NWR is a 75,000 ha oasis of extensive freshwater marshes, flood-irrigated meadows, and large lakes within the intermountain arid shrub-steppe landscape of the northern Great Basin in southeastern Oregon (Fig. 1). Most cranes nest in the 25,000 ha Blitzen Valley and 7,600 ha Double-O units where habitats are intensively managed using flood irrigation, haying, cattle grazing and prescribed fire. Wetland habitats at Malheur NWR are largely dependent on melting snow packs from Steens Mountain (Blitzen Valley units) and the Blue Mountains (Double-O unit). The study area was divided into a set of fenced fields which included meadow and marsh habitats and served as habitat management units.

Data Collection

During 1990-1998, we searched for nests from early April through early June on foot (~95% of nests found) and from fixed-winged aircraft (~5%). Both fidelity to nesting territory (Littlefield and Ivey 1995) and adult survival of Sandhill Cranes are high (Drewien 1973; Tacha *et al.* 1992); consequently, the location of most crane territories was known before nest searching began each year. We located nests by searching a sample of territories until we found either an active or inactive nest (Littlefield 2003). When found, each nest platform was recorded as active (egg laying or incubating, hatched [at least one egg]), failed (destroyed or abandoned), or inactive. Inactive nests were platforms located before egg laying. These were revisited and if they were later active or had failed they were included the sample. We identified failed nests as those with evidence of broken or missing eggs at the nest. Successful nests were determined from the presence of egg membranes in the nest, while active nests contained undeveloped or warm incubated eggs and abandoned nests contained cool but developed eggs (Littlefield 1995a). For each active nest, we floated eggs to estimate incubation stage (Westerskov 1950; Fisher and Swengel 1991), which allowed estimation of initiation and hatching dates. We revisited active nests after the estimated hatch date to determine nest fate. Thus, each nest was visited no more than twice each year to minimize disturbance which can lead to nest abandonment (GLI, pers. obs.).

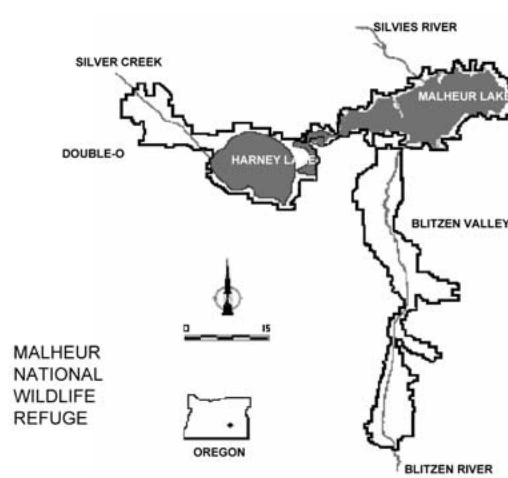

Figure 1. Breeding Greater Sandhill Cranes (*Grus canadensis tabida*) were studied at Malheur National Wildlife Refuge in southeastern Oregon.

In addition to information on nest fate, we collected data on habitat characteristics at the nest and on land use practices in the field where the nest was located. We recorded dominant vegetation within one meter of the nest (cattail, burreed, bulrush or meadow), water depth (cm), nest concealment based on an ocular estimate of how many sides of the nests were obscured from view (0, 1, 2, 3 or 4) at a distance of 3 m, and shortest distance to a change in plant community (as an index of nest isolation) at each nest. Vegetation at the nest site provides concealment, but is also related to water depth. We characterized surrounding land-use as hayed, cattle grazed, burned, or idle. Haying of upland meadows occurred in late summer (after 10 August) after all crane nests had hatched, and livestock grazing occurred from October through December. Grazed fields were first hayed and hay was raked into piles for winter cattle grazing. Consequently, the management practice applied the year prior to nest initiation was used when modeling nest success. Controlled burns primarily occurred in fall and early spring; wildfires usually occurred in summer. Fields not subject to any of these practices were categorized as idle.

Control of Coyotes (*Canis latrans*), Raccoons (*Procyon lotor*) and Common Ravens (*Corvus corax*) occurred annually at Malheur NWR during 1986-1993 while no predator control occurred during 1994-1998. The impact of predator control on relative predator density was not measured; however, during the predator control years, 1,800 Coyotes, 113 Raccoons and an estimated 503 ravens were removed from the study area (GLI, unpubl. data).

Analyses

We calculated apparent nest success (100 × no. nests with at least one egg hatched/total no. nests with known fates) for each year. Reporting apparent nest success is appropriate if nest detection is independent of nest fate (Johnson and Shaffer 1990), an assumption generally met for cranes that have large, visible nests. We plotted nest success by year over the 32 year period (1966-1998) for which apparent nest success estimates were available to look for trends in nest success in the Malheur NWR population. Estimates for 1966-1989 came from Littlefield (1976) and Littlefield (1995b). When visual inspection suggested a linear trend, we fit a line to the data using general linear modeling techniques.

We used logistic regression (SAS Institute, Inc. 2002) to determine factors that influenced nest success (Hosmer and Lemeshow 2000). The dependent variable in our analyses was nest fate (0 = failed, 1 = successful). We developed a list of explanatory variables based on earlier crane work (Littlefield 1976; Littlefield and Paullin 1990; Littlefield 2003; Austin *et al.* 2007) and personal experience that included predator control (CONT), land-use type (LU), dominant vegetation at the nest (VEG: hardstand bulrush [*Scirpus acutus*], cattail {*Typha* spp.], broad-fruited burreed [*Sparganium eurycarpum*], and meadow [grasses and sedges]), nest concealment (CONC: calculated as the number of sides of the nest concealed from a distance of 3 m), distance to habitat edge (EDGE), water depth (WAT) as well as water supply and weather factors.

We fit generalized linear mixed models with a binomial response distribution and the logit link function and used model weights (w_i) and AIC*c* values along with an information theoretic approach to compare support among competing models (Burnham and Anderson 2002). We considered models within two AIC values of the best model competitive. While evaluations of β's and odds ratios provide the same results, we chose to use odds ratios to examine the strength of each variable because they are widely used in logistic regression and are a useful measure of effect size. Percent change in the odds of nest survival for each one-unit change in an independent variable was calculated by subtracting one from the odds ratio and multiplying this value by 100.

While we hypothesized that annual water supply, temperature and precipitation likely influenced nest success but there were several options for measuring each, some of which were correlated (GLI, unpubl. data). We suspected that low water supplies might cause birds to spend more time feeding and less time in nest attendance and that high water supplies can lead to increased incidences of nest loses to flooding. Also, cranes seem to be more likely to abandon nests during periods of bad weather (GLI, pers. observ.). Rather than including all variables in the final model set, or arbitrarily selecting one measure, we modeled the influence of all potential temperature, precipitation and water supplies variables, chose the best covariate from each climate category using AIC*c* and model weights, and included the best measure in our final model set.

We modeled two measures of water supply, the March Palmer Drought Index (PDI) and annual peak snow water equivalent index (SNO). We hypothesized that nest success might be lower under extreme conditions (both wet and dry), thus we included both the linear and quadratic function for both variables. We modeled three measures of temperature (average low temperature, number of nights below freezing, and the average temperature of the three coldest consecutive nights during April and May) and six measures of precipitation (total precipitation in April [cm], total precipitation in May, April + May precipitation, and total days of precipitation in April, May, and April + May). We used National Oceanic and Atmospheric Administration (NOAA) Oregon Zone Seven for PDI data, Natural Resource Conservation Service's Fish Creek Snotel site on Steens Mountain for SNO data, and Oregon Climate Service's summary of NOAA's National Weather Service Cooperative Observer Program data from the south end of the Blitzen Valley for temperature and precipitation. For twelve missing data points, we substituted data from the nearest weather station.

Our final model set included most combinations of one, two and three-factor additive models (89 models). We did not hypothesize any interaction effects *a priori* and did not include potential confounding variables in the same model (e.g., vegetation type which is influenced by water depth) or year with other annual variables (predator control, water supplies, or temperature and precipitation during nesting season). We could not calculate initiation date for all nests (e.g., those found already failed or hatched); therefore, we did not include nest initiation date in our initial modeling. We assessed the influence of initiation date in a secondary modeling exercise, using the subset of nests with initiation dates (n = 380) and the explanatory variables that occurred in competitive models of the entire data set and evaluated one, two, three and four factor models.

We calculated variable importance weight, a measure of the relative importance for each variable, by summing model weights for all models containing that variable (Burnham and Anderson 2002). We used estimates of slope coefficients (ß), odds ratios, and their

95% confidence intervals to assess direction, magnitude, and reliability of relationships (Hosmer and Lemeshow 2000; Burnham and Anderson 2002) and we reported Nagelkerke's R^2 as a measure of model performance (Nagelkerke 1991). We calculated model-averaged point estimates to account for model selection uncertainty and provide a more robust estimate of the effect of each variable on nest success and generated odds ratios using the model-averaged coefficients. We calculated model-averaged coefficients as the sum of coefficients multiplied by AIC weights (w_i) and used zero for a coefficient when a model did not contain the explanatory variable; thus, model-averaged coefficients represented the contribution of the explanatory variable across the entire set of candidate models (Burnham and Anderson 2002). We generated model-averaged odds ratios by calculating unconditional variance estimators for each model-averaged coefficient (Burnham and Anderson 2002) and converted these coefficients and their standard errors to odds ratios and corresponding CIs (Hosmer and Lemeshow 2002).

RESULTS

Our sample included 506 nests found over nine years (1990-98; Table 1); 75% of nests were active when found, 16% had hatched and 9% had failed. We excluded eight nests from the analysis that we believe failed because of researcher disturbance. The majority of nests were in marsh vegetation types (88%); median water depth at nests was 25 cm (range 0-100 cm). Snow pack levels were below normal during the first four years, near normal during the fifth year, and above normal during the last four years. The mean palmer drought index was -1.3 during the study (range = -6.10 to 3.17). Temperatures varied considerably among years; the coldest nest season temperatures (three-day average) ranged from -8.3 to -1.5°C. For 380 nests with initiation data, the mean initiation date was 19 Apr. (range 22 Mar. to 31 May). The yearly median initiation date ranged from 10-25 April. Apparent nest success averaged 72.4 ± 3.9% (range = 51 to 87%); of nests that failed, 69% were destroyed by predators and 31% failed due to factors such as flooding, abandonment and addled eggs (dead embryos; determined from actively incubated eggs). From 1966-1998, apparent nest success of Sandhill Cranes at Malheur NWR has steadily increased (1.2% per year, $P < 0.001$; $R^2 = 0.47$; Fig. 2).

Our initial modeling of weather and water supply covariates revealed that the best single-factor weather model for temperature was the coldest three-day period (COLD, w_i = 76%). The mean-centered quadratic Palmer Drought Index (PDIQ) was the best water supply covariate and the second best single variable model overall ($\Delta AICc$ = 2.9, w_i = 18%). Total precipitation in April and May (TP) was the best precipitation variable; however, it received much less support than the intercept only model ($\Delta AICc$ = 12.6, w_i = 1%). Consequently, we included COLD and PDIQ in our analyses with habitat variables.

Only one multivariate model received substantial support (w_i = 0.50) as a predictor of nest fate and included the variables LU, COLD and WAT (Nagelkerke's R^2 = 0.11; Table 2). Variable importance weights indicated strongest support for the effects of LU, followed in descending order by COLD and

Table 1. Sample size (n) and fates (%) of Greater Sandhill Crane (*Grus canadensis tabida*) nests monitored at Malheur National Wildlife Refuge, Oregon, 1990-98.

		Nest fate				
Year	n	Successful	Depredated	Flooded	Abandoned	Other[a]
1990	59	85	10	0	3	2
1991	77	51	26	10	5	8
1992	55	69	20	0	2	9
1993	62	84	8	3	0	5
1994	50	74	14	3	6	3
1995	61	72	26	2	0	0
1996	53	68	30	0	2	0
1997	50	62	34	0	2	2
1998	39	87	5	3	5	0

[a]Failed due to addled eggs or possibly infertile.

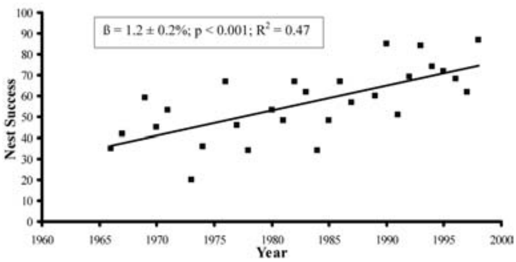

Figure 2. Trend in apparent nest success estimates for Greater Sandhill Cranes (*Grus canadensis tabida*) breeding at Malheur National Wildlife Refuge, 1966-1998 (data for 1966-1989 is from Littlefield 1976, 1995b).

WAT (Table 3). Variables YEAR, PDIQ, CONT, CONC, EDGE and VEG received no support.

Compared to idle fields, nests in fields burned the previous year were 70% less likely to hatch (Table 3). Confidence intervals around the odds ratios for nests in hayed and grazed fields included one, indicating neither practice had a strong influence on nest fate (Table 3). Also, nest success increased with April and May temperatures (COLD) and was higher for nests in deeper water (Fig. 3).

Because burning had the strongest influence on nest success, we conducted an *a posteriori* analysis to investigate the temporal affects of burning. We classified each nest based on time since the field was burned (B_0 = 0 growing seasons post burned, B_1 = 1 growing season post burn, B_2 = 2 growing seasons post burn, and B_3 = 3 growing seasons post burn) and unburned (>3 growing seasons post burn) and re-ran the analysis, substituting each of the burn categories for the land use variable and used unburned as the reference variable for comparisons. Nest success was 55% lower in burned fields the spring after burning (B_0 odds ratio = 0.45 [CI = 0.28-0.74]); however, burning had no influence on nest fate after one season's growth (Fig. 3).

Including nest initiation date (INIT) in our models increased the number of competitive models and the number of explanatory variables that occurred in competitive models (Table 2), but it did not significantly improved their performance (R^2 = 0.11 to 0.13). Along with LU, nest initiation date was included in all five models that were compet-

Table 2. Results of logistic regression analysis to identify factors that influenced nest success of Greater Sandhill Cranes (*Grus canadensis tabida*) breeding at Malheur National Wildlife Refuge, Harney Co., Oregon, 1990-1998. Models ranked according to Akaike's information criterion adjusted for small sample size (AIC*c*). The number of parameters (*k*), ΔAIC*c*, and AIC*c* weights (w_i) are given for all models. Models within two ΔAICc_i values of the best model are considered competitive.

Model structure[a]	*k*	ΔAICc_i	w_i	Nagelkerke's R^2
Full model set; n = 509				
LU COLD WAT	6	0.00	0.502	0.110
LU COLD	5	3.67	0.080	0.095
LU PDIQ WAT	7	3.68	0.080	0.106
NULL	1	30.00	0	—
Initiation model set; n =380				
INIT LU WAT	6	0.00	0.203	0.119
INIT LU	5	0.64	0.147	0.109
INIT LU PDIQ	7	0.92	0.128	0.123
INIT LU PDIQ WAT	8	1.22	0.110	0.129
INIT LU COLD WAT	7	1.31	0.105	0.121
INIT LU COLD	6	2.08	0.072	0.111
INIT LU PDIQ COLD	8	2.34	0.063	0.123
INIT PDIQ	4	2.96	0.046	0.091
INIT PDIQ WAT	5	3.49	0.035	0.098
NULL	1	21.25	0.000	—

[a]LU = land use (idle, hayed, grazed or burned); COLD = lowest 3-day average temperature during nesting season (April and May); WAT = water depth at nest site; PDIQ = mean centered quadratic form of the Palmer Drought Index; YEAR = year nest was active as a categorical variable; EDGE = distance to a change in plant community (a measure of nest isolation). CONT = categorical variable to indicate years when predator control program was ongoing; NULL = intercept only model, INIT = nest initiation date.

Table 3. Summary of variable importance weights and odds ratios for variables occurring in competitive models explaining variation in nest success for Greater Sandhill Cranes (*Grus canadensis tabida*) nesting at Malheur National Wildlife Refuge, Harney Co., Oregon from 1990-98. Values calculated as the summed weights of all models that include the each variable.

Variable code	Variable importance weight	Odds ratio[b]	95% Confidence interval[c]
Full model set; n = 509			
LU: Burn vs. Idle	0.996	0.30	0.15-0.60
Graze vs. Idle		0.92	0.56-1.51
Hay vs. Idle		1.48	0.78-2.75
COLD	0.776	1.10	1.03-1.17
WAT	0.630	1.01	1.01-1.02
Initiation model set; n = 380			
INIT	0.994	0.969	0.952-0.986
LU: Burn vs. Idle	0.739	0.431	0.256-0.725
Graze vs. Idle		1.175	0.807-1.710
Hay vs. Idle		1.587	0.988-2.550
WAT	0.503	1.010	1.006-1.022
PDI	0.416	1.001	0.891-1.125
PDIQ	0.416	0.977	0.940-1.016
COLD	0.300	1.024	1.033-1.223

[a]LU = land use (idle, hayed, grazed or burned); COLD = lowest 3-day average temperature during nesting season (April and May); WAT = water depth at nest site; INIT = nest initiation date; PDI = Palmer Drought Index; PDIQ = mean-centered quadratic form of PDI.
[b]Odds ratios >1 indicate positive relationship; <1 indicate negative relationship.
[c]Confidence intervals not including 1 indicate evidence of effects.

itive and the 15 models which included INIT were ranked in the top 15 models and received some support via model weight. Variable importance weight was highest for INIT, followed by LU, WAT, PDIQ and COLD. The odds ratio confidence intervals for the Palmer Drought Index included 1.0, suggesting a very weak effect (Table 3). Nest success declined 3%/day with increasing initiation date (INIT odds ratio = 0.97).

DISCUSSION

Early initiated nests located at moderate water depths (50-80 cm) during relatively warm springs were most successful. Studies consistently find that water depth influences crane nest success (e.g., Drewien 1973; Littlefield 1995a; Austin *et al.* 2007) indicating its fundamental importance for crane management. Water is a deterrent to many mammalian predators, helping limit access to nests (Arnold *et al.* 1993). The relationship between nest success and water depth also likely explains the influence of annual water conditions (PDIQ) and, in part, the influence of nest initiation date on nest success (later initiated nests at greater risk of drying). Additionally, the gradual decline in success with season is similar to many birds (Cooke *et al.* 1984; Flint and Grand 1996) reflecting a tendency for older, higher quality pairs to nest earlier (Nesbitt 1992; Blums *et al.* 1997; Mauck *et al.* 2004). Previous authors have hypothesized that temperature might influence nest success (Littlefield 1976; Drewien *et al.* 1995), but this is the first study to quantify that nest success is lower in years with colder spring low temperatures. Cold weather during incubation may influence incubation behavior, reduce nest attentiveness or expose eggs to greater mortality risks during incubation breaks.

We hypothesized haying, grazing, and burning would lower nest success by reducing the availability of vegetation needed to construct and conceal nests. Grazing and haying had no impact on nest success, but burning did lower success. Compared to grazing and haying, burning removes a greater percentage of vegetation on any treated area. Additionally, burning may reduce the abundance of alternate prey for

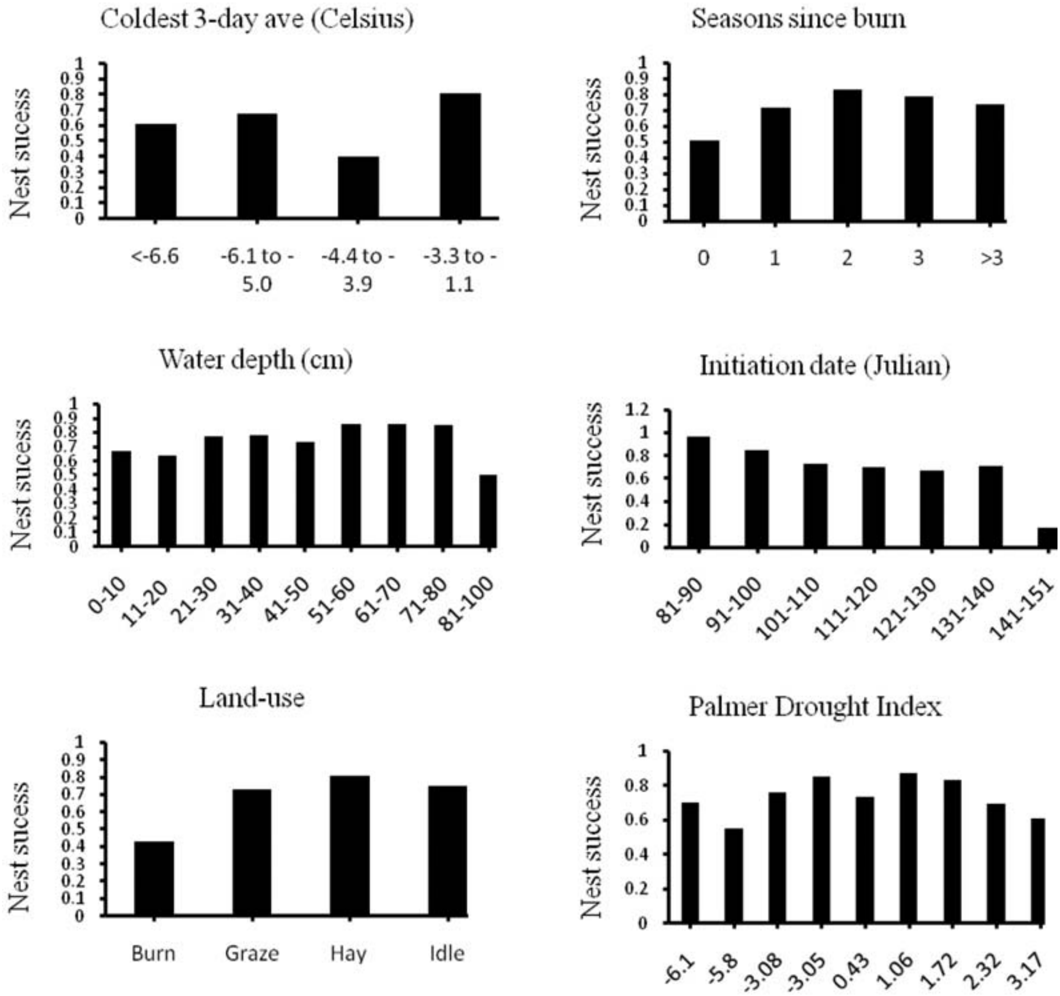

Figure 3. Variation in nest success with weather, habitat and nest initiation date variables for Greater Sandhill Cranes (*Grus canadensis tabida*) breeding at Malheur National Wildlife Refuge, Oregon.

predators, increasing pressure on crane nests (Ackerman 2002). Anecdotal accounts at both Gray's Lake and Malheur NWR indicate vole (*Microtus* spp.) abundance may impact crane nest success (Austin *et al.* 2007; GLI, pers. obs.) and work at Malheur NWR indicates vole abundance is influenced by vegetation cover (Cornely *et al.* 1983).

Contrary to our predictions, we found no relationship between nest concealment or vegetation type and nest success. While the role of concealment and vegetation type in protecting nests is intuitive, empirical data for sandhill cranes is conflicting with one study reporting higher nest success for better concealed nests (Littlefield 1995a) and others reporting no impact of concealment (Austin *et al.* 2007; this study). Together, these studies suggest the importance of concealment varies regionally (possibly depending on the relative importance of mammalian vs. avian predators), concealment has been over emphasized for cranes, or that researchers have been inconsistent or ineffective at measuring nest concealment in a biologically meaningful way for cranes.

Comparisons with Previous Malheur NWR Studies

Nest success during 1990-1998 was higher than previous estimates at Malheur NWR

(41% ± 5% and 54% ± 3%; Littlefield 1976; 1995b). In fact, success has steadily increased at Malheur NWR since monitoring began in 1966 (Fig. 2). This trend likely reflects long term changes in habitat conditions and management priorities on the refuge. Prior to 1972, the refuge was heavily grazed during winter, greatly reducing the vegetation cover needed by nesting cranes (Littlefield 1995a), and predators were controlled using compound 1080. Use of compound 1080 ended in 1971, predator control ended in 1972, and beginning in 1973 the stocking rate of cattle was reduced, allowing plant communities to begin recovering. This was followed by management that was focused on improving nesting conditions for cranes. Also, it is likely that predator community changes and predator-prey dynamics have influenced the trend.

Our findings differ from previous studies at Malheur NWR that reported higher nest success with predator control (Littlefield 2003), higher nest success in idle vs. hayed and grazed fields (Littlefield and Paullin 1990), and higher nest success in burned vs. unburned fields (Littlefield *et al.* 2001). Differences in methodologies among studies make direct comparisons difficult. Previous studies only included successful nests and those destroyed by predators; because we hypothesized several mechanisms might influence nest success (in addition to predation), we retained all failed nests in our analysis. It is also possible the relative importance of various factors has changed as nest success rates have increased.

Studies of nesting Sandhill Cranes at Malheur NWR and elsewhere are consistent in attributing most nest losses to predation (Drewien 1973; Stern *et al.* 1987; McMillen 1988; Littlefield 2003; Austin *et al.* 2007); however, nest success was not related to predator control in our study (95% confidence interval for the model averaged odds ratio 0.6-1.7). Average nest success in predator control and non-predator control years during our study was nearly identical (72.3 vs. 72.6%, respectively), as were rates during another block of control (46.8%; 1966-1971) and non-control (43.4%; 1973-81) years (Fig. 2). Together these data suggest control of Coyotes and Common Ravens had little influence in crane nest success, but we did not conduct a controlled experiment, which limits the scope of our inference. For example, we can not discount the possibility that the lack of a predator control effect during our study was caused by protracted effects that influenced nest success for several years after control activities cease. Such an effect may be due to replacement of experienced Coyotes and Common Ravens with individuals inexperienced in finding crane nests (R. Drewien, pers. comm.). However, of the two studies that report higher crane nest success under predator control, one suffers from the same lack of experimental control as our study (Littlefield 2003) and the second lacked replication and was inconclusive (Littlefield and Cornely 1997). Taken together, we suggest the effect of predator control on crane nest success at Malheur NWR is unclear and recommend that if any future predator control actions are proposed they explicitly include plans for a controlled, replicated experiment to evaluate program efficacy and assure there are no unrecognized consequences. For example, at both Malheur NWR and Gray's Lake, periods of intense predator control were associated with a shift in the predator community structure (Drewien and Bouffard 1990; GLI, unpubl. data). The eight-year Coyote and Common Raven control program at Malheur NWR that occurred during this study was correlated with an increase in the abundance of Striped Skunk (*Mephitis mephitis*) and Mink (*Mustela vison*) while Coyote populations appeared stable and ravens declined (GLI, unpubl. data). Mink were an important predator on crane colts during this time (Ivey and Scheuering 1997). The primary reason for low productivity during this study was low colt survival (GLI, unpubl. data).

Future studies need to report metrics on model performance to help interpret the comparative results generated by ranking competing models. We focused on factors that could be influenced by wildlife managers; however, relatively low model R^2 for our competitive models indicates that other variables or additional interactions among variables need to be considered. Future studies should investigate the influence of adult quality, breeding crane density, and availability of alternate prey for predators.

Management Implications

Despite high nest success, population productivity at Malheur NWR averaged only 7.5 young fledged per 100 pairs from 1991-1998 (GLI, unpubl. data), considerably lower than estimates from previous years (Littlefield 2003). The primary reason for low productivity during this study was low colt survival (GLI, unpubl. data). Thus, additional efforts to increase crane nest success at Malheur NWR are unnecessary, rather there is a need to study crane brood-rearing to expand our understanding of crane breeding ecology that leads to a more balanced management strategy for enhancing crane productivity. Specifically, what are the sources of colt mortality and how do habitat management activities implemented to improve nest success influence colt survival? It is possible that actions designed to improve nest success have negative consequences to overall crane productivity.

If improving crane nest success is desirable, managers could encourage early nesting by early application of water to crane territories, because Greater Sandhill Cranes typically delay nesting until water is available within their territories. Managers should maintain water levels around crane nests through the entire nesting season because drying can cause failure. When a mix of meadow and marsh habitat is available in crane territories, managers may increase nest placement in deeper-water marsh sites by haying or grazing meadows (where appropriate and feasible) to reduce the attractiveness of meadow habitat for nesting. We advocate continued use of prescribed burning in wetland habitats used by nesting cranes. The short term decline in nest success is offset by the long term benefits of fire, which is an important process driving ecosystem function in the intermountain west. Also, burning may provide forage benefits to adults and colts as soils in burned sites tend to thaw earlier facilitating early availability of invertebrates and high protein vegetation. Predator control is not necessary on an annual basis, particularly in systems where crane nest success is relatively high.

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