

Do artificial nests simulate nest success of greater sage-grouse?

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Abstract: Artificial nests have been used to study factors affecting nest success because researchers can manipulate them more than natural bird nests. Many researchers have questioned the validity of generalizing the results from artificial nests onto naturally occurring nests. Other studies have assessed the validity of artificial nest studies by simultaneously comparing overall depredation or daily survival rates, depredation timing, predator species, or habitat characteristics of artificial and natural nests. To evaluate how well artificial nests simulated nest success of greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), we used the unique approach of monitoring artificial nests (n = 69) placed in the natural nest bowls of sage-grouse in southern Wyoming, USA, during 2010 to 2011. Brown chicken eggs were placed in natural sage-grouse nests 7 to 14 days after the hatch or depredation of natural sage-grouse nests to compare artificial nest fate to the fate of natural sage-grouse nests. As secondary objectives, we placed cameras next to a subset of artificial nests to identify which predator species were depredating nests, and we assessed the effects of corvid (black-billed magpie [*Pica hudsonia*] and common raven [*Corvus corax*]) density, nest-site characteristics (i.e., anthropogenic development, landscape variables, and microhabitat) date of depredation, and presence of a camera near nest bowls on the depredation rate of all artificial nests. We found that depredation of artificial nests paralleled the fate of natural sage-grouse nests. Depredations were more likely to occur earlier in the summer (June to early July rather than late July to early August). Depredation of artificial nests was negligible as time progressed past the typical sage-grouse nesting season, supporting the hypothesis of predators using a search image to detect eggs. We also found that shorter perennial grass height and greater magpie densities were positively associated with the depredation rates of artificial nests. Camera-recorded depredation events verified that 4 badgers (*Taxidea taxus*), 2 magpies, and 1 domestic cow depredated artificial nests. Artificial nests may give managers insight into the expected nest success rates of sage-grouse in areas of conservation interest. However, care must be taken regarding placement and timing of artificial nests for reliable conclusions to be drawn from artificial nest studies. Furthermore, identifying predators based on artificial nests likely leads to inaccurate assessment of local species composition of nest depredators.

Key words: artificial nest, *Centrocercus urophasianus*, sage-grouse, human–wildlife conflicts, nest predator, nest success, search image

QUANTIFICATION OF FACTORS affecting nest success have been central to the conservation of many avian species, including greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse; McKee et al. 1998, Jiménez and Conover 2001, Schroeder and Baydack 2001, Connelly et al. 2011). Low rates of nest success have concerned management authorities regarding sensitive and threatened avian species, because nest success is an integral component of avian recruitment (Cote and Sutherland 1997, Jiménez and Conover 2001, Evans 2004, Frey and Conover 2006). Artificial

nests have been used traditionally to study nest success because researchers can manipulate them more than natural bird nests. For example, cameras have been used to document the species of nest predators at artificial nests without fear of causing researcher-induced nest failure at real bird nests (Vander Haegen et al. 2002, Richardson et al. 2009). Artificial nests traditionally have been used to study the effects of egg size and color, habitat fragmentation, nest density, nest-site characteristics (e.g., proximity to anthropogenic development, fragmentation, topography, and concealment

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cover), and predator composition on nest success of multiple avian species (Burger et al. 1994, DeLong et al. 1995, Rangen et al. 2000, Vander Haegen et al. 2002, Zanette 2002, Borgo and Conover 2009). However, the validity of projecting results from artificial nests onto naturally occurring nests has been questioned because artificial nests do not have the same appearance as natural nests (Zanette 2002, Borgo and Conover 2009). Several studies have assessed the validity of artificial nest studies by simultaneously comparing overall depredation rates or daily survival rates (King et al. 1999, Moore and Robinson 2004, Borgo and Conover 2009), depredation timing (Thompson and Burhans. 2004, Welstead et al. 2005), predator species (Maier and Degraaf. 2001, Vander Haegen et al. 2002, Zanette 2002, Thompson and Burhans. 2004), or habitat characteristics (Rudnicky and Hunter 1993, DeLong et al. 1995, Watters et al. 2002, Welstead et al. 2005, Ruzicka and Conover 2011) of artificial and real nests.

During artificial nest studies, the relative depredation rates of artificial and natural nests have been assumed to be equivalent over space and time (Zanette 2002). For example, structural characteristics of nests associated with higher depredation rates of natural nests should lead to higher depredation of artificial nests. This assumption of parallel depredation rates allows researchers or management agencies to study factors that affect nest success without disturbing natural bird nests. For artificial nests to accurately predict the fate of real nests, researchers need to replicate the appearance, odor, structure, and location of natural nests, which should then produce relative depredation rates that are parallel. Many discrepancies between artificial and natural nests may attract or deter predators from encountering artificial nests (Skutch 1985, Rangen 2000, Maier et al. 2001, Zanette 2002).

Nest-sites selected and constructed by researchers may or may not simulate the nest success of real bird nests, due to the lack of an incubating bird and researcher bias in site selection and preparation (Rudnicky and Hunter 1993, King et al. 1999, Zanette 2002). While previous studies have simultaneously monitored artificial and real nests to test the assumption that artificial nest depredation rates parallel those of natural nests, these studies were

unable to conclusively determine if artificial nests had the same pattern of depredation (hatched versus failed) compared to natural nests. Our primary objective was to determine if the fate of artificial nests mimicked that of natural sage-grouse nests. Thus, we monitored artificial nests placed in nest bowls constructed by sage-grouse to evaluate how well an artificial nest (without an incubating bird) simulated nest success observed when the sage-grouse was incubating her eggs. We also recorded nest predators with cameras, counted the number of corvids (i.e., black-billed magpies [*Pica hudsonia*] and common ravens [*Corvus corax*]), measured microhabitat characteristics (i.e., bare ground, grass, forb, and shrub cover; and grass and shrub height), calculated topographic ruggedness, and calculated the distance to anthropogenic development (e.g., oil and gas structures, power lines, and roads) and riparian and forested habitat at each nest. This series of variables, which commonly are used in other studies of artificial and natural nests, allowed us to test whether our artificial nest study had the ability to detect factors contributing to low nest success as secondary objectives, while additionally evaluating whether the effect of these factors aligned with results from the natural nests. Secondary objectives were (1) to identify nest predators with cameras; and (2) to evaluate the effects if depredation rates of artificial nests are influenced by corvid (ravens and magpies) densities measured at the landscape-scale, microhabitat characteristics surrounding artificial nests, presence of a camera in a nest bowl, and calendar date of exposure. We expected that depredation events would decrease as calendar date progressed past the typical nesting season of sage-grouse, which would be consistent with the search-image hypothesis.

Study area

We conducted artificial nest experiments in 12 circular study sites in Carbon, Lincoln, Sweetwater, and Uinta counties of Wyoming. Eight nests were 16 km in diameter and four were 24 km in diameter. Study sites in Lincoln and Uinta counties were 16-km diameter and approximately centered around leks where hens were captured based on results found by Holloran and Anderson (2005). Study sites in

Carbon and Sweetwater counties were 24 km in diameter, because sage-grouse were captured at several nearby leks over a larger area. The landscape surrounding artificial nest locations was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), black sagebrush (*A. nova*), and dwarf sagebrush (*A. arbuscula*). Other shrub species near our artificial nest locations included: alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Common forb species included arrowleaf balsamroot (*Balsamorhiza sagittata*), buckwheat (*Eriogonum* spp.), common yarrow (*Achillea millefolium*), dandelion (*Taraxacum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), lupine (*Lupinus* spp.), sego lily (*Calochortus nuttallii*), and wild onion (*Allium* spp.). Common grass species included: bluegrasses (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*). There were isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) at the higher elevations and on north-facing hillsides. Most of this study was conducted on land that was federally owned and administered by the Bureau of Land Management and included a small percentage of private lands. The dominant land-use near artificial nests was domestic sheep and cattle grazing. Artificial nests were near anthropogenic development, which consisted mostly of unimproved roads. There were conventional natural gas, coalbed methane natural gas, and conventional oil extraction activities present within 5 km of 57% of our artificial nests.

Methods

Sage-grouse capture and monitoring

We monitored sage-grouse hens during the nesting season in 2010 and 2011. Hens were captured, radio-collared, and released in April of each year. We captured hens at night using

ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen 1992). Sage-grouse hens were fitted with 17.5- or 22-g (<1.5% body mass) necklace radio collars (Holohil Systems Ltd., RI-2D, Ontario, Canada, and Advanced Telemetry Systems Inc., A4060, Isanti, Minn.).

Sage-grouse hens were located on a weekly basis with Communications Specialists receivers and 3-way Yagi antennas (Communications Specialists, Orange, Calif.). We identified potential nests with binoculars from ~15 m by circling a radio-marked hen until she was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. We continued monitoring nests weekly until the nest hatched or failed. We assessed nest fate as successful or unsuccessful after a hen had left her nest. A successful nest was defined as having evidence that at least 1 egg hatched as determined by shell membrane condition (Wallestad and Pyrah 1974).

Artificial nest construction and placement

We set up an equal number of artificial nests in the existing nest bowls of successful and unsuccessful sage-grouse nests, where nest fate of natural sage-grouse nests had been verified by radio-telemetry monitoring. The nest bowls of successful and unsuccessful sage-grouse used as artificial nests were randomly chosen from 195 natural sage-grouse nests found during 2010 to 2011 (Dinkins 2013). Four brown chicken eggs were placed in each artificial nest 7 to 14 days after hatch or failure of the natural sage-grouse nest. This period of time was intended to allow odor from the sage-grouse hen to dissipate, which normalized the initial odor at artificial nests. Each artificial nest was monitored for 14 days to determine the time of depredation. Eggs at artificial nests were placed on a timing mechanism to determine the exact date of depredation (see Borgo and Conover 2009 for details). A cotton ball with ~1 ml of grouse scent was placed in each artificial nest to mimic the presence of a sage-grouse hen to olfactory predators.

We used Cuddeback infrared cameras (No Flash, Cuddeback, De Pere, Wis.) with motion-activated triggers to identify the species

of nest predator in a random subset of our artificial nests ($n = 24$); we equally distributed cameras to artificial nests that had successful and unsuccessful natural sage-grouse nest fates. The cameras were camouflaged and attached discretely to the interior portion of the nest shrub, which positioned each camera approximately 25 cm away from each nest bowl. Cameras took 1 still photograph and a 10-second video clip on every occasion that the motion sensor was triggered.

Corvid variables

Raven and magpie densities were quantified by conducting point count surveys at random locations within each study site between May 1 and August 1 of each year. Point counts were 10 minutes in length and were conducted during daylight hours on a weekly basis. We quantified ravens and magpies separately, but will refer to them collectively as corvids for ease of discussion. We used standard distance sampling techniques to count all corvids observed during point counts (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), and we followed the point count methods described in Dinkins et al. (2012) and Dinkins (2013). Corvid density variables used in analyses were calculated from the raw point-count data within effective detection radii estimated with DISTANCE (version 6.0, release 2; Thomas et al. 2010), as specified in Dinkins et al. (2012) and Dinkins (2013). Thus, we calculated raven and magpie densities separately within 600 m and 300 m, respectively, of each random point count location within a study site.

To restrict random locations to habitat considered available to sage-grouse for nesting, we used ArcMap 10.0 (ESRI Inc., Redlands, Calif.) to generate random locations only in sagebrush-dominated habitat. Sagebrush habitat was classified by the Northwest ReGAP landcover data from 2008 (Lennartz 2007). Random locations were designated to be $>1,000$ m apart; however, random selection led to average nearest neighbor distances among random point count locations of >2000 m (Dinkins et al. 2012, Dinkins 2013). We generated 12 random locations in each 16-km diameter study site and 18 random locations in each 24-km diameter study site per year. A new set of random locations was generated each year

to avoid spatial autocorrelation; thus, random locations among years were independent.

Nest-site characteristics

Anthropogenic development variables. We used ArcMap 10.0 to calculate anthropogenic development variables as the distance from artificial nests to the nearest oil and gas structure (i.e., energy well, compressor station, transfer station, refinery, or other energy extraction related buildings), major roads (i.e., paved, improved gravel, and railroad), other road (major road and unimproved, 4-wheel-drive accessible roads), communication tower, power line, and rural house. We obtained information on oil and gas structures, including date construction started and date when structures were removed, from the Wyoming Oil and Gas Conservation Commission (WOGCC; 2012). Ongoing energy development was occurring in half of our study sites; thus, we used WOGCC data to precisely add and remove specific oil and gas structures from our dataset by date. Most ($>95\%$) oil and gas structures were energy wells. From summer 2006 and August 2009, we verified the existence and digitized the spatial location of anthropogenic development with color aerial satellite imagery obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture [USDA] 2010). Aerial imagery from NAIP was produced by the USDA on a 3-year rotation; thus, we used WOGCC data and on-the-ground GPS units to map energy development that occurred after August 2009. Energy development reported to WOGCC after August 2009 had better reporting of location, initial construction date, and removal date compared to energy development constructed >15 years prior to the start of this study. All power lines and roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units.

Landscape variables. Similar to anthropogenic development variables, we used ArcMap 10.0 to calculate the distance from every artificial nest to forest (deciduous and conifer stands) and riparian habitats. Forested and riparian habitats were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007). We verified the existence and location of forested and riparian habitat with NAIP imagery from 2009. We also used

ArcMap 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion; TRI variables were developed using a moving window analysis at 0.27-, 0.54-, 1-, and 3-km radii (0.23 km², 0.92 km², 3.14 km², and 28.26 km² scales, respectively). Riley et al. (1999) created TRI to describe the roughness of landscapes; and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map and then averaged over a user-defined area.

Microhabitat variables. Vegetation was measured at artificial nests directly before their construction in natural sage-grouse nest bowls during June and July, and sampling occurred ~1 to 2 weeks after natural sage-grouse nests hatched or failed. We recorded the maximum height and the average canopy cover of the nest shrub. We quantified vegetation within 5 m surrounding sage-grouse nests by orienting 2 vegetation transects—each 10 m in length—at the cardinal directions and intersecting at an artificial nest (Canfield 1941). Average total shrub cover—including antelope bitterbrush, greasewood, rabbitbrush, sagebrush, Saskatoon serviceberry, and snowberry—was calculated by dividing the total shrub intercepted line length (cm) by the total line length (2,000 cm) and then multiplying by 100. Gaps <3 cm were not recorded (Wambolt et al. 2006), and no section of shrub cover was measured more than once. Average shrub height was calculated by averaging the height of all shrubs that intersected the vegetation transect; shrub heights excluded inflorescences. We calculated percentage cover of grass, perennial grass, forbs, bare ground, and litter in 6 cover classes (1 = 0 to 1%; 2 = 1.1 to 5%; 3 = 5.1 to 25%; 4 = 25.1 to 50%; 5 = 50.1 to 75%; and 6 = 75.1 to 100%; Kirol et al. 2012) by averaging nine, 20-cm × 50-cm quadrats placed along vegetation transects at 2, 4, 5, 6, and 8 m (Daubenmire 1959). The height of perennial grass was measured by recording the maximum grown height excluding flowering stalks within 1 m of the 9 quadrats. An index of general line-of-sight obstruction was measured by recording the lowest visible 5-cm section of a Robel pole (hereafter, visual obstruction) that was placed in the center of a artificial nest (Robel et al. 1970). We recorded visual obstructions from 1

m off the ground and 5 m away at the 4 cardinal directions, then averaged these values to report 1 visual obstruction measurement per site.

Data analysis

We analyzed the effect of nest fate (hatch or fail; hereafter, real fate) of a natural sage-grouse nest, calendar date of depredation (hereafter, date of depredation), corvid density, camera presence, and nest-site characteristics on depredation of artificial nests with Cox proportional hazard (Cox PH) models. Cox PH models were fit using function “coxph” in package SURVIVAL version 2.36-14 in R (R 2.14.2; R Foundation for Statistical Computing 2009). Cox PH models are robust semi-parametric models that are commonly used to analyze time-to-event data (Cox 1972), such as nest failure based on time to depredation. The risk of mortality (hazard ratio [h(t|x_i)]) is a function of the non-parametric baseline hazard (h₀(t)) and the parametric covariates (x's) affecting nest depredation (Hosmer and Lemeshow 1999) with the Cox PH equation expressed as:

$$h(t|x_i) = h_0(t) \times \exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \beta_k x_{ik})$$

The baseline hazard is allowed to vary with time in Cox PH; however, covariates in Cox PH models are assumed to have proportional mortality hazard over time (proportional hazard assumption; Hosmer and Lemeshow 1999). Thus, we used function “cox.zph” in package SURVIVAL in R (Therneau and Grambsch 2000) to test the proportional hazard assumption for each covariate in all models; the proportionality of each covariate was validated with $P > 0.05$ for each covariate. Coefficient values were expressed as mortality hazard; thus, positive values were associated with greater risk of nest depredation.

In addition, we calculated dfbetas and generated leverage plots to evaluate if there were influential observations; no observations were omitted as a result of high influence. We prevented multicollinearity by not including any 2 variables that co-varied in any Cox PH model ($r > 0.65$) as determined with a Pearson's correlation matrix. Variance inflation factors for all predictor variables were ≤ 2 , indicating that the variances of coefficient values were not

drastically increased by the inclusion of any predictor variable; thus, collinearity was not a problem.

Modeling of variables affecting depredation of artificial nests was conducted with an information theoretic approach (Anderson 2008). We compared Cox PH models with Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i ; Burnham and Anderson 2002) with function "aictab" in package AICCMODAVG (version 1.25 in R). Prior to comparing *a priori* models, we analyzed each covariate individually in a Cox PH model to assess which covariates were informative. We included real fate, date of depredation, corvid density (magpie and raven, separately), camera presence, and nest-site characteristic (maximum nest shrub, average total shrub, and average perennial grass heights; average nest shrub, total shrub, grass, forb, bare ground, and litter cover; visual obstruction; distance to oil and gas structure, communication tower, power line, major road, any road, rural house,

forested habitat, and riparian habitat; and the TRI variable with the lowest AIC_c among TRI variables measured at 0.27-, 0.54-, 1-, or 3-km radii) variables in individual Cox PH analyses. Non-informative covariates (85% confidence intervals [CI] of parameter estimates overlapped 0) were eliminated from further AIC_c model selection, as suggested by Arnold (2010). We then compared additive models describing depredation of artificial nests using only informative covariates.

The date-of-depredation variable was calculated as the number of days transpired between the day when the first artificial nest was setup each year to the day that an artificial nest was either depredated or reached 14 days. We evaluated potential bias in depredation of artificial nests with cameras by including camera as a binomial variable in AIC_c model selection. The best spatial scale describing the effect of TRI was determined by comparing Cox PH models with individual TRI variables measured at 0.27-km, 0.54-km, 1-km, and 3-km radii with AIC_c ; the TRI variable scale with the

Table 1. Model comparison of Cox proportional hazard (Cox PH) models describing depredation rates of artificial nests; only the 10 best models are shown. Cox PH models with explanatory variables were compared with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w_i). Variables included in modeling were real fate (nest fate = hatch or fail of the natural sage-grouse nest), date of depredation, corvid density (magpie and raven separately), camera presence, and nest-site characteristics. Nest-site characteristics included (1) maximum nest shrub; (2) average total shrub; (3) average perennial grass heights; (4) average nest shrub; (5) total shrub; (6) grass; (7) forb; (8) bare ground; (9) litter cover; (10) visual obstruction; (11) distance to oil and gas structure; (12) communication tower; (13) power line; (14) major road; (15) any road; (16) rural house; (17) forested; (18) riparian habitat; and (19) topographic ruggedness index, measured at 0.27-km radii. Artificial nest data were collected at 67 nest locations previously occupied by sage-grouse hens in southern Wyoming, USA, during 2010 to 2011. $AIC_c = 93.75$.

Models	k	ΔAIC_c	w_i	Deviance
Real fate+date of fate+camera+magpie+grass height	5	0.00	0.27	82.80
Real fate+date of fate+magpie+grass height	4	0.39	0.22	85.52
Real fate+date of fate+grass height	3	1.85	0.11	89.22
Real fate+date of fate+magpie	3	2.20	0.09	89.58
Real fate+date of fate	2	2.25	0.09	91.82
Real fate+date of fate+camera+grass height	4	2.84	0.06	87.96
Real fate+date of fate+camera+magpie	4	3.39	0.05	88.52
Real fate+date of fate+camera	3	3.85	0.04	91.22
Real fate+camera+magpie+grass height	4	4.53	0.03	89.66
Real fate+magpie+grass height	3	5.40	0.02	92.78
Intercept-only model		$\Delta AIC_c = 14.15$		

lowest AIC_c was used in all further modeling. We based our inference on Cox PH models within 4 AIC_c of the top selected model, and we conducted model averaging of parameter estimates from models within 4 AIC_c of the top selected model (Burnham and Anderson 2002). Variable importance was calculated for each parameter estimate that was model averaged by summing the w_i across all models with that variable (Arnold 2010).

Results

We found 195 natural sage-grouse nests during 2010 and 2011, and set up artificial nests in 32 successful and 37 unsuccessful nests of those sage-grouse. One artificial nest from a successful sage-grouse nest was eliminated from analyses because information on that artificial nest’s fate was not recorded by observers. There were 13 (19%) depredations of artificial nests within the 14-day observation period. To assess the effect of corvid densities on depredation of artificial nests, we conducted 1,690 point count surveys at 336 random locations during 2010 and 2011. We counted 277 ravens and 45 magpies within species specific EDRs (600 m and 300 m, respectively). Cameras were deployed at 24 artificial nests, with eight of these nests having depredation events (4 badgers, 2 magpies, 1 domestic cow, and 1 camera failure; Figure 1). We did not statistically analyze our camera results due to



Figure 1. Nest camera images of a magpie and badger depredating an artificial nest that was previously occupied by a sage-grouse hen.

the limited number of depredations.

Eight models describing the depredation of artificial nests were within 4 AIC_c of our top AIC_c selected model and incorporated 0.93 of the cumulative w_i (Table 1). Thus, we accounted for model uncertainty among the

Table 2. Model averaged parameter estimates of Cox proportional hazard models describing depredation of artificial nests. Model averaging was calculated for all parameters in models that were within 4 Akaike’s information criterion units (adjusted for small sample sizes; AIC_c) of the top AIC_c selected model. Parameters included in model averaging were real fate (nest fate = hatch or fail of the natural sage-grouse nest), date of depredation, magpie density, average perennial grass height, and camera presence. Artificial nest data were collected at 67 nest locations previously occupied by sage-grouse hens in southern Wyoming, USA, during 2010 to 2011.

Parameter	Estimate	SE	95% CI		Variable importance ^a
			Lower	Upper	
Real fate	2.22	0.86	0.54	3.90*	0.99
Date of fate	-0.08	0.03	-0.14	-0.02*	0.93
Grass height	-0.13	0.07	-0.26	0.00*	0.71
Magpie density	4.00	2.00	0.08	7.91*	0.69
Camera presence	0.86	0.64	-0.39	2.11	0.45

*Denotes a 95% confidence interval that does not include zero.

^aAkaike weights from all models containing each variable were added to calculate variable importance. Maximum value for variable importance was 1.

most supported variables by model averaging the parameter estimates of variables from those models. We found that the most supported variables were real fate, date of depredation, magpie density, average height of perennial grass, and camera presence (Table 1). No anthropogenic development or landscape variables described differences in depredation of artificial nests (parameter estimates had 85% CIs that overlapped 0).

Real fate and date of depredation were the most important variables describing depredation of artificial nests with variable importance values of 0.99 and 0.93, respectively (Table 2). We found that the fate of artificial nests mimicked that of natural sage-grouse nests, because an artificial nest placed in a natural sage-grouse nest that failed was more likely to be depredated during the 14-day observation period (real fate parameter estimate = 2.22; 95% CI = 0.54 to 3.90; Table 2). This indicated that the depredation rates of artificial nests paralleled that of natural sage-grouse nests, and the lack of an incubating bird did not bias the pattern of depredation at artificial nests. Our date of depredation results indicated that artificial nests were less likely to be depredated within 14 days as the calendar date increased (i.e., higher values of the date of depredation variable; Table 2; Figure 2).

We found that average height of perennial grass and magpie density were the next most important variables describing depredation of artificial nests with variable importance values of 0.71 and 0.69, respectively (Table 2). Lower heights of perennial grass were correlated with more depredations of artificial nests (Table 2, Figure 2). Average height of perennial grass at depredated artificial nests was 17.4 cm (1.47 SE) compared to 20.26 cm (0.69 SE) at artificial nests that were undisturbed within the 14-day observation period. No other nest-site characteristic accurately explained variation in the depredation of artificial nests. Greater magpie density within study sites was associated with more depredations of artificial nests (Table 2; Figure 2). Average magpie density at depredated artificial nests was 0.14 magpies per km² (0.05 SE) compared to 0.08 magpies per km² (0.01 SE) at artificial nests that were undisturbed within the 14-day observation period. We did not find any effect

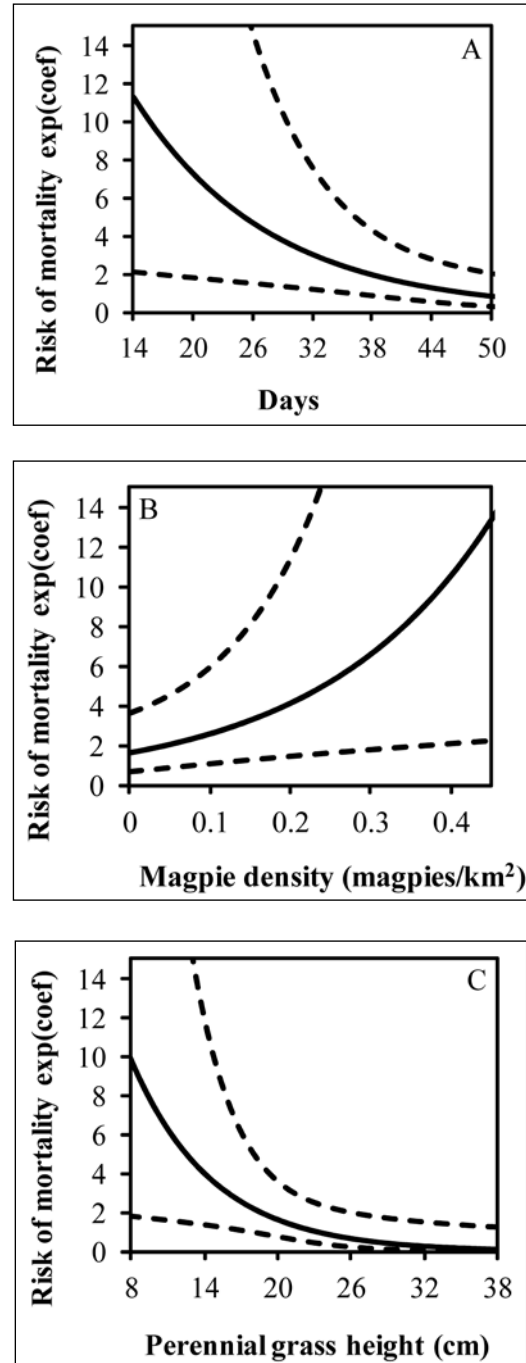


Figure 2. Predicted effects of (A) date of depredation (1 corresponds to June 13), (B) magpie density (magpies/km²), and (C) average perennial grass height (cm) on depredation rates of artificial nests with 95% confidence intervals. Predicted effects were from the best Cox proportional hazard model (see Table 2) and were displayed as the risk of mortality with the y-axis units plotted as exp(coefficient values). Artificial nest data were collected at 67 nest locations previously occupied by sage-grouse hens in southern Wyoming, USA, during 2010 and 2011.

of raven density on depredation of artificial nests.

Camera presence was the least important variable (variable importance = 0.45) within the top AIC_c ranked models and imprecisely explained depredation of artificial nests (Table 2). We included the camera presence variable in modeling because it was determined to be slightly informative when analyzed individually (i.e., 85% CI did not overlap 0 when camera presence was assessed individually). After incorporating uncertainty with model averaging, the parameter estimate of the camera presence variable had 85% CIs that overlapped 0. The parameter estimate of the camera presence variable indicated that the presence of a camera in a nest bowl was associated with more depredations (Table 2); however, we did not have enough data on depredations to decisively determine if this effect was legitimate.

Discussion

Due to low cost and logistic simplicity, artificial nest studies have long been used to study the dynamics behind low nest success of multiple bird species. Many researchers have approached results from these types of studies with skepticism because evidence that the principle criteria ensuring legitimate conclusions may frequently be violated—lack of parallel rates of depredation in space and time (Wilson et al. 1998, Zanette 2002, Moore and Robinson 2004, Thompson and Burhans 2004). Concurrently, results from artificial nest studies continue to be used to address management concerns related to poor nest success. This has necessitated a thorough evaluation of the assumptions behind artificial nest studies. Inconsistencies related to artificial nest resemblance of real nests are the central reasons for violations of parallel depredation. The 3 primary factors contributing to this are poor or incorrect placement (within shrub and on the landscape); appearance (i.e., physical nest structure, egg sightability, lack of incubating hen, and olfactory characteristics); and vulnerability (i.e., egg size, eggshell thickness, and lack of hen defending nest), which affect the probability of an artificial nest being encountered and destroyed by a predator.

Other studies have looked at the mimicry of

depredation pattern by monitoring both artificial and real nests in tandem, which has the intent of observing how well researchers can place and construct artificial nests to produce parallel depredation rates. This approach still has the potential for the introduction of researcher bias in placement, appearance, and vulnerability of artificial nests, which can influence patterns of depredation. Our methods allowed us to evaluate depredation pattern after eliminating potential observer bias in placement by using nest bowls created by natural sage-grouse. We found that depredation rates of artificial nests paralleled that of natural sage-grouse nests. This indicated that the appearance and vulnerability of artificial nests did not bias the relative pattern of hatch or fail at artificial nests, which suggests that placement maybe a greater source of researcher induced bias than appearance or vulnerability for artificial nests aimed at mimicking sage-grouse nests. Our unique approach of comparing natural to artificial nests by using the exact same nest bowls also allowed us to postulate that nest depredation was not a random process as suggested in the literature (Filliater et al. 1994, Wilson and Cooper 1998). It has been difficult to test the randomness of depredation patterns because most nests are only used once; our assessment allowed nests to be tested twice with a nonrandom pattern of depredation between the real and artificial nests providing evidence that not all sage-grouse nests are equally likely to be depredated.

Studies designed to simultaneously monitor artificial and natural nests have found mixed results regarding spatial and temporal correlation of depredation rates at artificial and natural nests (Wilson et al. 1998, King et al. 1999, Vander Haegen 2002, Zanette 2002, Thompson and Burhans 2004). In both fragmented and intact sagebrush steppe habitat, artificial songbird nests paralleled the general pattern of depredation between artificial nests and real nests of Brewer's sparrows (*Spizella breweri breweri*), sage sparrows (*Amphispiza belli*), sage thrashers (*Oreoscoptes montanus*), and Vesper sparrows (*Poocetes gramineus*; Vander Haegen et al. 2002). However, there was substantial variance in depredation rates among individual study sites. The variability seen in depredation rates at individual study sites could have been

a remnant of poor placement of artificial nests at random, which was overwhelmed when looking at their study as a whole. Regardless, this type of error is undesirable in a research method intended to precisely address research questions regarding factors contributing to low nest success. In contrast, Zanette (2002) found no evidence of parallel depredation rates in space or time between artificial nests and natural nests of eastern yellow robins (*Eopsaltria australis*). These results bring doubt onto the validity of the assumption that depredation rates between artificial and natural nests are at least relative spatially and temporally, especially when there is potential for bias in placement of artificial nests. There was no detectible difference or substantial variance of depredation pattern as a result of space or year among the fates of our nests whether incubated by sage-grouse or as artificial nests with brown chicken eggs.

There have been many examples of studies illustrating that predator identification often varies between artificial and natural nests (Wilson et al. 1998, Zanette 2002, Thompson and Burhans 2004). This could lead to different depredation patterns and erroneous interpretations of the effects of local predator compositions. In Missouri, average daily survival rates of artificial and natural nests were the same; however, mice (*Peromyscus* spp.) and raccoons (*Procyon lotor*) preyed on artificial nests, while snakes (black rat snake [*Elaphe obsoleta*], prairie kingsnake [*Lampropeltis calligasteri*], blue racer [*Coluber constrictor*], speckled kingsnake [*Lampropeltis getulus holbroki*], and *Thamnophis* spp.), and raccoons preyed on natural nests of field sparrows (*Spizella pusilla*) and indigo buntings (*Passerina cyanea*; Thompson and Burhans 2004). Eastern yellow robin nests were depredated primarily by large avian predators compared to artificial nests that were primarily depredated by small avian predators (Zanette 2002). Even though our study illustrated high correlation of spatio-temporal correlation between artificial and natural nests, the species of corvid impacting our artificial nests was different from the natural sage-grouse nests determined by comparing our artificial nest results to success of natural sage-grouse nests from Dinkins (2013) during 2008 and 2011. Depredation of natural sage-grouse nests was positively correlated with the

presence of ravens (Dinkins 2013); whereas, magpie density was positively associated with depredation of artificial nests with no effect from raven density (Table 1; Figure 2). Our magpie density results were verified by a small sample ($n = 2$) of images showing magpies depredating two of our artificial nests (Figure 1). Lack of consistent identification of predators makes artificial nests useless at giving insight on the predator composition preying on bird nests included in our study. However, it is worth noting that magpies were the only avian predators detected by cameras and that the alignment of corvid-density effects with camera detections indicates that measures of avian predator density provide an accurate means of testing the effect of avian predators. These results are similar to raven-density effects verified by camera from sage-grouse nests in Nevada (Coates and Delehanty 2010).

The ability of birds, including sage-grouse, to hide their nests in areas that provide better concealment from visual predators influences the success of their nests (Sargeant et al. 1995, Schroeder and Baydack 2001, Evans 2004, Manzer and Hannon 2005, Coates and Delehanty 2010, Conover et al. 2010). Thus, quantifying the effects of nest-site characteristics have been common objectives of artificial nest studies. Habitat factors, such as greater sagebrush, forb, and grass heights, have been associated with increased nest success of artificial and natural sage-grouse nests (DeLong et al. 1995, Watters et al. 2002). Watters et al. (2002) found increased depredation of artificial nests after experimentally cutting grass that surrounded artificial nests constructed to resemble sage-grouse nests. Our artificial nest results confirmed that grass height was an important factor influencing depredation rates (Figure 2). However, grass height seemed to be more important to artificial nests than to natural nests because Dinkins (2013) did not find an effect of grass height on the success of natural sage-grouse nests (mean grass height was slightly higher at successful nests compared to unsuccessful nests). This dichotomy in the effect of grass height may imply that concealment of artificial nests is innately lower than that of natural nests because hens are typically cryptic in behavior and coloration. Alternatively, artificial nests have greater exposure to

depredation by small visual predators, such as magpies, as opposed to nests with incubating hens that proactively protect their nests against smaller predators.

When assessing the effect of calendar date, we found that depredations were more likely to occur earlier in the summer (June to early July rather than late July to early August); thus, depredation of artificial nests was negligible as time progressed past the typical sage-grouse nesting season (Table 2; Figure 2). By examining depredation of artificial nests in relation to calendar date, we were able to provide evidence supporting the hypothesis of predators using a search image (nests) to efficiently detect nests during the nesting season (Tinbergen 1960, Gibb 1962, Alcock 2005).

Artificial nests may give managers a logistically amenable way to study nest success rates of birds, such as sage-grouse, in areas of conservation interest. However, managers need to approach information from these studies with caution. We found that artificial nests may not be good at identifying the species of nest depredator at natural nests. Even though results from artificial nest studies need to be considered with scrutiny, these types of studies have the potential to provide useful information to direct conservation measures.

Acknowledgments

Research funding was provided by the Anadarko Petroleum Corporation, Jack H. Berryman Institute, Lincoln County Predator Management Board, Predatory Animal District of Sweetwater County, School of Energy Resources at the University of Wyoming, South Central Wyoming Local Sage-Grouse Work Group, Uinta County Predator Management Board, Utah Agricultural Experiment Station (journal #8598), Wyoming Animal Damage Management Board, and Wyoming Game and Fish Department. We especially thank J. Borgo for development of nest timers, and M. Holloran for contributing to our sage-grouse nest dataset. We greatly appreciate the logistical support provided by C. Polfus, R. Pyles, N. Schwertner, and D. White, and our many other field technicians who are too numerous to list. We also give a special thanks to the cooperation of the many landowners throughout southwest

and south-central Wyoming for allowing access to private lands.

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