Daily nest survival rates of Gunnison Sage-Grouse (*Centrocercus minimus*): assessing local- and landscape-scale drivers

DAILY NEST SURVIVAL RATES OF GUNNISON SAGE-GROUSE (*CENTROCERCUS MINIMUS*): ASSESSING LOCAL- AND LANDSCAPE-SCALE DRIVERS

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ABSTRACT.—The Gunnison Sage-Grouse (*Centrocercus minimus*) is a species of conservation concern and is a candidate for listing under the U.S. Endangered Species Act because of substantial declines in populations from historic levels. It is thought that loss, fragmentation, and deterioration of sagebrush (*Artemisia* spp.) habitat have contributed to the decline and isolation of this species into seven geographically distinct subpopulations. Nest survival is known to be a primary driver of demography of Greater Sage-Grouse (*C. urophasianus*), but no unbiased estimates of daily nest survival rates (hereafter nest survival) exist for Gunnison Sage-Grouse or published studies identifying factors that influence nest survival. We estimated nest survival of Gunnison Sage-Grouse for the western portion of Colorado's Gunnison Basin subpopulation, and assessed the effects and relative importance of local- and landscape-scale habitat characteristics on nest survival. Our top performing model was one that allowed variation in nest survival among areas, suggesting a larger landscape-area effect. Overall nest success during a 38-day nesting period (egg-laying plus incubation) was 50% (daily survival rate; SE = 0.982 [0.003]), which is higher than previous estimates for Gunnison Sage-Grouse and generally higher than published for the closely related Greater Sage-Grouse. We did not find strong evidence that local-scale habitat variables were better predictors of nest survival than landscape-scale predictors, nor did we find strong evidence that any of the habitat variables we measured were good predictors of nest survival. Nest success of Gunnison Sage-Grouse in the western portion of the Gunnison Basin was higher than previously believed. *Received 9 January 2014. Accepted 13 August 2014.*

Key words: *Centrocercus minimus*, Gunnison Sage-Grouse, habitat, landscape-scale models, local-scale models, nest success, nest survival.

  Subpopulations of Gunnison Sage-Grouse (*Centrocercus minimus*) have declined substantially from historic levels, and only ~4,400 (not all breed) Gunnison Sage-Grouse remain across seven geographically isolated subpopulations in Colorado and Utah (U.S. Department of the Interior 2010). Most birds (~3,800) reside within the Gunnison Basin (U.S. Department of the Interior 2010). Loss, fragmentation, and deterioration of sagebrush habitat have contributed to declines and isolation of these subpopulations (Braun 1995, Oyler-McCance et al. 2001, Gunnison Sage-Grouse Rangewide Steering Committee 2005), resulting in elevated conservation concern and listing as a candidate species under the U.S. Endangered Species Act (U.S. Department of the Interior 2010). This resulted in the U.S. Fish and Wildlife Service developing a proposed rule to list the species as endangered (U.S. Department of the Interior 2013a), and a proposed critical habitat rule (U.S. Department of the Interior 2013b) for Gunnison Sage-Grouse.

  Researchers have studied nest survival for many populations of the larger-bodied Greater Sage-Grouse (*C. urophasianus*; Aldridge and Boyce 2007, Moynahan et al. 2007, Kolada et al. 2009a) and have shown the influence of nest survival on population growth (Taylor et al. 2012), but there are no published daily nest survival rate (hereafter nest survival) estimates that are also unbiased for Gunnison Sage-Grouse. The only published estimate of nest success for Gunnison Sage-Grouse reported an apparent nest success rate of 43% in the Gunnison Basin (Young 1994). Apparent nest success of Greater Sage-Grouse varies widely (i.e., 15–86%) across its range, but is typically between 30–60% (Schroeder et al. 1999, Connelly et al. 2011). Apparent nest success estimates are based on the proportion of nests found that survive to fledge at least one chick, and are typically positively biased (Mayfield 1961, 1975), because some nests may

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fail before they are discovered. In addition, re-nesting rates, which may affect seasonal breeding success, vary widely across the species' range (Schroeder et al. 1999). Unbiased estimates of nest survival specific to Gunnison Sage-Grouse would help inform conservation efforts, and allow for careful assessment of vegetation and land-scape features associated with nest survival. This would help guide management of habitats to enhance nest survival and productivity, which likely have strong influences on population growth rates (Taylor et al. 2012).

Little work specific to vegetation characteristics at Gunnison Sage-Grouse nest sites has been published, but nest site habitat characteristics and their influence on nest site selection have been extensively examined for Greater Sage-Grouse. These studies have largely focused on resources directly at the nest site, or the habitat surrounding the nest, with more recent emphasis on landscape-scale assessments. In the area that surrounds a nest site, Greater Sage-Grouse have been shown to select for greater sagebrush (Wallestad and Pyrah 1974, Aldridge and Brigham 2002, Aldridge 2005, Hagen et al. 2007) or shrub canopy cover (including sagebrush; Gregg et al 1994, Sveum et al. 1998, Holloran et al. 2005, Kolada et al. 2009b), and tall grass cover (Aldridge 2005, Holloran et al. 2005, Hagan et al. 2007) compared to available habitats. The concealment cover provided by grasses and available shrubs (often sagebrush) is thought to reduce nest predation by providing visual and scent barriers and has similarly been linked to increased nest success (Gregg et al. 1994, DeLong et al. 1995, Aldridge and Brigham 2002, Watters et al. 2002, Aldridge 2005), but effects may depend on the predator community present (Coates and Delehanty 2010). However, animals inherently select habitat at multiple spatial scales (Johnson 1980), and sage-grouse have been shown to select nest sites across spatial scales (Aldridge and Boyce 2007, Kolada et al. 2009b, Doherty et al. 2010, Aldridge et al. 2012). Public lands are typically managed at greater spatial extents than the fine scale detail provided by most previous nest site selection studies (i.e., a small <15-m patch around the nest), and management actions directed at sage-grouse conservation would have greater applicability if the links between habitat influences and demographics across spatial scales could be ascertained (Wiens 1989; Orians and Wittenber-ger 1991; Boyce 2006; Aldridge and Boyce 2007,

2008; Aldridge et al. 2012). Mechanistic drivers are beyond the scope of our study, but it is important to note that even though vegetation conditions and structure across regions may be similar, predator communities may ultimately have varied effects on nest survival (Coates and Delehanty 2010, Conover et al. 2010).

Our objective was to estimate daily nest survival rates of Gunnison Sage-Grouse for the western portion of Colorado's Gunnison Basin subpopulation, and to assess the effects of local- and landscape-scale habitat characteristics on nest survival. We have previously shown that resources assessed at scales beyond a few meters surrounding a nest site affect nest site selection (Aldridge et al. 2012), and we predicted that vegetation characteristics in the immediate vicinity of the nest will most strongly affect nest survival in comparison with remotely-sensed vegetation variables summarized across large landscapes. We also predicted that nests in landscapes with anthropogenic features nearby will experience reduced survival rates, possibly the result of increased disturbances or elevated predator activity associated with anthropogenic features (Andrén and Angelstam 1988).

Finally, we investigated whether daily nest survival rates differed between two geographically distinct areas containing the majority of nests in the study area: Kezar Basin and Sapinero Mesa. These areas differ in grazing management practices, past habitat treatments, elevation, and overall productivity.

METHODS

Study Area.—The Gunnison Basin is a high-elevation valley on the eastern edge of the Colorado plateau, and ranges in elevation from ~2,200–3,100 m asl. The average annual temperature within the basin is 3.1 °C with 27 cm of average annual precipitation. Gunnison Sage-Grouse currently occupy ~2,400 km² of habitat within the Gunnison Basin, 70% of which is public land (Gunnison Sage-Grouse Rangewide Steering Committee 2005). Our study area was ~845 km² in size, ~58% (492 km²) of which was public land. Nesting data for our study were collected in the western portion of the Gunnison Basin and focused on the Curecanti National Recreation Area managed by the National Park Service, and the surrounding area (Fig. 1; from Aldridge et al. 2012).
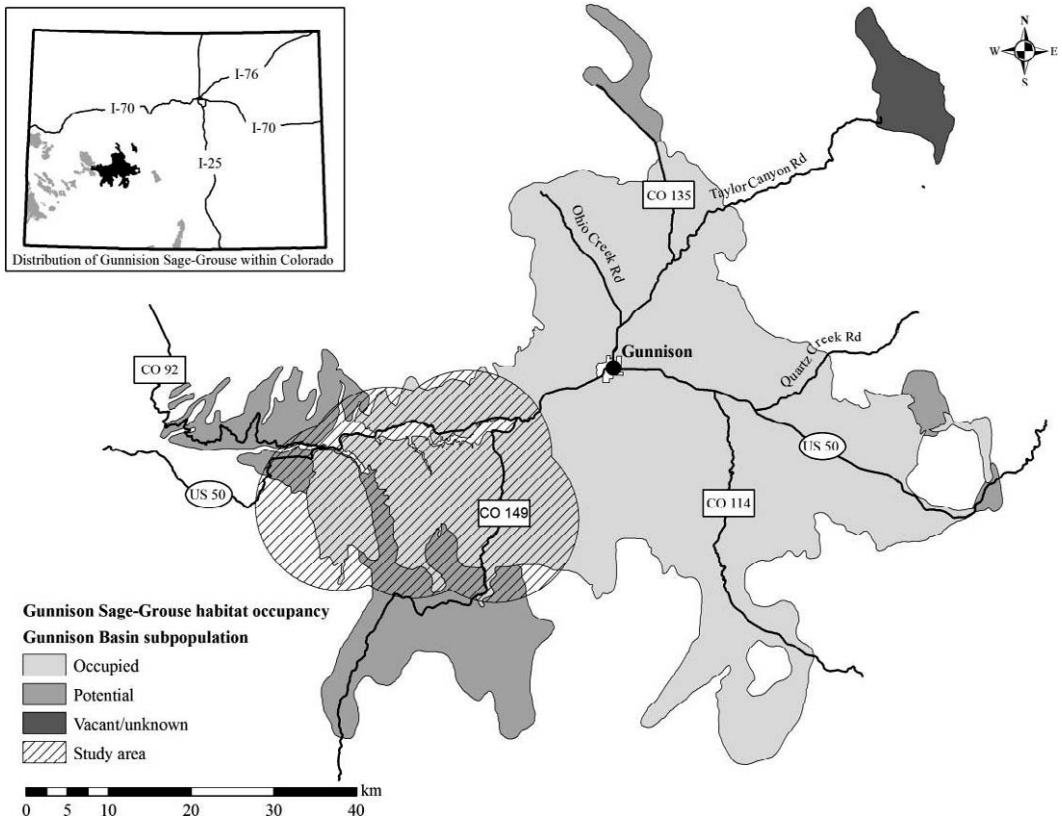
FIG. 1. Nesting data were collected in the western portion of the Gunnison Basin, Colorado (From Aldridge et al. 2012).

Sagebrush-steppe is prevalent throughout the Gunnison Basin with big sagebrush (*A. tridentata* spp.) dominant. Intermixed within the sagebrush community are riparian areas and drainages containing narrowleaf cottonwood (*Populus angustifolia*), Rocky Mountain juniper (*Juniperous scopulorum*), Gambel oak (*Quercus gambelii*), serviceberry (*Amelanchier utahensis*), and wild rose (*Rosa woodsii*). Most of the valley bottoms along major drainages have been converted to hay fields and pastures. Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), spruce (*Picea* spp.), and quaking aspen (*P. tremuloides*) forests occur at higher elevations.

Nesting Data Collection.—We captured adult and yearling female Gunnison Sage-Grouse during April and the first week of May near seven of 10 known active leks within the study area from 2000–2009 using spotlighting techniques (Giesen et al. 1982). We fitted captured birds with a necklace-style radio transmitter (RI-2BM - Holohil Systems, Carp, Ontario, Canada; A4050 -

ATS, Isanti, MN, USA). We located marked hens on average every 4.2 days (range = 1–30 days, SD = 4.5) during the trapping and nest initiation period. Once hen movements became localized to a relatively small area, we located hens every 1–3 days (average = 1.7 days, range = 1–20 days, SD = 1.6) using triangulation and by obtaining visual confirmation of the hen's location using binoculars.

We assumed a location was a nest when we observed a hen in the same location on consecutive days. We assumed hens were on a nest when we detected a strong radio signal on an established transect intersecting the estimated nest location from a location marked with a rock cairn ≥20 m (but typically farther) from the nest location. This was done to minimize disturbance that could have led to nest abandonment or predation. Once the hen vacated the nest, we examined eggshells for evidence of hatching or predation, and we confirmed hatching when we located brooding hens on the evening of the hatch/nest location date

and saw chicks present. We recorded the Global Positioning System (GPS) coordinates of the nest and post-processed locations using Trimble Pathfinder Office software (Trimble Navigation Limited, Sunnyvale, CA, USA) to increase spatial location accuracy (~0.5 m). All animal handling methods and protocols were approved by the U.S. Geological Survey Fort Collins Science Center's Institutional Animal Care and Use Committee.

Local-scale Habitat Data Collection.—We collected habitat data at each nest shortly after the nest was vacated ($\bar{x}$ = 6 days after eggs hatched or failed, range = 0–22 days) to characterize habitat conditions that contributed to the fate of each nest (Gregg et al. 1994, Sveum 1998, Aldridge and Brigham 2002, Watters et al. 2002, Crawford et al. 2004, Aldridge 2005, Holloran et al. 2005, Moynahan et al. 2007). We measured vegetation characteristics at each nest along a 30-m transect centered on the nest and oriented perpendicularly to the slope aspect of the nest site (e.g., for a nest on a slope with a south aspect we oriented the transect east-west). We used the line-intercept method (Canfield 1941) to estimate overall live and dead sagebrush canopy cover. We classified canopy cover as 'live' if any layer was alive and classified it as 'dead' only if all layers were dead or multiple layers of live and dead sagebrush canopy intersected the transect.

We used the Daubenmire (1959) method to estimate percent graminoid (new and residual) and forb cover. We estimated the percent cover of both graminoids and forbs within 10, 20 × 50-cm microplots placed at 3-m intervals along the downslope side of the 30-m transect, beginning at 2 m. We assigned estimated graminoid and forb cover to one of 12 cover categories (≤1, >1–10, >10–90% in eight 10% increments, >90–99, and >99%). The median value of graminoid and forb cover categories from each microplot was averaged across all 10 microplots to produce a mean graminoid and forb cover metric for each nest. We calculated mean grass height by averaging the maximum droop height of all grasses occurring in all microplots. Average forb height was calculated by measuring the height of one forb closest to the down-slope edge of each microplot and averaging forb heights across all 10 microplots.

Visual obstruction at the nest has been shown to be a significant factor influencing Greater Sage-Grouse nest and chick survival (Aldridge 2005, Aldridge and Boyce 2008). We measured visual obstruction of vegetation at the nest using a Robel pole marked in 10-cm increments (Robel et al. 1970) centered in the nest bowl, and recorded vegetation obstruction from a distance of 15 m in each of the four cardinal directions. We averaged these measurements to produce an overall estimate of visual obstruction at the nest site and computed the coefficient of variation of the four measurements to use as a measure of the uniformity of the visual obstruction.

Landscape-scale Habitat Data Collection.—The landscape-scale spatial predictor variables that we used for our nest survival analysis were a subset of those previously developed for investigation of nest site habitat selection of Gunnison Sage-Grouse (Aldridge et al. 2012). These data were either directly available digitally or were derived from remotely-sensed information, and were used to describe the vegetation, anthropogenic, and topographic characteristics of our study area. We selected variables based on their potential effect on nest survival. We evaluated these metrics at spatial scales ranging from a 3 × 3 grid (30 m × 30 m pixels) to a spatial window extent that encompassed an area with a radius of 6.4 km. We did not consider individual pixel values given that we had local-scale data measured on the ground.

Variables used for modeling varied broadly in one of two categories: (1) those that contributed to nest concealment and (2) those that facilitated predation. Vegetation variables came from products developed specifically for the Gunnison Basin using remotely sensed information (Aldridge et al. 2012, Homer et al. 2013). Shrub metrics included mean percent cover, standard deviation of cover (a surrogate for patchiness), and proportion of area with >5, 10, 15, and 20% shrub cover (all species), sagebrush (all species combined), and all big sagebrush (all subspecies combined) over the full range of spatial windows. Other vegetation metrics included mean percent cover of herbaceous vegetation and bare ground over the 3 × 3 grid extent. Nest predation on Greater Sage-Grouse has been shown to be correlated negatively with the amount of herbaceous cover surrounding the nest (Gregg et al. 1994, Coates and Delehanty 2008); however, there is evidence that increased herbaceous cover may lead to higher predation rates by American badgers (*Taxidea taxus*) (Coates and Delehanty 2010). We also investigated the effect of proximity (Euclidian distance measured in km) to

conifer/juniper classed habitat and water on the nest success of Gunnison Sage-Grouse. Patches of coniferous habitat can provide perching opportunities for avian predators, and riparian areas can act as travel corridors for both avian and mammalian predators (Connelly et al. 2004, Aldridge and Boyce 2007). Habitat selection studies (Aldridge et al. 2012) have indicated the relationship between distance to water and habitat use as non-linear, so we considered both linear and quadratic forms of this variable.

We also examined metrics that captured the potential impact of residential development on nest survival. A wide array of anthropogenic development has been shown to attract Common Ravens (*Corvus corax*) (Bui 2009), a known nest predator of sage-grouse (Schroeder and Baydack 2001, Holloran et al. 2005, Coates 2007). Residential metrics included both density and proximity. Density was calculated over the range of spatial windows, and both linear and quadratic forms of the distance variable were considered. Similarly, roads have the potential to influence nest survival through disturbance of nesting hens and facilitation of predator dispersion into a landscape (Knight and Kawashima 1993, Forman and Alexander 1998, Connelly et al. 2004). We looked at linear road density across all spatial windows as well as linear and quadratic forms of road proximity.

The effect of vegetation productivity on nest survival was assessed using NDVI (Normalized Difference Vegetation Index) and CTI (Compound Topographic Index). NDVI is a measure of greenness derived from spectral images using a tasseled cap transformation, whereas CTI is a terrain derived index correlated with soil moisture and vegetation productivity (Gessler et al. 1995). We make the assumption that more productive areas would provide greater concealment of nests at a small scale, and perhaps make searching by predators more difficult at larger scales. The mean and standard deviation of both productivity variables were calculated over all spatial windows. Values associated with each nest site were extracted from spatial data sets using the Spatial Analyst extension in ArcMap 10.0 (ESRI, Redlands CA, USA).

Statistical Analyses.—We estimated daily nest survival rates using the likelihood-based model of Dinsmore et al. (2002) with a logit link to accommodate individual covariates. We selected this model for analysis because it does not have the intrinsic bias of apparent survival estimates, and because of its generality; other commonly used models such as Mayfield (1961, 1975), Johnson (1979), and Schaffer (2004) are special cases of this model. An additional benefit of the Dinsmore et al. (2002) model is the availability of software (i.e., Program MARK; White and Burnham 1999) for modeling individual covariates and obtaining point and error estimates.

We performed a correlation analysis of covariates prior to model building to assess for possible collinearity; all variables retained for *a priori* analyses had a $|r| \leq 0.50$. We identified a set of 32 *a priori* models that we believed could potentially explain variation in nest survival (Appendix). Twelve of these models were at the local-scale and 17 were at the landscape-scale. Three additional models were an intercept only (i.e., null) model, an area-specific model (i.e., Kezar, Sapinero, other), and an age-specific model (i.e., adult, yearling). We evaluated several *post hoc* exploratory models in addition to the *a priori* models.

We compared alternative models using Akaike's Information Criterion corrected for small sample size (AIC_c), and computed model weights (w_i; Burnham and Anderson 2002). ΔAIC_c, computed as the difference between the AIC_c value of the model of interest and the AIC_c of the best model (i.e., $AIC_{c\ min}$), along with model weights (w_i), provided a measure of the relative strength of evidence for each model given the data and our candidate set of models. Models with $\Delta AIC_c \leq 2$ were considered to have substantial support with the exception of those that differed from the best model by one additional parameter and which had essentially the same values of the maximized log-likelihood as the best model (Burnham and Anderson 2002, Arnold 2010). These latter models provide no net reduction in AIC_c (Arnold 2010), and we excluded them from consideration. We report only results for models with $\Delta AIC_c \leq 2$.

We computed 85% confidence intervals (CIs) for parameters (β) on the logit scale and present them as $\beta \pm 1.44(SE)$ based on the recommendation of Arnold (2010). We computed 95% confidence intervals with Program MARK using the appropriate logit-linear model and the delta method (Seber 1982, Cooch and White 2010) for daily nest survival rates. We defined nest success as daily nest survival rate exponentiated by the estimated number of days in the both the egg

TABLE 1. Model selection results for *a priori* models reporting only results for models with $\Delta AIC_c \leq 2$; k is the number of parameters in the model. All non-null models have an intercept term that is omitted from the table.

Model[a]	AIC_c	ΔAIC_c	w_i	k
areaO + areaS	291.24	0.00	0.215	3
mugrsht	291.87	0.63	0.157	2
mugrsht + lsagecc + dtotgras + muforbht	291.97	0.73	0.149	5
null	292.48	1.24	0.115	1
dist_res + dist_res^2	292.61	1.37	0.108	2
dist_cj	293.06	1.82	0.087	2
lsagecc	293.10	1.85	0.085	2
dtotgras	293.12	1.88	0.084	2

[a] areaO = other areas (i.e., non Kezar, non Sapinero); areaS = Sapinero area; dist_cj = distance from nest to nearest conifer/juniper (km); dist_res = distance from nest to nearest residential classed habitat (km); dtotgras = total grass cover (%); lsagecc = live sagebrush canopy cover (%); muforbht = average forb height (cm); mugrsht = average grass height (cm); null = intercept only model.

laying and incubation stages under the assumption that nest survival was constant across both stages.

RESULTS

We trapped and monitored 73 hens during breeding seasons from 2000–2010; 24 hens nested in Kezar Basin, 33 hens nested on Sapinero Mesa, and 11 hens nested in surrounding areas (hereafter labeled 'other'). We found no evidence of nesting for 5 hens (7%). We monitored 98 nests, of which 57 survived to produce at least 1 chick; 36 nests failed, 1 was abandoned, and 4 were not monitored because of staffing shortages in 2001. We did not flush hens from potential nest sites, and it is possible that some nests that failed in the laying or early incubation stage were missed. Six of the 98 nests we monitored were censored from the sample (4 unknown fate, 2 vegetation transects were not completed), and of the 92 nests remaining, 65 were incubated by adults and 27 by yearlings. Some hens initiated nests in multiple years of the study. Twenty-two hens initiated nests in 2 years, while five hens initiated nests in three consecutive years. We considered all nests to be statistically independent and all nests with complete data sets were included in our nest survival analysis. We observed only one re-nest attempt throughout the course of our study. We did not include this attempt in our analysis.

We collected incubation period data from 50 of the 57 successful nests. Average incubation periods were 28.7 days (range = 28–30 days). Mean clutch size, based on nest contents after hatch and a count of chicks brooded by the marked hen on the hatch day, was 6.0 eggs/clutch (range = 3–9 eggs/clutch) for 50 of the 57 successful nests, and 6.1 eggs/clutch (range = 3–9 eggs/clutch) for 27 of the 36 depredated nests with

sufficient egg shell evidence to assign clutch size, giving an overall weighted average clutch size of 6.0 eggs/clutch ($n = 77$) for nests in the study. Egg viability (percentage of eggs hatching in all 57 successful nests) was 93% (343 of 370 eggs).

A Priori Model Results.—Model selection results for the *a priori* models we evaluated (Appendix), where only results for models with $\Delta AIC_c \leq 2$ are reported, varied (Table 1). The best model from among those evaluated was one that allowed for variation in nest survival among areas ($AIC_c = 291.24$). Daily nest survival rates for Kezar Basin ($n = 30$ nests), Sapinero Mesa ($n = 46$ nests), and the other areas ($n = 16$ nests) were 0.978 (SE = 0.006), 0.980 (SE = 0.004), and 0.995 (SE = 0.004), respectively. Assuming a 9.0-day egg laying period, computed as the product of our estimate of 6.0 eggs/clutch and an assumed 1.5-day interval between laying of consecutive eggs, and adding to this our estimated 28.7-day incubation period, we had an estimated nesting period of 37.7 days that we rounded to 38 days. Nest success for Gunnison Sage-Grouse for Kezar Basin, Sapinero Mesa, and other areas using this 38-day estimate, was 43% (SE = 10%), 46% (SE = 7%), and 83% (SE = 13%), respectively.

The second- and third-ranked models contained local-scale variables that included: average grass height (cm; mugrsht), live sagebrush canopy cover (%; lsagecc), total grass cover (%; dtotgras), and average forb height (cm; muforbht). Parameter estimates and 85% CIs for these variables indicated daily nest survival rates increased as mean grass height increased ($\beta = 0.057$; 85% CI = 0.005, 0.110; estimate taken from higher ranked model) but decreased as mean forb height ($\beta = -0.066$; 85% CI = -0.118,
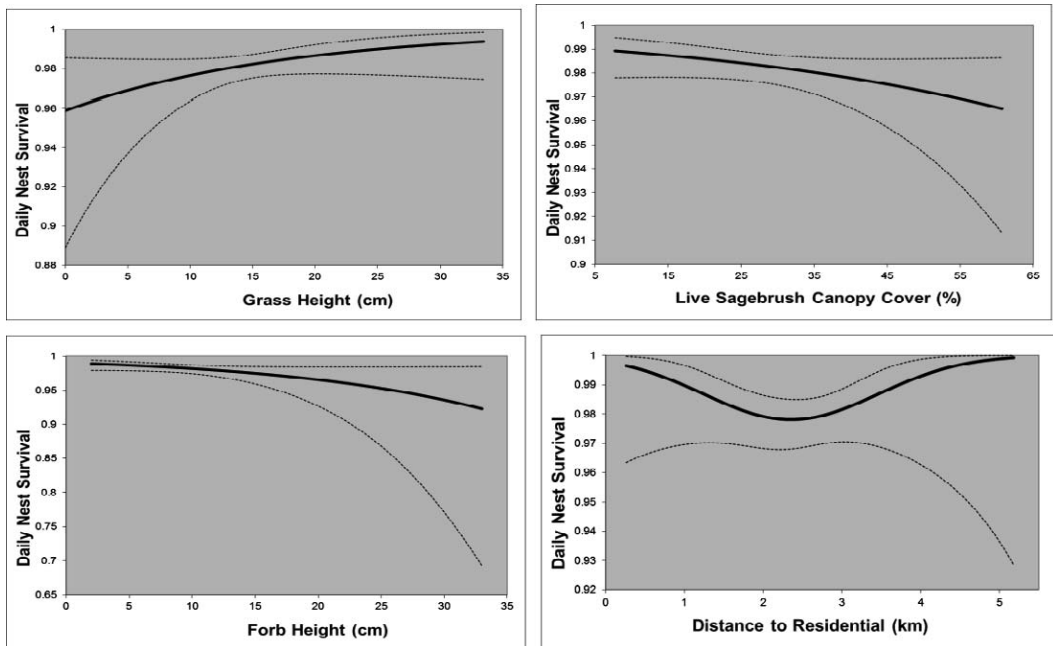
FIG. 2. Effects of local-scale and landscape-scale vegetation variables on daily nest survival rates (95% CI) of Gunnison Sage-Grouse within the western portion of the Gunnison Basin, Colorado.

−0.014) and live sagebrush canopy cover (β = −2.282; 85% CI = −4.416, −0.147) increased (Fig. 2). The parameter estimate and 85% CI for total grass cover (β = 1.250; 85% CI = −0.292, 2.792) did not support an effect.

The fourth-ranked null model, equivalent to the top model but with all sites pooled (n = 92 nests), yielded a daily nest survival rate of 0.982 (SE = 0.003) and a 50% (SE = 6%) nest success over the 38-day nesting period.

The fifth- and sixth-ranked models contained landscape-scale variables that included distance from nest to nearest residential classed habitat (km; dist_res) and distance from nest to nearest conifer/juniper (km; dist_cj) classed habitat. Parameter estimates and 85% CIs for these variables indicated daily nest survival rates decreased and then increased (i.e., the pattern is quadratic) as distance to residential-classed habitat (β_1 = −1.99; 85% CI = −3.848, −0.132; and β_2 = 0.423; 85% CI = 0.027, 0.819) increased (Fig. 2). The parameter estimate and 85% CI for distance to conifer/juniper-classed habitat (β = −0.939; 85% CI = −2.052, 0.174) did not support an effect.

The final two models (Table 1) contained local-scale variables that already appeared in the third-

ranked model. The parameter estimate and 85% CI for live sagebrush canopy cover (lsagecc) in the seventh-ranked model was (β = −1.848; 85% CI = −4.057, 0.361) and for total grass cover (dtotgras) in the eighth-ranked model was (β = 1.203; 85% CI = −0.310, 2.716) and there was no support for an effect in either case.

Post Hoc Exploratory Model Results.—We evaluated eight *post hoc* exploratory local-scale models and compared them to our *a priori* models. Only one of the exploratory models appeared to explain variation in nest survival better (AIC$_c$ = 290.56) than our best *a priori* model (AIC$_c$ = 291.24) (Table 1). That model contained only a single covariate representing grass volume: grass cover (%) × grass height (cm). The parameter estimate and 85% CI for this variable indicate daily nest survival increased as grass volume increased (β = 0.010; 85% CI = 0.022, 0.177).

We evaluated a total of 134 *post hoc* exploratory models (all of which were univariate or bivariate additive) at the landscape-scale to examine how certain variables performed relative to the variables appearing in our *a priori* analysis. Eighty-six of these 134 models were based on shrub variables, 21 were based on productivity

variables, 5 were based on proximity to and density of residential development, and 22 were based on road variables. We found three shrub variable models (all univariate) based on comparisons of the exploratory model AIC_c values with the best *a priori* model (i.e., the area model; Table 1) to be better supported by the data, and no productivity, residential, or road variable models.

The shrub variables in all three of these models were highly correlated (i.e., $|r| \geq 0.76$) and we report only the top ranked model, where the predictor variable was the proportion of pixels with $>15\%$ big sagebrush (all subspecies) cover across a 6.4-km radius window. The parameter estimate and 85% CI for this variable indicated that nest survival increased as the proportion of big sagebrush increased ($\beta = 431.1$; 85% CI = 63.3, 798.9).

DISCUSSION

Overall nest success over a 38-day nesting period (egg-laying plus incubation) under the null model was 50% (daily survival rate = 0.982), which is higher than the only available apparent nest success estimate for the species (43%; Young 1994) and is generally higher than published results for the closely related Greater Sage-Grouse where mean nest success was 46% for 29 published radio telemetry studies (both apparent and unbiased estimates; Connelly et al. 2011). Much of the early literature for Greater Sage-Grouse presents apparent estimates of nest success (ranging from 15–86% (Schroder et al. 1999, Connelly et al. 2011), and our unbiased estimate of nest success for the laying and incubation period (50%) is slightly higher than comparable unbiased estimates from Wyoming (37% over 34 days; Holloran et al. 2005), and Nevada (41% over 37 days; Coates and Delehanty 2010). Similarly, nest success in our study of Gunnison Sage-Grouse for the incubation period only (rounded to 29 days) was estimated at 59% (SE = 5%), and was higher than similar estimates from northern Montana (23–41%; Moynahan et al. 2007) and Alberta (39%; Aldridge and Boyce 2007). Thus, at least for our study population in the western portion of the Gunnison Basin, nest success of Gunnison Sage-Grouse is higher than previously believed.

The top performing model from among those evaluated in the *a priori* analyses was one that allowed for variation in nest survival among areas, and likely captures a larger landscape area effect.

There was little difference in nest survival for nests in Kezar Basin and on Sapinero Mesa, but nest survival was greater in the outlying areas (labeled 'other'). However, the sample size of nests for the outlying areas was relatively small ($n = 16$), and we are uncertain whether this result is real or is an artifact of sampling variation. Additional research confirming our result, as well as examining possible explanatory factors if the result is real, would be useful.

Current sage-grouse research identifies landscape-scale issues such as habitat loss and fragmentation as being the predominant threats to Greater Sage-Grouse populations (Braun 1998, Connelly et al. 2004, Stephens et al. 2004, Aldridge and Boyce 2007, Moynahan et al. 2007, Wisdom et al. 2011). More specifically, resources and disturbances across large landscapes affect nest site selection by sage-grouse (both species; Connelly et al. 2004, Aldridge and Boyce 2007, Kolada et al. 2009b, Doherty et al. 2010, Aldridge et al. 2012); therefore, large-scale habitat characteristics may also affect nest survival (Aldridge and Boyce 2007, Moynahan et al. 2007). We predicted that local scale vegetation characteristics would be better predictors of nest survival than remotely-sensed vegetation characteristics summarized across large landscapes. This was based on numerous studies investigating the importance of shrub (Wallestad and Pyrah 1974, Gregg et al. 1994) and grass cover (Gregg et al. 1994, Sveum et al. 1998) in concealing Greater Sage-Grouse nests from predators.

The *a priori* local-scale vegetation models slightly outperformed our *a priori* landscape-scale models, but the margin was small and is somewhat equivocal. The top two local-scale models had ΔAIC_c values of 0.63 and 0.73, and our top two landscape-scale models had ΔAIC_c values of 1.37 and 1.82 (Table 1). These values are <2, and the corresponding models should be considered competitive with each other as well as competitive with the best model. The presence of the mean grass height variable (mugrsht) in the top two local-scale models may have caused the local-scale models to perform better than expected. Data representing mugrsht were measured at the time of loss for nests that failed and were measured at the time of hatching for successful nests. This is common practice in similar studies, but the median difference in time of measurement between failed and successful nests was 12 days.

It is possible that increases in grass height for successful nests over those 12 days made mugrsht appear to be a better predictor of nest survival than it actually was. For example, if mugrsht had been measured at nest initiation or on the expected hatch date for all nests regardless of nest fate, it is conceivable there would be no difference in mugrsht between failed and successful nests. Thus, the variable would have no predictive value with respect to nest survival. Consequently, there is insufficient evidence that local-scale variables performed better than landscape-scale variables.

Despite relatively high nest success when compared to apparent nest success estimates of Gunnison Sage-Grouse, and the more robust estimates of Greater Sage-Grouse, understanding factors that influence nest survival of Gunnison Sage-Grouse is important, because it may allow managers to focus on specific habitat requirements to increase productivity and recruitment for small or declining populations. Local-scale models in our study containing the covariates grass height, live sagebrush canopy cover, and forb height performed slightly better than a null model with no covariates, and the 85% CI on the parameter estimates did not cover zero, suggesting these variables influenced nest survival.

Increases in grass height were associated with increased nest survival rates. This is consistent with previous findings for Greater Sage-Grouse throughout the species' range (Gregg et al. 1994, Aldridge 2005). Grass cover during nesting is provided predominantly by residual grass from the previous growing season (Crawford et al. 2004). Lateral cover provided by tall residual grasses likely conceal nests from non-avian predators (Wallestad and Pyrah 1974, Gregg et al. 1994, Aldridge and Brigham 2002, Crawford et al. 2004, Aldridge 2005), acting as either visual or scent barriers and enhancing nest survival. However, Coates and Delehanty (2010) found badger predation of Greater Sage-Grouse nests increased with visual obstruction of understory vegetation at nest sites in Nevada. Crawford et al. (2004) recommended the maintenance of tall residual bunchgrass (>18 cm) to ensure suitable screening cover for nests, which has been linked to increased nest success in Oregon (Gregg et al. 1994). Our measurements of grass height may have confounded grass phenology with nest fate. Consequently, we are unable to conclude that grass height is a good predictor of nest fate.

Increases in forb height were associated with decreased nest survival rates. This is the opposite of what we expected because, like taller grasses, we expected taller forbs to produce a more effective visual barrier that would make nests harder for predators to detect. Recent research suggests that Greater Sage-Grouse conceal their nests from visual predators but not olfactory predators (Conover et al. 2010). Nests with greater vertical and horizontal cover and taller shrubs work well to hide nests from visual predators but prevent updrafts, high turbulence, and greater wind speeds, thus making these nest sites easier for olfactory-based mammalian predators to discover (Conover 2007). Coates and Delehanty (2010) showed that Greater Sage-Grouse nest sites with greater visual obstruction and a higher dry biomass of forbs and grasses increased the likelihood of predation by badgers. Badgers are not abundant in the Gunnison Basin, but other common mesopredators, such as coyotes (*Canis latrans*), may use olfactory cues to discover nests.

Our finding that nest survival was associated negatively with live sagebrush canopy cover was surprising, because most sage-grouse nests (both species) are placed under sagebrush and we have previously shown strong selection for sagebrush surrounding nest sites in this Gunnison Sage-Grouse population (Aldridge et al. 2012). Research on Greater Sage-Grouse shows that nest success increases as sagebrush (Wallestad and Pyrah 1974, Connelly et al. 1991) or shrub (Gregg et al. 1994, Delong et al. 1995, Aldridge 2005, Coates and Delehanty 2010) cover increases. However, sagebrush cover had no apparent effect on nest survival in Washington (Sveum et al. 1998). We re-examined the data we used to model nest survival as a function of live sagebrush canopy cover, and suspected two extreme observations were perhaps exerting undue influence on the results. We re-ran model three (Table 1) without these observations and the resulting 85% confidence interval on live sagebrush canopy covered zero. Thus, we are uncertain whether the negative effect of live sagebrush canopy cover on nest survival we observed is real. We note our landscape-scale *post hoc* exploratory model suggests big sagebrush cover might be important in our study area.

The only other model in which the 85% CI on the parameters did not cover zero was the dist_res + dist_res[2] model (Table 1). This model and the

remaining lower ranked models had even less support than the null model containing no covariates. Thus, it seems unlikely these variables strongly affected nest survival in the system we studied. None of the local-scale or landscape-scale variables we investigated seemed to be strongly associated with nest survival. The candidate models had AIC_c values that were close to the null model in all cases and we agree with Arnold (2010) that 85% CIs are appropriate for analyses like ours; if we had instead reported 95% CIs, the intervals would have covered zero for every habitat variable we investigated. Possible reasons for the lack of a strong association would include a small sample of nests (98), inappropriate habitat variables or methods for measuring those variables, variables were characterized at an inappropriate scale, insufficient variability among nests to allow correlations to be detected (e.g., because of strong selection for some characteristics, Aldridge et al. 2012), or the variables do not affect nest survival.

Our sample population of nests in this study is representative of only those nests in our study area (Fig. 1), and statistical inferences with respect to nest survival and factors associated with nest survival may apply only to that area and not the greater Gunnison Basin or smaller subpopulations. The relatively high rate of nest survival we observed is encouraging, and suggests nest success is less of a concern for Gunnison Sage-Grouse than it is for Greater Sage-Grouse. Consequently, if resources for research and management are limited, investigation of other vital rates could be given priority.

ACKNOWLEDGMENTS

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APPENDIX. The set of 32 *a priori* models of nest survival of Gunnison Sage-Grouse we hypothesized could potentially explain variation in nest survival within the Gunnison Basin, Colorado, where each model represents a different hypothesis; *k* is the number of parameters in the model. All non-null models have an intercept term that is omitted from the table.

Model[a]	*k*
null	1
areaO + areaS	3
agej	2
Local-scale models	
mugrsht	2
mugrsht + lsagecc + dtotgras + muforbht	5
lsagecc	2
dtotgras	2
lsagecc + mugrsht + robmu	4
muforbht	2
robcv	2
dtotforb	2
dsagecc	2
robmu	2
lsagecc + lsagecc^2	3
lsagecc + dsagecc + lsagecc*dsagecc	4
Landscape-scale models	
dist_res + dist_res^2	3
dist_cj	2
herb_am	2
dist_rd1_4 + dist_rd1_4^2	3
sage_bm	2
herb_am + dist_res + dist_res^2	4
dist_wat	2
dist_res	2
dist_rd1_4	2
dist_res + dist_res^2 + dist_rd1_4	4
herb_am + sage_bm	4
sage_bm + sage_bs	3
dist_cj + dist_res + dist_wat + dist_res^2	5
sage_bm + dist_wat	3
sage_bm + dist_wat + dist_res + dist_res^2	5
sage_bm + dist_cj + dist_rd1_4	4
sage_bm + dist_wat + dist_res	4

[a] agej = 0 if adult, 1 if yearling; areaO = other areas (i.e., non Kezar, non Sapinero); areaS = Sapinero area; dist_cj = distance from nest to nearest conifer/juniper (km); dist_res = distance from nest to nearest residential classed habitat (km); dist_rd1_4 = distance from nest to nearest maintained road (i.e., classes 1–4; km); dist_wat = distance from nest to nearest water (km); dsagecc = dead sagebrush canopy cover (%); dtotforb = total forb cover (%); dtotgras = total grass cover (%); herb_am = mean herbaceous cover in a 3 × 3 pixel grid centered on the nest (%); lsagecc = live sagebrush canopy cover (%); muforbht = average forb height (cm); mugrsht = average grass height (cm); null = intercept only model; robcv = coefficient of variation in the Robel pole reading; robmu = average of the Robel pole reading (cm); sage_bm = mean sagebrush cover within a 564-m radius of the nest (%); sage_bs = SD of mean sagebrush cover within a 564-m radius of the nest.