# A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats

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The distribution and range of the greater sage-grouse *Centrocercus urophasianus* have been reduced by 56% since the European settlement of western North America. Although there is an unprecedented effort to conserve the species, there is still considerable debate about the vegetation composition and structure required for nesting and brood-rearing habitat. We conducted a meta-analysis of vegetation characteristics recorded in studies at nest sites (N = 24) and brood habitats (N = 8) to determine if there was an overall effect (Hedge's d) of habitat selection and to estimate average canopy cover of sagebrush *Artemisia* spp., grass and forbs, and also height of grass at nest sites and brood-rearing areas. We estimated effect sizes from the difference between use (nests and brood areas) and random sampling points for each study, and derived an overall effect size across all studies. Sagebrush cover ($d_{++}$ = 0.39; 95% C.I.: 0.19-0.54) and grass height ($d_{++}$= 0.28; 95% C.I.: 0.13-0.42) were greater at nest sites than at random locations. Vegetation at brood areas had less sagebrush cover ($d_{++}$ = -0.17; 95% C.I.: -0.44 - +0.18), significantly taller grasses ($d_{++}$ = 0.31; 95% C.I.: 0.14-0.45), greater forb ($d_{++}$ = 0.48; 95% C.I.: 0.30-0.67) and grass cover ($d_{++}$= 0.17; 95% C.I.: 0.08-0.27) than at random locations. These patterns were especially evident when we examined early (< 6 weeks post hatching) and late brood-rearing habitats separately. The overall estimates of nest and brood area vegetation variables were consistent with those provided in published guidelines for the management of greater sage-grouse.

*Key words: Artemisia spp., breeding habitat, effect size, greater sage-grouse, Hedges' d, meta-analysis, sagebrush*

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The distribution and range of greater sage-grouse *Centrocercus urophasianus* have been reduced by 56% since the European settlement of western North America (Connelly & Braun 1997, Schroeder et al. 2004). Although loss and fragmentation of sagebrush *Artemisia* spp. habitats have been cited as the primary causes for the decline of the species, degradation of existing habitat also has been considered an important factor (Braun 1998). Guidelines for protection and management of nesting and brood-rearing habitat have been provided to land managers (Connelly et al. 2000). In general, a range of 15-25% sagebrush, > 10% forb, > 15 % grass canopy cover and, a herbaceous height of 18 cm are needed for breeding habitats of greater sage-grouse.

Techniques used to measure vegetation characteristics have not always been consistent (Wamboldt et al. 2006). Additionally, some researchers and managers have questioned the applicability of management guidelines (Connelly et al. 2000) across the range of the greater sage-grouse, as well as the techniques used to derive the earlier estimates of vegetative cover and height (Bates et al. 2004, Schultz 2004). In particular, subsequent debate over the quantitative properties of the recommended vegetative characteristics required for greater sage-grouse has become a hindrance to implementing conservation actions. To address these concerns and examine the relevance of management guidelines additional analyses are needed. One potential analytical method that was not used when producing the earlier guidelines (Braun et al. 1977, Connelly et al. 2000) was the research synthesis or meta-analysis, which allows an evaluation of the generality of a given effect as a result of combining parameter estimates (effect sizes) from a set of studies (Hall et al. 1994). The use of meta-analysis can advance our knowledge and understanding of observed findings, and contribute to the advancement of more theoretical issues (Hedges & Olkin 1985).

Schultz (2004) analysed the data set in Connelly et al. (2000) and used the analysis to critique the published guidelines. However, since these articles were published, more data have become available. Because the interpretation of earlier research is a fundamental tool in the development of appropriate guidelines to management, we employed meta-analytic techniques to the research summarized by Connelly et al. (2000) as well as research conducted more recently. The purpose of our meta-analysis was to estimate the effect of habitat selection of breeding habitats (i.e. nesting and brood rearing) of greater sage-grouse. To this end we compared vegetation characteristics at use sites to random points, to evaluate the similarity of effect sizes across studies, and to determine if the overall effect size for each vegetation characteristic is statistically or biologically meaningful.

# Methods

## Literature review and data selection

We reviewed peer-refereed articles and graduate research theses (N = 15) and non-refereed agency reports (N = 4) that pertained to greater sage-grouse habitat use during the nesting and brood-rearing periods (Tables 1 and 2). Because studies reported significant differences in vegetation between years (Fischer 1994, Apa 1998, Sveum et al. 1998, Holloran 1999) or study areas (Gregg 1991, Drut 1992, Slater 2003) we estimated effect size for each significant unit. We included estimates from studies that reported actual cover values (e.g. 32.3%) and excluded values from one study (Klott et al. 1993) that used ranked cover values (e.g. 1-5 from Daubenmire (1959) readings). In some studies, a limited number of vegetative characteristics were recorded, thus sample sizes in Tables 1 and 2 vary for each estimate of effect size. We examined the relationship of sagebrush cover, grass cover, forb cover and grass height at nest sites and brood-use sites compared to their respective random points. These variables were consistently reported across studies and provided the largest sample sizes for our comparisons. Several articles reported only shrub cover (e.g. Drut 1992, Gregg 1993, Fischer 1994, Hanf et al. 1994, Sveum et al. 1998), which may have included a mix of sagebrush and other shrubs. Because of limited sample sizes, we estimated effect sizes and parameter estimates for sagebrush only and shrub cover (i.e. sagebrush and other shrub cover) and present results for each. Canopy cover was sometimes estimated with line-intercept or quadrats. However, because we used a standardized metric in our meta-analysis, we could compare studies that used these different methodologies (Hedges & Olkin 1985, Gurevitch & Hedges 1999). Because brood survival rates and habitat use differ between 0-6 weeks post hatching and > 6 weeks post hatching (Holloran 1999, Lyon 2000), we estimated effect sizes for brood-use by early and late periods for studies that differentiated between them. We estimated a pooled effect size for studies that did not differentiate between early and late brood-rearing periods.

## Data analysis

A general equation for an effect size is the treatment mean minus control mean divided by the pooled variance (Hedges 1982). The effect size for each study serves as a dependent variable that can be modeled as a function of discrete or continuous explanatory

Table 1. Studies and vegetation data used in meta-analyses of greater sage-grouse nesting habitats throughout North America. Sagebrush (shrub), grass and forb canopy cover (in %) and grass height (in cm) were vegetation variables considered in the analyses. Vegetation community was described in each study as silver sagebrush (SS), mountain big sagebrush (MT) or Wyoming big sagebrush (WY). ND means that no data were available or had been reported in a manner that was usable in the meta-analysis.

| | Nest site vegetation | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Study | Vegetation community | N | Shrub cover | SD | Grass cover | SD | Forb cover | SD | Grass height | SD |
| Aldridge 2005 | SS | 93 | 25.46 | 18.52 | 19.56 | 16.59 | 3.82 | 5.30 | 33.94 | 20.25 |
| Aldridge & Brigham 2002 | SS | 29 | 31.90 | 21.92 | 31.90 | 21.33 | 8.10 | 6.03 | 30.90 | 19.28 |
| Apa 1998 (1989) | MT | 11 | 22.00 | 12.60 | 16.20 | 9.95 | 11.50 | 5.64 | 23.00 | 4.97 |
| Apa 1998 (1990) | MT | 10 | 18.80 | 6.32 | 17.00 | 6.01 | 9.00 | 5.06 | 32.40 | 6.01 |
| Apa 1998 (1991) | MT | 18 | 16.70 | 7.64 | 13.50 | 5.09 | 8.60 | 12.73 | 41.90 | 7.64 |
| Fischer 1994 (Postburn) | WY | 67 | 17.90 | 38.08 | 29.30 | 10.64 | 4.30 | 4.09 | 22.10 | 7.37 |
| Fischer 1994 (Preburn) | WY | 71 | 29.00 | 1.20 | 7.20 | 25.85 | ND | ND | 19.80 | 6.74 |
| Gregg 1991(Jackass Creek) | WY | 51 | 56.00 | 22.00 | 11.10 | 10.00 | 12.80 | 11.00 | ND | ND |
| Gregg 1991 (Hart Mountain) | MT | 47 | 51.00 | 15.00 | 18.00 | 20.00 | 6.50 | 5.00 | ND | ND |
| Hanf et al. 1994 | WY | 20 | 44.00 | 8.90 | 15.00 | 8.94 | 5.00 | 8.94 | 22.00 | 13.42 |
| Hausleitner 2003 | MT | 93 | 26.90 | 13.50 | 3.70 | 3.86 | 6.90 | 7.71 | 13.80 | 6.75 |
| Heath et al. 1998 | WY | 42 | 19.00 | 12.90 | 8.20 | 4.73 | 2.04 | 2.33 | 16.60 | 3.56 |
| Holloran 1999 (1997) | WY | 32 | 24.90 | 11.80 | 5.50 | 3.53 | 6.70 | 3.64 | 20.80 | 4.25 |
| Holloran 1999 (1998) | WY | 45 | 25.20 | 9.72 | 4.10 | 1.74 | 7.80 | 3.65 | 17.10 | 2.73 |
| Klott et al. 1993 | WY | 8 | 24.47 | 15.75 | ND | ND | ND | ND | 16.69 | 8.70 |
| Lyon 2000 | WY | 50 | 25.60 | 991 | 10.60 | 11.70 | 8.20 | 9.21 | 21.30 | 4.25 |
| Popham & Gutiérrez 2003 | WY | 40 | 14.50 | 18.97 | 12.50 | 15.81 | ND | ND | 23.10 | 18.97 |
| Schroeder 1995 | WY | 78 | 17.24 | 9.76 | 51.03 | 15.94 | 20.64 | 13.35 | 107.88 | 28.62 |
| Slater 2003 (Collett Creek) | WY | 64 | 22.24 | 11.68 | 6.23 | 3.36 | 7.96 | 6.88 | 18.21 | 3.04 |
| Slater 2003 (Salt Creek) | WY | 21 | 24.80 | 8.29 | 3.26 | 2.84 | 1.33 | 1.47 | 16.23 | 3.16 |
| Sveum et al. 1998 (1992) | WY | 21 | 51.00 | 27.50 | 26.00 | 20.62 | 12.00 | 13.75 | ND | ND |
| Sveum et al. 1998 (1993) | WY | 45 | 59.00 | 26.83 | 27.00 | 20.12 | 21.00 | 20.12 | ND | ND |
| Wakkinen 1990 | WY | 49 | 21.50 | 41.08 | 6.50 | 24.65 | ND | ND | 18.20 | 7.00 |
| Wik 2002 | WY | 38 | 21.00 | 8.63 | 58.00 | 17.88 | ND | ND | 25.00 | 7.40 |

variables or used to estimate a cumulative effect size. The effect size magnitude can be ranked small (0.2), medium (0.5) or large (0.8) standard deviations from a null effect size of zero, as a general rule (Cohen 1969).

We used Hedges' d (Hedges 1982) to estimate effect sizes for sagebrush cover, grass height, grass cover and forb cover for each study because it is conducive to estimating an effect between paired treatments. With E as the treatment group and C as the control, Hedges' d was calculated as:

$$d = \frac{\overline{X}^E - \overline{X}^c}{S} J$$

where S is the pooled standard deviation and the variance ($v = \sqrt{S}$) of Hedges' d is:

$$v = \frac{N^c + N^E}{N^c N^E} + \frac{d^2}{2(N^c + N^E)}$$

and J is the correction for small sample sizes:

$$J = 1 - \frac{3}{4(N^c + N^E - 2) - 1}$$

We estimated cumulative effect size $d_{++}$ as:

$$d_{++} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i}$$

where the weight $w_i$ for study i is the reciprocal of the variance ($w_i = 1/v$). We used random sites as the 'control' group and use (nests or brood) sites as the 'treatment' group; thus, a positive estimate of d indicates that the variable was greater at use sites than at random points. Confidence limits (95% C.I.) were

Table 2. Studies and vegetation data used in the meta-analyses of greater sage-grouse brood-rearing habitats throughout North America. Sagebrush (shrub), grass and forb canopy cover (in %) and grass height (in cm) were vegetation variables considered in the analyses. Dominant vegetation community was described in each study as silver sagebrush (SS), mountain big sagebrush (MT) and Wyoming big sagebrush (WY). ND means that no data were available or had been reported in a manner that was usable in the meta-analysis.

| | Brood-rearing area vegetation | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Brood period/study | Vegetation community | N | Shrub cover | SD | Grass cover | SD | Forb cover | SD | Grass height | SD |
| Early | | | | | | | | | | |
| Drut 1992 (Hart Mt) | MT | 87 | 23.00 | 8.00 | 15.00 | 7.00 | 11.00 | 7.00 | ND | ND |
| Drut 1992 (Jackass) | WY | 84 | 26.00 | 8.00 | 9.00 | 5.00 | 13.00 | 6.00 | ND | ND |
| Hausleitner 2003 | MT | 31 | 12.70 | 10.02 | 5.80 | 2.78 | 7.50 | 3.90 | 21.70 | 5.57 |
| Heath et al. 1998 | WY | 16 | 14.40 | 8.80 | 12.50 | 13.20 | 2.80 | 2.80 | 16.10 | 4.80 |
| Holloran 1999 | WY | 67 | 15.83 | 8.67 | 5.89 | 5.74 | 9.25 | 4.93 | 18.59 | 4.94 |
| Lyon 2000 | WY | 23 | 21.50 | 7.35 | 14.20 | 18.10 | 8.30 | 9.91 | 23.30 | 4.90 |
| Sveum 1995 | WY | 53 | 11.00 | 7.28 | 17.00 | 21.84 | 22.00 | 14.56 | ND | ND |
| Late | | | | | | | | | | |
| Drut 1992 (Hart Mt) | MT | 38 | 24.00 | 9.50 | 16.00 | 7.00 | 20.00 | 8.00 | ND | ND |
| Drut 1992 (Jackass) | WY | 38 | 29.00 | 15.00 | 8.00 | 5.00 | 8.00 | 6.00 | ND | ND |
| Hausleitner 2003 | MT | 28 | 8.40 | 7.41 | 9.10 | 9.52 | 8.90 | 5.29 | 20.00 | 5.82 |
| Heath et al. 1998 | WY | 22 | 11.10 | 10.79 | 15.60 | 19.23 | 10.10 | 11.73 | 15.60 | 6.10 |
| Holloran 1999 | WY | 59 | 17.40 | 12.10 | 5.26 | 2.83 | 9.01 | 5.17 | 16.53 | 4.35 |
| Sveum 1995 | WY | 19 | 7.00 | 8.72 | 18.00 | 13.08 | 23.00 | 13.08 | ND | ND |
| Both | | | | | | | | | | |
| Aldridge 2005 | SS | 139 | 8.85 | 7.90 | 21.20 | 13.56 | 8.88 | 9.08 | 8.85 | 7.90 |
| Aldridge & Brigham 2002 | SS | 91 | 20.90 | 15.55 | 34.20 | 19.56 | 10.90 | 11.45 | 20.90 | 15.55 |
| Apa 1998 | MT | 49 | 14.10 | 11.90 | 10.00 | 9.80 | 8.00 | 11.20 | 14.10 | 11.90 |
| Klott et al. 1993 | WY | 13 | 16.76 | 5.72 | ND | ND | ND | ND | 10.60 | 11.51 |
| Hausleitner 2003 | MT | 92 | 10.60 | 11.51 | 6.50 | 5.75 | 8.00 | 6.71 | 16.48 | 4.21 |
| Slater 2003 | WY | 13 | 13.50 | 13.41 | 6.81 | 5.77 | 5.45 | 6.20 | 13.50 | 13.41 |
| Wik 2002 | WY | 46 | 15.00 | 10.17 | 50.00 | 14.24 | 16.00 | 10.17 | 20.00 | 6.78 |

estimated for d, and we used bias-corrected bootstrap sampling to estimate confidence limits for $d_{++}$, to account for replicate years or areas within studies. We evaluated the plausibility of using additional explanatory variables to explain the observed differences in effect sizes across studies. The $Q_T$ statistic is based on the total sum of squares and specifically tests for equal effect sizes across studies. If $Q_T$ is greater than would be expected at random ($\chi^2$-distribution), then additional variables (e.g. nest success rates) might help explain the observed variation in the data. We assumed that random variation occurred across nesting studies and estimated effect sizes using random effects models (Hedges 1982). However, we used mixed models to identify if there was a common effect size across brood-rearing periods (categorical data) for each cover type. The basic assumption for this analysis is that random variation occurs among effect sizes within a brood period, but may differ between periods (Gurevitch & Hedges 1999). Here the statistic $Q_B$ can be used to assess the amount of variation accounted for between groups. If $Q_B$ is significantly large, it suggests that effect sizes are larger between groups than expected from random. Applications of mixed-model meta-analysis are uncommon in ecological studies, but likely are the most appropriate for such data sets (Gurevitch & Hedges 1999). All meta-analytic calculations were conducted in MetaWin 2.0 (Rosenberg et al. 2000).

The quality of a research synthesis hinges on the quality of the publications available to analyse, as well as on studies not published because of a lack of significant results (Rosenberg 2005). This is referred to as publication bias and can overestimate the effect size if a large number of non-significant studies are not published or accessible. One of the simplest methods to evaluate the potential impact of publication bias is the calculation of a fail-safe number ($N_+$). A fail-safe number indicates the number of non-significant, unpublished (or missing) studies that would need to be added to a meta-analysis to reduce an overall statistically significant observed result to non-significance (Rosenberg 2005). We estimated fail-safe numbers for each significant effect size using Fail-Safe Number Calculator (Rosenberg 2005), and considered an effect size robust if $N_+ > 5N + 10$, where N is the observed number of studies used to estimate the effect size.

To add biological relevance to the meta-analysis, we used a weighted general linear model (PROC GLM; SAS Institute 2000) and estimated the mean and 95% C.I. for sagebrush cover, grass cover, forb cover and grass height at nest and brood-use sites.

## Results

### Effect sizes

Greater sage-grouse females selected nest sites with generally more sagebrush cover ($d_{++}$ = 0.39; 95% C.I.: 0.19-0.54) and taller grass height ($d_{++}$ = 0.28; 95% C.I.: 0.15-0.41) than random sites (Fig. 1). Grass ($d_{++}$ = 0.13; 95% C.I.: -0.03 - +0.25) and forb cover ($d_{++}$ = 0.15; 95% C.I.: -0.06 - +0.37) were greater at nest sites, but neither effect was significantly large. An examination of $Q_T$ indicated that d was homogenous (P > 0.2) among studies for each variable and that additional information would not explain the observed effect sizes (Table 3). Shrub cover had a larger effect size than sagebrush only ($d_{++}$ = 0.74; 95% C.I.: 0.39-1.13).

Vegetation at brood areas combined among all periods had greater forb cover ($d_{++}$ = 0.46; 95% C.I.: 0.30-0.66), grass cover ($d_{++}$ = 0.19; 95% C.I.: 0.09-0.30), significantly taller grasses ($d_{++}$ = 0.29; 95% C.I.: 0.13-0.42), and less sagebrush cover ($d_{++}$ = -0.17; 95% C.I.: -0.44 - +0.18) than random locations (see Fig. 1). However, females exhibited some variation in habitat selection for sagebrush between these periods ($Q_B$ = 6.12, df = 2, P = 0.046). Generally, early brood-use areas were comprised of greater forb cover ($d_{++}$ = 0.57; 95% C.I.: 0.23-0.80), grass cover ($d_{++}$ = 0.27; 95% C.I.: 0.11-0.50), and taller grass ($d_{++}$ = 0.39; 95% C.I.: 0.26-0.60), but less sagebrush cover ($d_{++}$ = -0.46; 95% C.I.: -0.75 - -0.19) than random sites. Effect size for shrub cover changed moderately when using all studies ($d_{++}$ = -0.61; 95% C.I.: -0.95 - -0.31). During late brood rearing, forb cover ($d_{++}$ = 0.55; 95% C.I.: 0.23-0.79) and grass cover ($d_{++}$ = 0.16; 95% C.I.: 0.05-0.30) were greater at use sites, but sagebrush cover ($d_{++}$ = -0.08; 95% C.I.: -0.48 - +0.12) and shrub cover ($d_{++}$ = -0.04; 95% C.I.: -0.31 - +0.15) were similar between use and random sites. For studies that pooled estimates across both periods, forb cover was greater ($d_{++}$ = 0.27; 95% C.I.: 0.04-0.54) and grass height taller ($d_{++}$ = 0.34; 95% C.I.: 0.20-0.48) than at random sites. Sagebrush cover ($d_{++}$ = 0.15; 95% C.I.: -0.36 - +0.77) and grass cover ($d_{++}$ = 0.11; 95% C.I.: -0.01 - +0.32) were greater at brood use areas but neither of these factors was significant. Examination of $Q_T$ values indicated that effect sizes were homogenous (P > 0.25) except for shrub cover, and additional explanatory variables would not explain variation in effect sizes across all studies (see Table 3). The test of heterogeneity is conservative with small sample sizes and therefore interpreted in an appropriately conservative manner.

### Publication bias

We conducted fail-safe calculations for 12 effect sizes that were significant (see Table 3). The effect size of disproportional use of sagebrush and grass height was robust for nest sites as was forb cover at early and late brood-rearing areas (see Table 3). Grass cover and height effect sizes for brood-rearing areas were not

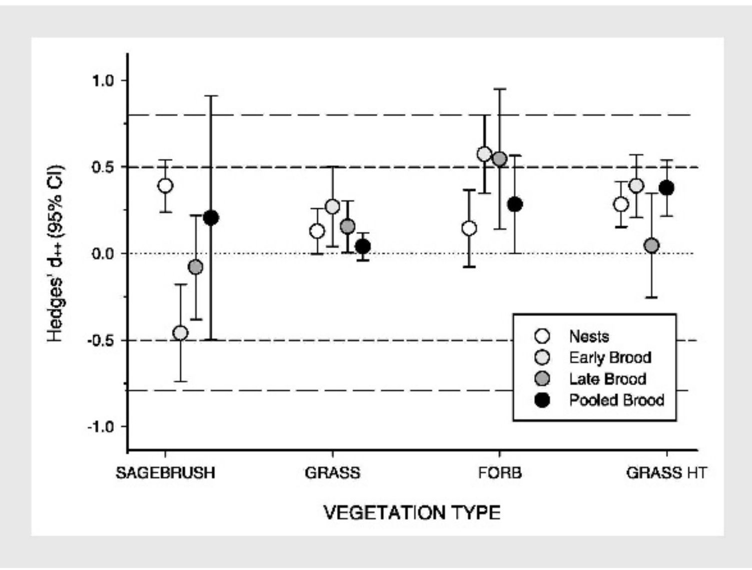


Figure 1. Cumulative effect sizes ($d_{++}$) by vegetation types and across nesting and brood-rearing habitats. Long-dashed lines indicate large (d > 0.8), small-dashed lines indicate medium (0.8 ≥ d > 0.5), and dotted line indicates small (0 < d < 0.5) effects. Significant positive and negative effects indicate selection for or against a vegetation type, respectively. Estimates with 95% C.I. including 0, indicate no effect of habitat selection.

Table 3. Estimates of vegetation characteristics at greater sage-grouse use sites from 19 studies across the species range, and diagnostic statistics ($Q_T$, $N_+$) for meta-analysis. Means and confidence intervals were derived from a weighted mean linear model where the inverse of the variance was the weighting factor. The 'early' period was defined as brood habitat used < 6 weeks post hatching, the 'late' period as > 6 weeks post hatching, and 'both' were studies that pooled estimates across both periods. An asterisk (*) indicates that a fail-safe number ($N_+$) is robust (> 5N + 10). The fail-safe number is equivalent to the number of studies of null effect and mean weight necessary to reduce the observed significance level to $\alpha = 0.05$.

| | | | Parameter estimates | | Diagnostics | | | |
|---|---|---|---|---|---|---|---|---|
| Cover type | Period | N | $\bar{x}$ | 95% C.I. | $Q_T$ | df | P | Fail safe ($N_+$) |
| Forb (%) | Nest | 19 | 4.02 | 2.05-5.99 | 21.3 | 18 | 0.27 | NA |
| | Early | 7 | 6.74 | 3.91-9.56 | 4.5 | 6 | 0.61 | 94* |
| | Late | 6 | 10.78 | 6.50-15.06 | 5.3 | 5 | 0.38 | 49* |
| | Both | 6 | 8.51 | 2.92-14.10 | 4.4 | 5 | 0.50 | 13 |
| Grass (%) | Nest | 23 | 6.75 | 4.53-8.98 | 25.9 | 22 | 0.26 | NA |
| | Early | 7 | 7.56 | 4.35-10.76 | 7.5 | 6 | 0.28 | 14 |
| | Late | 6 | 7.57 | 4.17-10.98 | 3.6 | 5 | 0.61 | 1 |
| | Both | 6 | 11.44 | 5.79-17.10 | 5.4 | 5 | 0.38 | NA |
| Sagebrush (%) | Nest | 19 | 21.51 | 19.91-23.93 | 13.7 | 16 | 0.62 | 270* |
| | Early | 4 | 16.84 | 9.59-24.08 | 3.2 | 3 | 0.37 | 14 |
| | Late | 3 | 10.92 | 1.67-20.16 | 1.9 | 2 | 0.38 | NA |
| | Both | 7 | 14.15 | 8.39-19.92 | 5.1 | 6 | 0.53 | NA |
| Shrub cover (%) | Nest | 24 | 25.13 | 20.35-29.91 | 35.3 | 23 | 0.05 | 1133* |
| | Early | 7 | 18.07 | 13.31-22.83 | 5.3 | 6 | 0.50 | 204* |
| | Late | 6 | 13.71 | 7.53-19.88 | 5.3 | 5 | 0.38 | NA |
| Grass height (cm) | Nest | 20 | 19.77 | 17.36-22.18 | 16.6 | 19 | 0.61 | 193* |
| | Early | 4 | 19.78 | 15.91-23.65 | 2.8 | 3 | 0.41 | 5 |
| | Late | 3 | 17.24 | 12.58-21.90 | 1.6 | 2 | 0.45 | NA |
| | Both | 7 | 19.16 | 15.17-23.15 | 7.5 | 6 | 0.28 | 40 |

robust for missing studies. However, these were relatively small effect sizes (see Fig. 1). The effect size of sagebrush cover at brood-rearing areas was robust.

### Parameter estimates

Sagebrush canopy cover was apparently greater at nest sites (21.5%) than at brood areas (< 16.9%; see Table 3). Combined forb (4.1%) and grass cover (6.5%) was less at nest sites than at brood areas (forb > 6.7%, grass > 7.6%). However, grass height was comparable (~19 cm) in nest and brood areas. During brood rearing, sagebrush cover decreased from early to late periods, forb cover increased, whereas grass cover and height did not change appreciably (see Table 3).

## Discussion

Our study provides the first quantitative assessment of available data for greater sage-grouse habitat selection during the nesting and brood-rearing periods. We found a general effect for habitat selection across the range of these studies, as evidenced by low levels of variation in effect sizes across studies and regions. Many of our estimated effect sizes were robust to the potential impacts of publication bias, lending considerable support to the generality of our findings. There was a medium to large effect (d = 0.37-0.74) of selection for vegetation characteristics, with greater sagebrush cover for nest concealment and forb cover for females with broods. There were smaller effects (d ~ 0.2) for selection of grass height and cover by nesting and brood-rearing females. The variation of effect sizes in sagebrush cover was more substantial between brood periods, signifying a seasonal shift in habitat use.

### Effect sizes

Because random variation was as expected, we can infer that greater sage-grouse females were selecting for similar nesting vegetation (greater sagebrush cover, grass cover and/or taller grasses) throughout the geographic range of these studies. This quantitative assessment supports earlier qualitative reviews of sage-grouse habitat requirements during the nesting period (Braun et al. 1977, Connelly et al. 2000) that suggested the importance of sagebrush and grass cover as well as grass height. Our study also indicated the importance of reporting sagebrush cover separately from other shrub species as there was a moderate change in effect size and increase in variance of effect size, when comparing studies reporting sagebrush versus shrub cover. Although the measurement of grass height has only recently been standardized (Connelly et al. 2003), we identified an overall selection for taller grasses at nest sites. Additionally, the relatively small selection effect of greater grass cover may have been confounded with grass height. Many short stature grasses may have been included in the estimates of grass cover, and may contribute to the relatively small effect size of grass cover at use sites.

Brood females selected early and late habitats with less sagebrush cover and greater herbaceous cover (grass and forbs) than random sites. This generalized effect for greater herbaceous cover during brood rearing is likely a result of mesic plant communities with an abundance of invertebrates and foods that are critical to the growth and development of chicks (Johnson & Boyce 1991, Drut et al. 1994). Alternatively, this effect may have been correlated with broods seeking habitats with less shrub cover and greater understory in more xeric sites. Taller grasses were selected more so during early brood rearing than during late brood rearing. The proximity of early brood rearing to nesting sites may have contributed to this result, or because females were selecting sites with less sagebrush cover, the use of taller grasses may have provided greater vertical screening and protection. However, as broods mature tall stature grasses appeared to become less important, as did sagebrush cover. For studies that pooled vegetation measurements across both brood periods the effect sizes were generally small and may have been confounded by potential effects between early and late broods. Sagebrush cover was greater at brood use sites for pooled studies and was likely due to selection for silver sagebrush *A. cana* sites in Alberta where the extent of sagebrush could be a limiting factor (Aldridge & Brigham 2002, Aldridge 2005).

## Publication bias

Generally, our findings were robust to publication bias with respect to vegetation needs for each life stage. Our evaluation of potential impacts of publication bias indicated that habitat usage by greater sage-grouse at nest sites was robust for sagebrush cover and grass height, each effect requiring two to several hundred studies of 'no effect' to nullify our results. Similarly, our estimated effects of less shrub cover and greater forb cover during brood rearing were robust to publication bias. The effects of grass cover were relatively small and more susceptible to non-significant or missing studies. These findings may help guide future work to identify vegetation characteristics that should be evaluated more carefully and perhaps reduce some of this ambiguity (e.g. grass cover).

## Parameter estimates

The weighted average of cover and height values were within the range specified by the greater sage-grouse management guidelines for breeding habitats (Connelly et al. 2000). Our analysis indicated that the range (95% C.I.s) of vegetation measurements encompassed those in the guidelines published by Connelly et al. (2000), recommending 15-25% sagebrush cover, $>$ 10% forb cover, $>$ 15% grass cover and $\geq$ 18-cm grass height (see Table 3). Estimates of sagebrush were not markedly different when we included studies that reported only shrub cover. Despite criticisms of the established guidelines (Bates et al. 2004, Schultz 2004), our quantitative analysis that includes new data published after 2000 strongly suggests that these values for describing breeding habitats are reasonable. Because these measurements are generally recorded over relatively small scales ($<$ 30 m), identifying the appropriate proportions of these vegetative characteristics in a larger landscape is paramount (Bates et al. 2004).

## Conclusions and recommendations

The magnitude of effects sizes combined with the parameter estimates in our meta-analyses demonstrated a shift in habitat selection by females between nesting and brood-rearing periods, primarily a shift in sagebrush and forb canopy cover. However, most studies have not quantified the spatial distribution or juxtaposition of these vegetative communities. Understanding the optimum mix and spatial arrangement of these communities and their effects on demographic rates in a landscape could substantially enhance management of the greater sage-grouse. More importantly, studies of breeding habitats need to begin to examine the relationship between vegetative communities, landscape metrics (e.g. habitat patch size, fragmentation and distance to roads) and demographic rates. Similarly, as more studies begin to compare vegetation and other differences between successful and unsuccessful nests, a meta-analysis could prove useful in identifying a general effect for factors contributing to nest success.

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