AN ABSTRACT OF THE THESIS OF

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

Abstract approved:

Bruce D. Dugger

I developed *a priori* hypotheses and used logistic regression to model Greater Sandhill Crane (*Grus canadensis tabida*) nest success in relation to weather, habitat and management variables for cranes breeding at Malheur National Wildlife Refuge (MNWR) in southeast Oregon. My primary interest was to investigate the effects of habitat conditions and management practices on nest success as these factors can be influenced by managers. However, I also included variables for weather, water supply, and nest initiation date to provide a context for understanding the relative importance of management actions and habitat conditions. I monitored 506 nests over 9 breeding seasons; mean apparent nest success was 72% ± 4% and varied from 51 to 87%. Nest success varied by habitat management within a field, nest-season temperatures, and water at the nest site. A second analysis which included a subset of nests with nest initiation data revealed that nest success declined with initiation and was higher during years of moderate precipitation. Variable importance analysis indicated initiation date had a greater influence on nest success (0.99) than land use (0.74), water depth (0.50), water supply (0.42), or temperature (0.30). Grazing, haying and predator control had no effect on nest success, while burning had a negative effect, but only during the nesting season following the burn. The lack of a predator control effect may have been due to elimination of individual problem animals before the study commenced, and a protracted effect of the control program. It may also be due to the relatively smaller importance of predator control at higher nest success rates.

Nest success at MNWR was higher during my study than in most studies and the low proportion of failed nests may have reduced my ability to detect influences of some variables such as land use practices and predator control. My study is the first to quantify the effect of temperature and moisture conditions on nest success and the results suggest adequate water availability is important for nesting cranes. It affirms the importance of water depth, but not concealment, indicating that the height of cover surrounding a nest is not very important.

During the 8-year coyote (*Canis latrans*) and Common Raven (*Corvus corax*) control program at MNWR non-target predator populations increased. Such control programs can have unforeseen consequences, such as release of mesopredator populations which can cause additional crane productivity problems. Nest success was relatively high during my study yet productivity was very low, averaging around 3.3 young per 100 pairs from 1995-1998 (GLI, unpublished data). Efforts to further increase nest success at MNWR using predator control are not warranted. The effect of predators on chick survival is likely of more importance and should be quantified to aid in the interpretation of predator control as a management tool.

Managers should focus on providing early water to crane territories to facilitate earlier nesting and water levels should be maintained through the nesting season to limit abandonment. Haying and grazing of meadows will likely encourage cranes to nest in deeper water marsh sites. Although burning showed negative effects on nest success during the first season following burns, I advocate continued, but careful use of this important habitat management tool. Lastly, in addition to management to improve nest success, managers should consider efforts to enhance chick and adult survival, as these factors are likely more important than nest success in maintaining populations.

Factors Influencing Nest Success of Greater Sandhill Cranes at

Malheur National Wildlife Refuge, Oregon

by

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I understand that my thesis will become part of the permanent collection of Oregon State University Libraries. My signature below authorizes release of my thesis to any reader upon request.

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1. Introduction

The Greater Sandhill Crane (*Grus canadensis tabida*) is one of six subspecies of Sandhill Cranes in North America. Historically the breeding distribution of this subspecies included 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 declines, the Greater Sandhill Crane was listed as endangered in Washington in 1981, threatened in California in 1983, sensitive in Oregon in 1989 (Littlefield and Ivey 2002), and a British Columbia Blue List species in 1998 (BCE, B. C. Environment 1998).

The breeding biology of all cranes is characterized by delayed maturity (first nesting usually delayed until ≥ 3 years), 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 growth of population (Drewien et al. 1995). Low recruitment has primarily been attributed to predation of nests and prefledged young (e.g., 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, Maxson and Riggs 1996a, Littlefield 2001), vegetation type around the nest (Littlefield and Ryder 1968, Drewien 1973, Stern et al. 1987, Littlefield 1995b, Urbanek and Bookhout 1992), nest concealment (Littlefield 1995a, Maxson and Riggs 1996a), and to a lesser extent land use practices (Littlefield and Paullin 1990, Littlefield et al. 2001). A few studies have suggested weather influences reproductive success (e.g., annual precipitation; Littlefield 1976, Drewien et al. 1995); however, formal evaluations of weather factor effects have not been reported. Presumably, these characteristics 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 (Paullin and Littlefield 1990) but not in Idaho (Austin et al. in press). 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 (e.g., Littlefield et al. 1994). Spring grazing can contribute directly to nest losses due to potential trampling of nests by cattle and by disturbance from cattle that can cause abandonment (e.g., Littlefield 1989). Indirectly, grazing, burning and haying may lower nest success by reducing nest cover thereby making nests easier for predators to detect (e.g., Littlefield and Paullin 1990). Predation is the most common source of nest loss, while predator control is a controversial management tool (e.g., Sargeant and Arnold 1984) 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 (Littlefield 2003) and Whooping Crane (*G. americana*) egg success (Drewien and Bouffard 1990); 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 (MNWR) is the most important breeding site for the Central Valley Population of Greater Sandhill Cranes, supporting 245 pairs in 2000 (Littlefield et al. 1994, Ivey and Herziger 2000). Similar to private ranchlands in the intermountain west, wetland habitat management at MNWR includes the use of haying, grazing and controlled burning. In this paper, I use data from 9 breeding seasons to estimate Greater Sandhill Crane nest success, determine the relative importance of the effects of weather, nest site, land-use and predator control and compare trends in success from earlier studies at MNWR (Littlefield 1976 and 1995b).

2. Methods

Study Area

MNWR 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 (Figure 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 MNWR 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, I searched for nests from early April through early June both from on foot (~95% of nests found) and from fixed-winged aircraft (~5%). Both fidelity to nesting territory (Littlefield and Ivey 1995, Drewien et al. 1995) and adult survival of Sandhill Cranes (> 80%; Bennett and Bennett 1990a) are high; consequently, the location of most crane territories was known before nest searching began each year. I located nests by searching a sample of territories until I 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 they were included the sample. I 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 (Rearden 1951, Littlefield 1995c). For each active nest, I floated eggs to estimate incubation stage (Westerskov 1950, Fisher and Swengel 1991), which allowed estimation of initiation and hatching dates. I revisited active nests after the estimated hatch date to determine nest fate. Thus, each nest was visited no more than twice each year; this minimized disturbance which can lead to nest abandonment (GLI, personal observation).

In addition to information on nest fate, I collected data on habitat characteristics at the nest and on land use practices in the field where the nest was located. At each nest, I 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). Vegetation at the nest site provides concealment, but is also influenced by water depth. I characterized surrounding land-use as hayed, cattle grazed, burned, or idle. Haying of upland meadows occurred in late summer (after Aug. 10) after all cranes nests had hatched, and livestock grazing occurred from October through December. Grazed fields were first hayed and hay was rake-bunched 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 MNWR 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 (Ivey 1993).

Analyses

Nest visitation protocol did not provide the data necessary to calculate exposure days for Mayfield nest success estimates (Miller and Johnson 1978), so I calculated apparent nest success (100 × no. nests with at least 1 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. I plotted nest success by year over the 32 year period (1966-1998) for which apparent nest success estimates are available to look for trends in nest success rates in the MNWR population. Estimates for 1966–1989 came from Littlefield (1976) and Littlefield (1995b). When visual inspection suggested a linear trend, I fit a line to the data using general linear modeling techniques.

I used logistic regression (SAS Institute, Inc. 2002) to determine factors that influenced nest success (Hosmer and Lemeshow 2000). The dependent variable for my analyses was nest fate (0 = failed, 1 = successful). I developed a list of explanatory variables based on earlier crane work (e.g., Littlefield and Ryder 1968, Littlefield 1976, Littlefield and Paullin 1990, Littlefield 1995a, 1995b; Maxson and Riggs 1996a; Littlefield 2003, Bradter et al. 2005; Austin et al. in press) and personal experience. Variables included were predator control (CONT), land-use type (LU), dominant vegetation at the nest (VEG), nest concealment (CONC), distance to habitat edge (EDGE), water depth (WAT) as well as water supply and weather factors (Table 1).

I 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). I considered models within ≤ 2 AIC values of the best model to be competitive. While evaluations of ß's and odds ratios provide the same results, I 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 the size of an effect. Percent change in the odds of nest survival for each one-unit change in an independent variable was calculated by subtracting 1 from the odds ratio and multiplying this value by 100.

While I hypothesized that annual water supply, temperature and precipitation likely influenced nest success, I had several potential measures of each variable type; many of which were correlated (G. Ivey unpubl. data). I 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 (G. Ivey, pers. observ.). Rather than including all covariates in my final set, or arbitrarily selecting one measure, I modeled the influence of weather and water supply first, identify the single most important variable for annual water supply, precipitation, and temperature.

I modeled two measures of water supply, the March Palmer Drought Index (PDI) and annual peak snow water equivalent index (SNO). I hypothesized that nest success might be lower under extreme conditions (both wet and dry), thus I included both the linear and quadratic function for both variables (SNOQ and PDIQ). I modeled 3 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; Table 1). I used National Oceanic and Atmospheric Administration (NOAA) Oregon Zone 7 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 12 missing temperature and precipitation data points, I substituted data from the nearest weather station. I chose the best covariate from these categories using AICc and AICc weights and include these covariates in my final model set.

My final model set included most combinations of 1, 2 and 3-factor additive models (89 models). I 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). I could not calculate initiation date for all nests (e.g., those found already failed or hatched); therefore, I did not include nest initiation date in my initial modeling. However, nest success has been shown to vary by initiation date (Maxson and Riggs 1996a). Thus, I 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 1, 2, 3 and 4 factor models.

I calculated relative importance for each variable by summing model weights for all models containing that variable (i.e., variable importance weight; Burnham and Anderson 2002). I 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, Anderson and Burnham 2002) and I reported Nagelkerke's R^2 as a measure of model performance (Nagelkerke 1991). I 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 (Anderson et al. 2000) and generated odds ratios using the model-averaged coefficients. I calculated model-averaged coefficients as the sum of coefficients multiplied by AIC weights (w_i) and used 0 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). I 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). Odds ratios measure the importance of a specific variable state (e.g., land use type = grazing) relative to a reference state (e.g., idle; Rosenberg and McKelvey 1999).

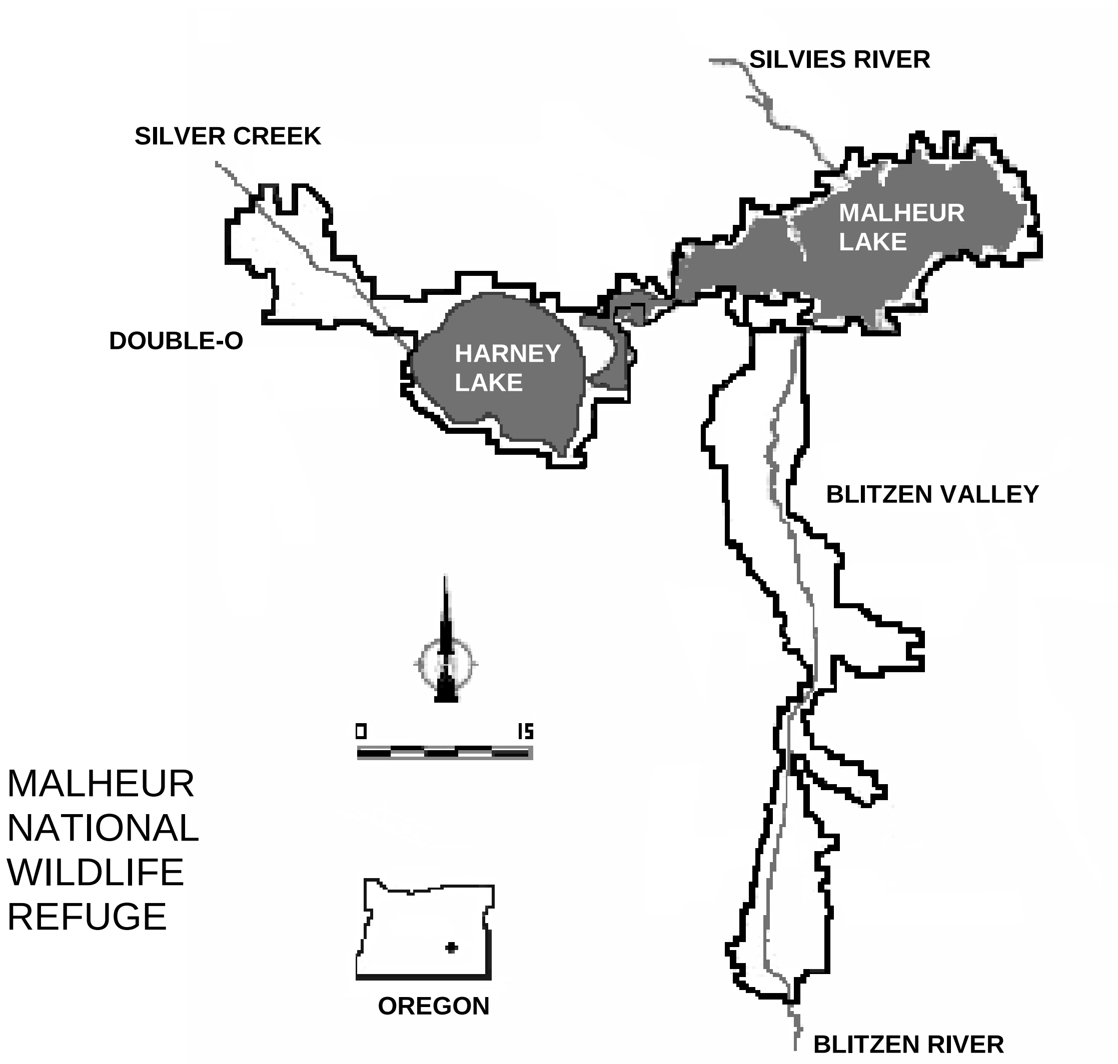

Figure 1. Breeding Greater Sandhill Cranes were studied at Malheur National Wildlife Refuge in southeastern Oregon.

Table 1. Definition of explanatory variables included in models of Sandhill Crane nest success.

Variable		Variable Description
NEST SUCCESS:		
	FATE	Successful hatch or failed nest.
WATER SUPPLY:		
	SNO	Annual snow index in March from Steens Mountain Snotel
	SNOQ	Mean-centered snotel index squared ($SNO + SNO^2$)
	PDI	Annual Palmer Drought Index for March
	PDIQ	Mean-centered Palmer Drought Index squared ($PDI + PDI^2$)
NESTING SEASON CLIMATE:		
	TEMP	Average daily low temperature during April and May
	COLD	Average low temperature during 3 coldest consecutive days during April and May
	FRZ	Number of nights when temperatures were below freezing
	TP	Total precipitation during nesting period (April + May)
	AP	Total precipitation during April
	MP	Total precipitation during May
	PDA	Total days of precipitation during April
	PDM	Total days of precipitation May
	PDT	Total days of precipitation during April and May
NEST SITE HABITAT:		
	WAT	Water depth at nest site (cm)
	VEG	Dominant plant species at nest site: *Scirpus acutus* (SCAC), *Sparganium eurycarpum* (SPEU), *Typha* spp. (TYPH), grasses and sedges (MDW)
	CONC	Estimate of nest concealment cover (scored 0-4)
	EDGE	Distance from nest to a change in plant community.
MANAGEMENT FACTORS:		
	CONT	Categorical variable indicating whether predator control occurred in a given year.
	LU	Categorical variable indicating land use at crane nest sites: nesting area was either grazed by livestock (G) hayed (H), burned (B), or idle (I; no manipulation).

3. Results

My sample included 506 nests found over 9 years (1990-1998; Table 2); 75% of nests were active when found, 16% had hatched and 9% had failed. I excluded 8 nests from the analysis that I believe failed because of researcher disturbance (determined by lack of change in incubation stage). Nest initiation ranged from March 21 through May 31, with a median date of April 18 (yearly median ranged from April 10 - 25). The majority of nests were in marsh vegetation types (88%); mean water depth at nests was 27.4 cm (range 0-100 cm). Snow pack levels were below normal during the first 4 years, near normal during the fifth year, and above normal during the last 4 years. Temperatures varied considerably among years; the coldest nest season temperatures (3-day average) ranged from -8.3 to -1.5 ^{o}C (Table 3). Apparent nest success averaged 72.4 ± 3.9% (range = 51 to 87%; Table 3); of nests that failed, 69% were destroyed by predators and 31% failed due to factors such as flooding, abandonment and addled eggs (dead embryos). Since 1966, apparent nest success of Sandhill Cranes at MNWR has steadily increased (1.2% per year, $p < 0.001$; $R^{2} = 0.47$; Figure 2).

During my initial modeling of weather and water supply variables, the best single-factor model for temperature was the coldest 3-day period (COLD, $w_i = 76\%$). The quadratic Palmer Drought Index (PDI2) 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 ($\Delta AICc = 12.6$, $w_i = 1\%$) than the intercept only model. Consequently, I included COLD and PDI2 in my analyses with habitat variables.

Only one multivariate model received substantial support (AICc wt. = 0.50) as a predictor of nest fate and included the variables LU, COLD and WAT (Nagelkerke's R^2 = 0.11; Table 4). No other model was competitive (i.e., within 2 AICc of best model); however, at least one of these variables were included in many models that performed better than the null model. Variable importance weights (VIW) indicated strongest support for the effects of LU, followed in descending order by COLD and WAT (Table 5). Variables YEAR, PDI2, CONT, CONC, EDGE and VEG received no support.

Compared to idle fields, nests in burned fields were 70% less likely to hatch (Table 5). 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 5). Nest success increased with April and May temperatures (COLD) and was higher in deeper water (WAT; Figure 3).

Because burning had the strongest influence on nest success, I conducted an *a posteriori* analysis to investigate the temporal affects of burning. I 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 (Table 6; Figure 3).

Including nest initiation date (INIT) increased the number of competitive models (5 models; Table 7), but did not significantly improved their predictive ability (R^2 = 0.11 to 0.13) but also increased the number of competitive models. Along with LU, nest initiation date was included in all 5 models that were competitive and the 15 models which included INIT were ranked in the top 15 models and received some support via model weight. Nest success declined 3%/day with increasing initiation date (INIT odds ratio = 0.97 [CI = 0.95 - 0.99]). 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 weak effect (Table 8).

Table 2. Sample size (n) and fates (%) of Greater Sandhill Crane nests monitored at Malheur National Wildlife Refuge, Oregon, 1990-1998.

		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.

Table 3. Summary statistics for nest success and continuous variables included in analysis of Greater Sandhill Crane nest success at Malheur National Wildlife Refuge, Oregon.

Parameter[a]	Units	Mean	Standard Error	Minimum	Maximum
SUCCESS	hatched	72.4	3.92	51	87
WAT	cm	27.4	0.87	0.00	100.00
COLD	^{o}C	-4.5	0.09	-8.3	-1.5
PDI	index	-1.3	0.15	-6.10	3.17
INIT	Julian Date	109 (Apr. 19)	0.72	81 (Mar. 22)	151 (May 31)

[a] SUCCESS = nest success; WAT = water depth at nest site; COLD = lowest 3-day average temperature during nesting season (April and May); PDI = Palmer Drought Index; INIT = date first egg was laid.

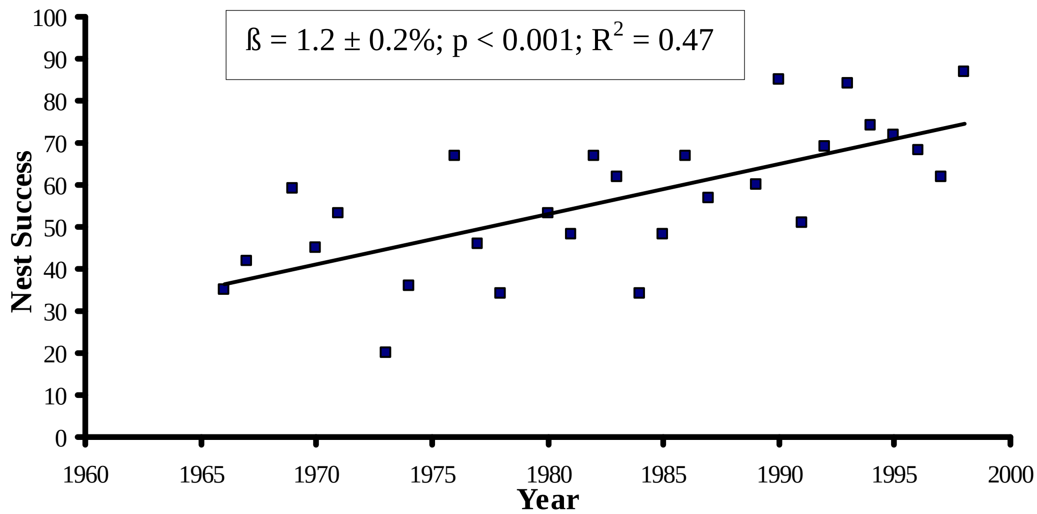

Figure 2. Trend in apparent nest success estimates for Greater Sandhill Cranes breeding at Malheur National Wildlife Refuge, 1966-1998 (data for 1966-1989 is from Littlefield 1976, 1995b).

Table 4. Results of logistic regression analysis to identify factors that influenced nest success of Greater Sandhill Cranes 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 2 ΔAICc_i values of the best model and AIC*c* weights indicate relative support for each model. The Nagelkerke's R^2 value is a measure of a model's ability to account for the variance.

Model structure[a]	*k*	ΔAICc_i	w_i	Nagelkerke's R^2
LU COLD WAT	6	0.00	0.502	0.110
LU COLD	5	3.67	0.080	0.095
LU PDI2 WAT	7	3.68	0.080	0.106
LU COLD EDGE	6	4.58	0.051	0.098
LU COLD CONT	6	4.84	0.045	0.097
LU COLD VEG	8	5.28	0.036	0.107
LU COLD CONC	6	5.40	0.032	0.096
LU WAT YEAR	13	5.51	0.027	0.134
LU PDI2	6	5.85	0.025	0.095
LU COLD PDI2	7	6.00	0.018	0.100
NULL	1	30.00	0	---

[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; PDI2 = 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.

Table 5. Variable importance weights and odds ratios for variables used to model factors influencing nest success of Sandhill Cranes from Malheur National Wildlife Refuge, Harney Co., Oregon from 1990-1998, calculated from model averaged estimates of betas.

Variable code	Variable importance weight	Odds Ratio [b]	95% Confidence Interval
LU: Burn vs. Idle	0.996	0.30	0.15 - 0.60[c]
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[c]
WAT	0.630	1.01	1.01 - 1.02[c]

[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;
[b] Odds ratios >1 indicate positive relationship; <1 indicate negative relationship.
[c] Confidence intervals not including 1 indicate evidence of effects.

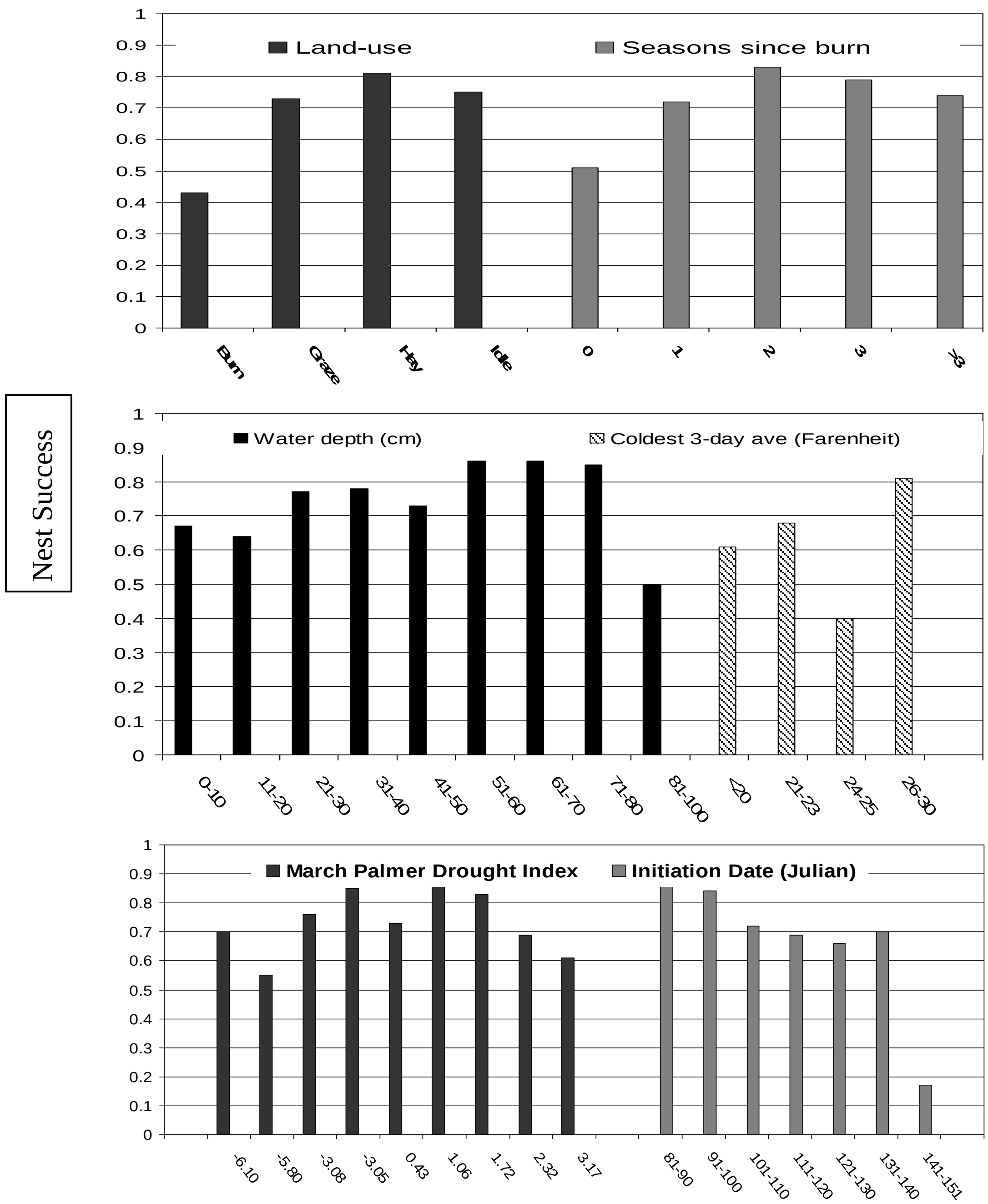

Figure 3. Variation in nest success with weather, habitat and nest initiation date variables for Greater Sandhill Cranes breeding at Malheur National Wildlife Refuge, Oregon.

Table 6. Summary of variable odds ratios for burning categories on Greater Sandhill Crane nest success from Malheur National Wildlife Refuge, Harney Co., Oregon from 1990-1998, calculated from the summed weights of models which include the variable in the entire model set.

Variable code	Odds Ratio[a]	95% Confidence Interval[b]
B_o vs unburned	0.45	0.28 – 0.74
B_1 vs unburned	1.01	0.62 - 1.64
B_2 vs unburned	1.48	0.58 – 3.82
B_3 vs unburned	1.30	0.72 – 2.35

[a] Odds ratios >1 indicate positive relationship; <1 indicate negative relationship.
[b] Confidence intervals not including 1 indicate evidence of effects.

Table 7. Model selection results for top 10 models relating initiation dates, climate, habitat and management variables to nest success of Greater Sandhill Cranes from Malheur National Wildlife Refuge, Harney Co., Oregon from 1990-1998. Models were 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 2 $\Delta AICc_i$ values of the best model and AIC*c* weights indicate relative support for each model. The Nagelkerke's R^2 value is a measure of a model's ability to account for the variance.

Model structure	K	$\Delta AICc_i$	w_i	Nagelkerke's R^2
INIT LU WAT	6	0.00	0.203	0.119
INIT LU	5	0.64	0.147	0.109
INIT LU PDI2	7	0.92	0.128	0.123
INIT LU PDI2 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 PDI2 COLD	8	2.34	0.063	0.123
INIT PDI2	4	2.96	0.046	0.091
INIT PDI2 WAT	5	3.49	0.035	0.098
INIT PDI2 COLD	5	4.96	0.017	0.091
NULL	1	21.25	0.000	---

[a] INIT = nest initiation date; 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; PDI2 = quadratic form of the Palmer Drought Index; NULL = intercept only model.

Table 8. Summary of variable importance weights and odds ratios for variables occurring in competitive models (including initiation date) explaining variation in nest success for Sandhill Cranes nesting at Malheur National Wildlife Refuge, Harney Co., Oregon from 1990-1998, calculated from the summed weights of models which include the variable in the entire model set.

Variable code[a]		Variable importance weight	Odds Ratio[b]	95% Confidence Interval
INIT		0.994	0.969	0.952 – 0.986[c]
LU:	Burn vs. Idle	0.739	0.431	0.256 – 0.725[c]
	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[c]
PDI		0.416	1.001	0.891 – 1.125
PDI2		0.416	0.977	0.940 – 1.016
COLD		0.300	1.024	1.033 – 1.223[c]

[a] INIT = nest initiation date; 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; PDI = Palmer Drought Index; PDI2 = 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.

4. Discussion

Mean apparent nest success (72% ± 4%) at MNWR during this study is within the range of apparent nest success estimates reported for Greater Sandhill Cranes (40-84%; Walkinshaw 1965, Drewien 1973, Littlefield 1976, Bennett 1978, Valentine 1982, Walkinshaw 1982, Nesbitt 1988, Bennett and Bennett 1990b, and Dwyer and Tanner 1992, Littlefield 1995b, Maxson and Riggs 1996a). Within the intermountain west, nest success during my study was higher than a comparable estimate for Rocky Mountain Population (RMP) Greater Sandhill Cranes breeding at Grays Lake, Idaho (60%, Austin et al. in press). Differences may reflect the greater use of publicly owned lands managed explicitly for cranes at MNWR compared to Grays Lake. Alternately, as nest losses in both studies were primarily attributed to nest predators, differences may reflect regional differences in the abundance and composition of predator communities (a larger percentage of failed nests were attributed to predators at Grays Lake [97%] compared to MNWR [69%]) and differences in prey resources (e.g., Ackerman 2002, Austin et al. 2007).

Studies of nesting cranes are generally consistent in attributing most nest losses to predation (Littlefield 1968, Littlefield and Ryder 1968, Drewien 1973, Littlefield 1976, Boise 1977, Stern et. al 1987, McMillen 1988, Littlefield 1995a, 1995b, Littlefield et. al. 2001, Littlefield 2003) and several studies on cranes report higher nest success with predator control (Drewien et al. 1985, Drewien and Bouffard 1990, Littlefield 2003); however, predator control was not an important covariate effecting nest success for MNWR. Average nest success in predator control and non-predator control years during my study was nearly identical (72.3 vs. 72.6%, respectively). Differences between studies may be caused by many factors. First, my results may indicate that predator control did not influence nest success when considered in a long-term context and in conjunction with a suite of explanatory variables. Alternately, all studies rely on signs at the nest to determine the cause of failure, which can be misleading (e.g., Sargeant et al. 1998). Nests scavenged after being abandoned or those destroyed by conspecifics (Drewien 1973, GLI pers. observ.) may be incorrectly classified as destroyed by coyotes or ravens (the main targets of predator control), so estimates of predation rates can be biased in all studies. Third, the effects of predator control may influence nest success for several years after control activities cease (R. Drewien, pers. comm.; GLI pers. observ.) which further confounds interpretation. The one controlled study that compared nest success between control and treatment plots in the same year collected data for only two years on one control and two treatment plots, and no other covariates were considered (Littlefield and Cornely 1997), making broad inferences tenuous. Even if predator control can improve nest success, it is not clear that it will result in higher crane productivity. The 8-year coyote and raven control program at MNWR that occurred during this study was correlated with an increase in the abundance of striped skunk (*Mephitis mephitis*) and mink (*Mustela vison*) (GLI, pers. observ.); mink are effective predators of crane colts (Ivey and Scheuering 1997) and colt survival and crane productivity was very low at MNWR during my study (mean = 7.5 colts fledged per 100 pairs; GLI, unpublished data). Thus, despite several studies, the effects of predator control on Sandhill Crane nest success and productivity remain unclear.

Nest success during 1990-1998 was higher than previous estimates at MNWR (41% ± 5% and 54% ± 3%; Littlefield 1976 and 1995b). In fact, success has steadily increased at MNWR since monitoring began in 1966 (Figure 2). This trend varies from the declining trend for RMP Greater Sandhill Cranes at Grays Lake that was attributed to changes in predator community following the end of an intensive control program in 1989 (Drewien et al. 1985, Austin et al. in press). Changes in predator community and predator-prey dynamics due to the MNWR predator control program is likely partly responsible for the increasing trend. The increase at MNWR may also reflect improved refuge habitat management, as habitat management changes were implemented in the mid-1970s to reduce intensive livestock grazing and provide improved nesting cover and later plans included management prescriptions specifically to benefit cranes (Rule et al. 1990, David and Ivey 1995).

Impact of land use

Some have challenged allowing cattle grazing and haying on public lands because of concerns for nesting birds (e.g. Ferguson and Ferguson 1983); consequently, understanding how these land use practices affect crane nesting success is important to wildlife managers. Grazing and haying had no effect on crane nest success. These results are consistent with work in Idaho (Austin et al. in press); however, they differ from a previous MNWR study that reported higher success in idle versus grazed fields (Littlefield and Paullin 1990). That study did not identify how grazing lowered nest success, but hypothesized that cattle trailing and bedding activities in robust emergent vegetation increased predator access to nests. Cattle stocking rates were similar between studies (mean = 1 animal/0.4 ha). Comparing between these studies is difficult as Littlefield and Paullin (1990) only included depredated and successful nests and did not consider other explanatory variables in their analysis.

A study of small mammals at MNWR documented that haying and grazing depressed the densities of small mammals (Cornely et al. 1983). This is likely because grazing reduced concealment cover and made small mammals more vulnerable to predators. The relative influence of grazing on crane nest success may vary with the availability of alternate prey (e.g., Ackerman 2002), as rodent populations fluctuate considerably at MNWR between years (GLI, personal observation). However, grazing did not influence nest success at Grays Lake despite large fluctuations in microtine (*Microtus* spp.) prey abundance.

Burning had the largest impact on nest success at MNWR. Compared to grazing or haying, burning removes more vegetation making it harder to conceal nests from predators. Burning may also lower the abundance of other prey species (e.g., microtines) increasing pressure on crane nests. However, the influence of fire was limited to the first nesting season following a burn. My results are consistent with work at Grays Lake; although in this case nest success was reduced for 2 years after burning (Austin et al. in press). Prescribed burning is a controversial management practice because ranchers see such burning as a waste of cattle forage and there is a risk of prescribed fires escaping to become wildfires and causing damage to adjacent private property. However, fire is an important factor that has shaped the evolution and maintenance of the vitality of plant communities in the intermountain west. Fire return intervals in the surrounding shrub-steppe habitats in this region are typically of 12 to 22 years (Miller and Rose 1999) and wetland plant communities imbedded in this habitat likely burned at least as frequently if not more often (Boone Kauffman, personal communication). Although crane nest success is lower following burns, long term maintenance of these ecosystems is dependent on fire and this management practice should be continued to maintain vigor in wetland plant communities that cranes depend on.

Nest-site characteristics

Consistent with other studies (Drewien 1973, Littlefield 1995a, Stern et al. 1987; Maxson and Riggs 1996a, Austin et. al. in press), crane nests at MNWR were more successful in deeper water. Water is a barrier to many mammalian predators, helping block access to nests (Sargeant and Arnold 1984, Bouffard et al. 1988, Maxson and Riggs 1996a) and some cranes abandoned their nests after water levels declined (GLI personal observation).

I found no relationship between nest concealment and nest success. While the role of concealment 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), another reporting the effect varied with habitat (Maxson and Riggs 1996a), and others reporting no impact of concealment (Urbanek and Bookhout 1992, Austin et al. in press, this study). Together, these studies suggest either the role of concealment has been over emphasized for cranes or researchers are inconsistent or ineffective at measuring nest concealment in a biologically meaningful way for cranes. An earlier MNWR study reported significantly higher nest losses to ravens and coyotes in nests with poor concealment compared to nests with good concealment (Littlefield 2001). My study affirms the importance of water depth, but not concealment, indicating that the height of cover surrounding a nest is not as important as water depth and the type of vegetation in which a nest is built.

Initiation date

Nest success declined with nest initiation date (Figure 3). Importantly, including nest initiation date in my modeling exercise increased the suite of variables that influenced nest success and reduced support for COLD and WAT.

Success varies with nest initiation date for many species of birds (e.g., Cooke et al. 1984, Flint and Grand 1996, Grand and Flint 1997, Dinsmore 2002, Traylor et al. 2004), including Sandhill Cranes (Maxson and Riggs 1996a) with earlier crane nests being more successful than later nests (Maxson and Riggs 1996a, this study). The gradual decline with season is consistent with other studies on birds (Cooke et al. 1984, Flint and Grand 1996) and likely reflects a tendency for higher quality pairs with better foraging conditions on their territories to nest earlier. The higher success for early nests may be due to more experienced crane pairs nesting earlier and because older, more experienced pairs are typically more successful (Nesbitt 1992). Numerous studies have reported that older birds tend to nest earlier (e.g., Boekelheide and Ainley 1989, Pyle et al. 1991, Blums et al. 1997, Mauck et al. 2004). Also, I speculate that pairs with better territories would tend to initiate nests earlier and be more successful. Spring temperatures and favorable weather facilitate early initiation for cranes and some waterfowl species (Drewien 1973, Raveling 1978, Hammond and Johnson 1984, Cowardin et al. 1985, Petersen 1992). Temperatures effect snow melt and soil thawing dates as well as water availability in crane territories (wetland conditions; e.g., Grand 1992). The presence of water in crane territories facilitates earlier soil thawing and the availability of invertebrates; the timing of water application to these irrigated areas likely influences nest initiation timing. These factors facilitate availability of food (as invertebrates and new vegetative growth become available when soils thaw and water is present) and help condition the female for egg-laying (e.g., as in Lesser Sandhill Cranes [*G. c. canadensis*]; Fox et al. 1995, and some waterfowl; e.g., Krapu and Reinecke

1992) which may indirectly effect when nests are initiated. Cranes typically delay nesting until after water is available in their territories (GLI, pers. observ.).

The trend with date was gradual until nest success sharply declined for birds nesting after mid May. The sharp decline for the last date interval is likely because many of those late nests represent renesting efforts which I would expect to have lower success as renesting birds might have less energy to attend to nests. It may also reflect declines in water levels for nests later in the season due to shortages of water, resulting in higher nest losses to predators.

Water supplies and weather

While the impact of weather on nest success of cranes has been hypothesized by some authors (Littlefield 1976, Drewien et al. 1995), this is the first study to quantify that temperature and moisture conditions correlate with nest success. Nest success was lower during extreme drought and flood years and during years with exceptionally cold springs. Because snow pack is a measure of water availability, I expected it might correlate with flood duration; however, snow pack data was not as important an influence as was the Palmer Drought Index. PDI is a measure of regional water conditions, while the snow data is site specific and may generally be a poorer estimate of water availability. Also, MNWR is a managed system, thus, water levels are manipulated by a series of control structures and levels are usually maintained through the nesting season unless water was very scarce. This may explain a weaker relationship between success and snow depth for my data set, however, the results still point to the importance of adequate water availability for nesting cranes.

Finally, future studies need to report metrics on model performance to help interpret the comparative results generated by ranking competing models. I focused on factors that could be influenced by wildlife managers; however, relatively low model R^2 for my competitive models indicate other variables or additional interactions among variables included in the analysis are more important determinants of nest success. Future studies should investigate the influence of adult quality (young pairs often fail; e.g.

Nesbitt 1992, Tacha et al. 1992), population density (which might cause low nest attentiveness; Littlefield and Thompson 1987, Ackerman et al. 2004), territory size and amount and quality of nesting habitat [within breeding territories] (Tacha et. al. 1992, Nesbitt and Tacha 1997), and availability of alternate prey for predators (e.g. Littlefield 1976, Ackerman 2002, Austin et al. in press).

5. **Management Implications**

The best models indicate that cranes nesting in areas of moderate water depths early in the season were most successful. Greater Sandhill Cranes typically delay nesting until water is available within their territories, so early nesting could be encouraged by early application of water to crane territories. No nests were located in water > 1.0 m; deeper habitats prevent cranes from wading to their nests. Managers should maintain water levels in crane territories through the entire nesting season because depth influences success and declining levels can lead to 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.

I advocate continued use of prescribed burning in wetland habitats used by nesting cranes. The short term decline in nest success is offset by gains in maintaining fire as an important process influencing the vitality of plant communities. Also, burning may provide forage benefits to adults as soils in burned sites tend to thaw earlier facilitating early availability of invertebrates and high protein vegetation.

Predator control programs can have unforeseen negative consequences, such as release of mesopredator populations which can cause additional predation problems as noted above (e.g., Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999). Predator control is not necessary on an annual basis, particularly in systems where crane nest success is relatively high. Managers considering predator control should target specific problem animals, as possible, and design programs to be of short duration to reduce chances of upsetting the predator community dynamics. Nest success was relatively high during my study yet productivity was very low and efforts to further increase nest success at MNWR using predator control are not warranted unless nest success significantly declines. An earlier Grays Lake study reported that predator control probably enhanced colt survival in years when good brood-rearing conditions prevailed (during years of good weather and water conditions), but had little effect in poor years (Drewien and Bouffard 1990). A better understanding of brood-rearing ecology is needed to develop a more balanced management strategy for enhancing crane productivity.

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