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Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival

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Conservation success often hinges on our ability to link demography with implementable management actions to influence population growth (λ). Nest success is demonstrated to be important to λ in greater sage-grouse *Centrocercus urophasianus*, an imperiled species in the North American sagebrush-steppe. Enhancing this vital rate through management represents an opportunity to increase bird numbers inside population strongholds. We identified management for grass height as an action that can improve nest success in an analysis of sage-grouse nests (n = 529) from a long-term study (2003–2007) in the Powder River Basin, southeast Montana and northeast Wyoming, USA. Average grass height by study area and year varied (11.4–29.2 cm) but its positive effects on nest survival were consistent among study years and study areas that differed in absolute rates of nest success. We tested the predictive ability of models by grouping output from log-link analyses (2004–2006) into two bins with nest success probabilities < 0.45 and > 0.55, and validated the relationship with additional data from 2003 and 2007. Nests with probabilities > 0.55 were 1.64 (2004–2006) to 3.11 (2007) times more likely to hatch than those < 0.45, except in 2003 when an early wet spring resulted in universally high grass height at nest sites (29.2 cm) and high predicted nest success (64%). The high predictive power of grass height illustrates its utility as a management tool to increase nest success within priority landscapes. Relationships suggest that managing grass height during drought may benefit sage-grouse populations.

Achieving desired conservation outcomes requires planning at scales that match the biological needs of wide-ranging focal species (Nicholson et al. 2013). Inherent in conservation success is our ability to link demography to implementable management actions that influence population growth (λ; Mills 2012). Implementing locally beneficial conservation practices inside intact ecosystems maximally benefits species for which landscape context matters (Wilson et al. 2007, Schultz 2010). Advances in spatial ecology make landscape prioritization more feasible (Millspaugh and Thompson 2009), but identifying intact targets is only a first step (Knight et al. 2008). Still missing in most plans is a demographic link between a conservation action and its ability to influence demographic traits influencing λ (Wisdom et al. 2000, Caswell 2001).

Greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) are native only to western arid and semiarid sagebrush *Artemisia* spp. landscapes (Schroeder et al. 1999), and extirpated from half their range (Schroeder et al. 2004), the species is a candidate for listing under the federal Endangered Species Act (US Fish and Wildlife Service 2010). Major fragmenting threats include energy development (Naugle 2012), wildfire (Bukowski and Baker 2013, Murphy et al. 2013), cultivation for row crop production (Foley et al. 2011) and others (Knick et al. 2013). The current sage-grouse distribution encompasses 76 million hectares, yet population densities are highly clumped across their range (Doherty et al. 2010a). In efforts to focus conservation actions, the US Fish and Wildlife Service identified "Priority Areas for Conservation" (PACs; US Fish and Wildlife Service 2013) by consulting US states to incorporate the best available population and habitat data into site delineation. Research has focused on reducing threats to populations within PACs (Baruch-Mordo et al. 2013, Copeland et al. 2013), yet management actions that aim to bolster populations within priority areas will be critical for a species with declining distribution.

The purpose of our paper is to increase conservation effectiveness by exploring linkages between demography and implementable actions to benefit populations. Nest success is demonstrably important to λ, and enhancing this vital rate through management may benefit populations (Taylor et al. 2012). Variation in nest survival may in part be explained by grass height (DeLong et al. 1995), a feature influenced by grazing (Rickard et al. 1975), and a preeminent landuse in sagebrush systems. We used generalized linear models to

estimate the influence of vegetation and nest characteristics on sage-grouse nest survival within a landscape context (Dinsmore et al. 2002, Rotella et al. 2004). Findings will help guide the US Dept of Agriculture's Sage Grouse Initiative (SGI) in implementing rotational grazing systems designed to increase hiding cover for nesting grouse inside PACs on 847 000 ha of privately-owned rangelands (<www.sagegrouseinitiative.com/our-work/proactive-conservation/> under Grazing Systems).

Material and methods

Study area

We sampled sage-grouse in two distinct study areas in Johnson and Sheridan Counties in northeast Wyoming (southern region), and Bighorn, Rosebud, and Powder River Counties in southeast Montana (northern region), USA. Northern study areas were dominated by sagebrush, with conifer encroachment in more rugged landscapes and overall larger grassland areas. Southern study areas were also dominated by sagebrush, but had no conifers and exhibited smaller grassland areas. Shrub–steppe habitats were dominated by Wyoming big sagebrush *A. tridentata wyomingensis* with an understory of native and non-native grasses. Land use in both study areas was dominated by cattle ranching and land tenure was a mix of federal, state and private. Doherty et al. (2008) provides detailed descriptions of study areas. Because of the differences in landscape context, study area was included as a categorical blocking variable.

Capture, radio-tracking and predictor variables

We captured sage-grouse in rocket-nets and walk-in traps (Giesen et al. 1982) and by spotlighting (Wakkinen et al. 1992) March–April and July–October in 2003–2007. We aged females, fitted them with necklace style VHF radio collars, and relocated sage-grouse to monitor nests by ground based radio-tracking throughout the breeding season. We used established protocols (Connelly et al. 2003) to quantify local vegetative features known to influence habitat selection within ≤15 m of nests (Connelly et al. 2000, Hagen et al. 2007; Table 1). Doherty et al. (2010b) provides a full description of nest monitoring.

Statistical analyses and model selection

We used generalized linear models with a binomial likelihood and a log-link to estimate the influence nest age, study area and grass height on the daily survival rates (DSR) of nests (Dinsmore et al. 2002, Rotella et al. 2004). We derived nest survival rates by multiplying DSR together over the 28 day predicted incubation time for sage-grouse. We divided samples into nests used to build the model (n = 383 nests in 2004–2006) and those used to test model stability and predictive capability (n = 146 in 2003 and 2007).

We followed an iterative system for model selection. We first included a variable that controlled for the known effect of a spring snow storm in 2005 on DSR in all variable screenings and final model selection (Walker 2008).

Table 1. List of variables used in model selection explaining sage-grouse nest survival, Powder River Basin, Montana and Wyoming, USA, 2004–2006.

Candidate variables	Description
Local scale habitat variables	
Shrub canopy cover	using the line-intercept method along two 30 m perpendicular transects centered at nest or random locations (Canfield 1941)
Shrub density	all shrubs > 15 cm within 1 m of transect line were counted, total /120 m^2
Quadratic shrub canopy cover	shrub canopy cover + (shrub canopy cover × shrub canopy cover)
Nearest shrub height	height of nearest shrub to Daubenmire quadrant location. There were 10 Daubenmire quads on each of the two 30 m transects for a total of 20 Daubenmire quads. They were spaced 3 m apart and started at 0 m
Visual obstruction at nest	height density readings at 0, 1, 3 and 5 m from nest or available shrub in each cardinal direction (Robel et al. 1970)
Nearest grass height	average of the vegetative droop height for the nearest grass from the 20 Daubenmire quadrants
Tallest grass height	average of the vegetative droop height for the tallest grass from the 20 Daubenmire quadrants
Average grass height	(nearest grass height + tallest grass height)/2
Nest characteristic variables	
Hen age	yearling or adult (Walker 2008)
Nest age	(nest age in days + nest age in days^2) (Walker 2008)
Snowstormmarker	grouped 7 nests that were abandoned following major snow event in May 2005
Abiotic site variables	
Study area	north or south Powder River Basin
Year	year of observation

We assigned predictor variables into 1 of 3 model categories: 1) habitat, 2) nest characteristic, and 3) site variables (Table 1). We first examined univariate selection for study area and the 8 habitat variables, and removed variables if 95% confidence intervals overlapped zero. If predictor variables were highly correlated ($r \geq |0.7|$), only the variable with the greatest biological merit was included in the model (Chatfield 1995). When variables were moderately correlated (i.e. $|0.3| \leq r < |0.7|$), we checked for stability and consistency of parameter estimates as predictor variables were added.

We allowed each variable that made it past variable screening to compete with all other combinations of variables to identify the most parsimonious model for habitat and study area. If variables made it past screening we determined if their addition improved model fit via Akaike's information criterion with a small sample size correction factor (AIC_c; Burnham and Anderson 2002). After obtaining the best habitat model using AIC_c values, we then tested if inclusion of nest characteristic variables (Table 1) and an additional abiotic site variable (year effect) documented in Walker (2008) were still important predictor variables when included with

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habitat covariates. We followed the exact variable screening and AIC methods described above to test if these variables improved model fit.

We tested the predictive strength of the final habitat model by grouping predicted nest survival probability from log-link analyses (2004–2006) into two bins with probabilities of nest survival, <0.45 and >0.55, generically representing low and high nest survival probabilities, respectively. We then compared observed nest success from independent data sets (2003 and 2007) between low and high validation bins, and calculated the ratio of observed nest success between the high and low bins. We reasoned that observed nest success should be higher in the top validation bin if the final model predicted nest success well across years, demonstrated by a ratio of observed nest success >1 between bins. We further evaluated the predictive model by comparing predicted nest success from our top model to observed nest success by year. Average grass height around nesting sage-grouse in a given year (Table 1) was the only continuous predictor variable included in our top model, thus we evaluated how well one variable served as an indicator of nest success. Statistical analyses were performed in program SAS ver. 8.0 (SAS Inst. <http://v8doc.sascom/sashtml/>).

We performed a bootstrap analysis to quantify precision and the effect size of grass height on nest survival, using beta coefficients from the best approximating model (Burnham and Anderson 2002). We used the logistic exposure equation (Rotella et al. 2004) to generate the predicted probability of successfully hatching a nest for each bootstrap dataset ($n = 5000$) by systematically varying grass height within the observed range of variation. We computed at each percentage the probability of successfully hatching a nest for each of 5000 simulations. We ordered these probabilities and used a rankit adjustment (Chambers et al. 1983) to estimate upper and lower 95% confidence intervals.

Results

Nearest, tallest and average grass height were the only variables with significant coefficients when tested univariately. Nearest, tallest and average grass height were all positively associated with nest success, but were highly correlated and could not be included in the same model. Average and nearest grass height had virtually identical univariate coefficient estimates, however average grass height showed less variation around the estimate (average grass height $\beta = 0.034$, SE = 0.013, 95% CI = 0.008–0.060 vs nearest grass height $\beta = 0.039$, SE = 0.019, 95% CI = 0.001–0.076). Further, average grass height outcompeted nearest and tallest grass measures based on AIC_c values, thus it was retained for additional modeling.

The addition of study area increased model fit, while hen age and year effects were removed from the model because they explained no additional variation in nest survival when included with habitat variables and confidence intervals around effect estimates overlapped zero. The inclusion of nest age increased model fit ($w_i = 0.974$; Table 2). Our final model included average grass height, nest age, study area and the variable that controlled for the known effect of a spring snow storm in 2005 on DSR.

Table 2. Comparisons of grass height, study area and nest age variables to identify the AICc best model explaining sage-grouse nest survival, Powder River Basin, Montana and Wyoming, 2004–2006[a].

Model	K	AIC_c	ΔAIC_c	w_i
Average grass height + study area + nest age	6	834.418	0.000	0.974
Average grass height + study area	4	841.634	7.216	0.026
Average grass height	3	866.099	31.681	0.000
Study area	3	927.881	93.463	0.000

[a]all models included a categorical blocking variable which controlled for nests abandoned in a heavy spring storm in 2005 (Walker 2008).

Estimates of average grass height tracked annual trends in nest success (Fig. 1; northern region 2003–2007, beta estimate = 0.036, p = 0.023; southern region 2004–2007, beta estimate = 0.079, p = 0.001). Bootstrap analyses showed the positive relationship between average grass height and nest success (Fig. 2). Our final model including grass height and study area demonstrated large effect sizes (Fig. 2). Nests with probabilities >0.55 were 1.64 (2004–2006) to 3.11 (2007) times more likely to hatch than those <0.45 (Table 3), except in 2003 when average grass height (29.2 cm) and apparent nest success reached their highest recorded levels (68%, Fig. 1).

Discussion

High predictive power of grass height illustrates its utility as a management tool to benefit sage-grouse populations. Findings show grass height is a strong predictor of nest survival inside intact landscapes, and increasing hiding cover can increase nest success, a demographic rate that explains a

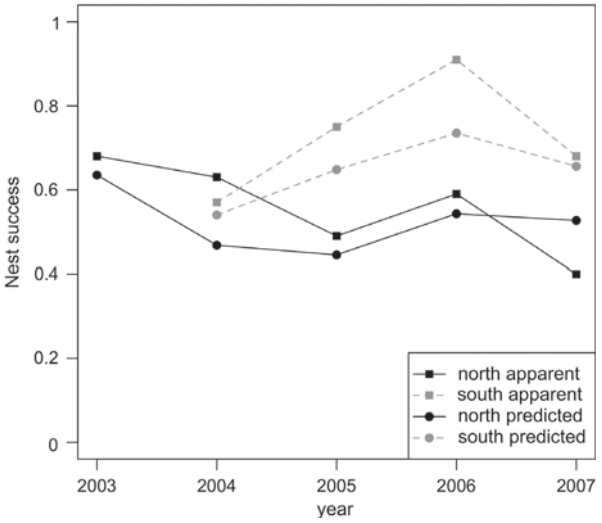


Figure 1. Apparent and predicted annual nest survival by year for sage-grouse in the Powder River Basin, Montana and Wyoming, US, 2003–2007. The final model included the effects of grass height, nest age, study area, and 2005 spring snow storm. Grass height measurements were averaged across nests within years to make annual predictions.

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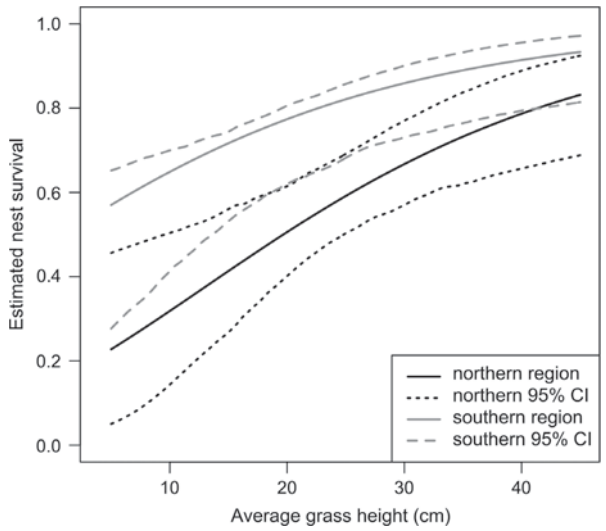


Figure 2. Relationship between average grass height and sage-grouse nest survival, Powder River Basin, Montana and Wyoming, USA, 2004–2006. Estimates of nest survival (95% confidence intervals [CIs]) in both study areas are based on 5000 bootstrap samples.

third of variation in λ (Taylor et al. 2012). Moreover, grass height is a reliable management tool because it explained variation (Fig. 2) despite variability in absolute rates of nest success between study areas. Positive effects of grass height should be evaluated on other important demographic rates including adult female and chick survival (Taylor et al. 2012) to see if benefits extend beyond what is now known.

Managing grass height in large and intact landscapes with grazing is a tool that may benefit populations in eastern Montana and northeast Wyoming. Positive effects of grass height in our study areas explained variation in nest success between years with large and precise effect sizes. Differing intercepts prohibit extrapolating of results to novel sagebrush systems because absolute effects likely depend upon regional conditions that influence grass and shrub composition. South and west of our study areas where sagebrush rather than grass provides most hiding cover, grass height had only a weak effect on nest success, and nest fates were dominated by year and site effects (Holloran et al. 2005). Grass height is positively related to nest success for other prairie grouse species and subspecies (Attwater's prairie-chickens *Tympanuchus cupido attwateri*, Lehmann 1941; plains sharp-tailed grouse *T. phasianellus jamesi*, Hillman and Jackson 1973; greater prairie-chicken *T. cupido pinnatus*, McKee et al. 1998).

Findings suggest that maintaining grass height during drought may provide the greatest benefits to populations. Average grass height and predicted nest success in this study is within the range of published literature (Schroeder et al. 1999, Connelly et al. 2000). Benefits may be negligible in years resembling 2003 when spring rains provided abundant grass and the correspondingly highest predicted nest success for the northern study area. High variation in pooled grass height by study area and years (11.4–29.2 cm) also suggested that modifying grazing practices to maintain nesting cover could improve a habitat feature that otherwise limits λ. We have identified a strong corollary of nest success in the Powder River Basin (PRB). If this relationship is validated in new study areas across different parts of the sage-grouse range, and if the relationship between grass height and nest success can be calibrated within these new areas, grass height may be useful as a surrogate to monitor nest success.

Findings emphasize the importance of an indirect effect of grazing on sage-grouse nest success. Results have broad implications because livestock grazing is the most widespread land use in the world (Holechek et al. 2003), affecting 70% of land area in the western US (Fleischner 1994). Effects of grazing on sage-grouse habitat may be wide-ranging depending upon current and historic timing and intensity of grazing, soil conditions, precipitation, plant communities and habitat features under consideration (Beck and Mitchell 2000, Connelly et al. 2000, 2004, Crawford et al. 2004). However, adjustments to duration and timing of grazing also may increase residual cover with the added benefit of increasing long-term rangeland health on which birds depend. For example, reducing the short-term stocking rate of sheep increased black grouse *Tetrao tetrix* numbers by 6% annually in Europe by increasing residual cover (Calladine et al. 2002). Replicated experiments to document sage-grouse response to different grazing systems are needed to help guide land managers to practices that are beneficial to sage-grouse and economically viable to producers (Krausman et al. 2011).

Habitat management within a PAC-based conservation strategy may benefit populations, but sage-grouse are a wildland species, and grass height is of little consequence if sagebrush systems continue to be replaced by anthropogenic land uses (Knick et al. 2013). Viability of ranching as a predominant land use may in part determine the future of sage-grouse conservation in the West. The SGI has increased by four-fold their implementation of rotational grazing systems by resting for up to 17 months the pastures used by nesting sage-grouse grouse within 488 000 ha inside Montana's PACs (J. Siddoway pers. comm.). Our findings suggest that these types of grazing systems that promote nest success may provide one mechanism to offset population losses by increasing bird numbers.

Table 3. Validation of grass height as a predictor for sage-grouse nest success, Powder River Basin, Montana and Wyoming, 2003–2007. We tested the AICc best model (Table 2) by calculating the predicted probability of hatching for each nest by applying grass height and region coefficients from log-link analysis (2004–2006) to observed grass heights at nests. We used the predicted probability (n is number of nests in each category) of hatching to group nests with probabilities of <0.45 and >0.55 and then compared apparent nest success ratios. We also validated the relationship with independent data sets (2003 and 2007). Nest age was excluded because we exponentiated daily survival rate for nests across the 28-day incubation period.

Predicted probability	Observed nest success		
	2003	2004–2006	2007
$p<0.45$ (low)	0.714 (n = 7)	0.486 (n = 70)	0.200 (n = 5)
$p>0.55$ (high)	0.667 (n = 30)	0.796 (n = 184)	0.623 (n = 52)
Ratio (high/low)	0.93	1.64	3.11

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