ACCOUNTING FOR FITNESS: COMBINING SURVIVAL AND SELECTION WHEN ASSESSING WILDLIFE–HABITAT RELATIONSHIPS

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ABSTRACT

Assessing the viability of a population requires understanding of the resources used by animals to determine how those resources affect long-term population persistence. To understand the true importance of resources, one must consider both selection (where a species occurs) and fitness (reproduction and survival) associated with the use of those resources. Failure to do so may result in incorrect assessments of habitat quality and inappropriate management activities. We illustrate the importance of considering both occurrence and fitness metrics when assessing habitat requirements for the endangered greater sage-grouse in Alberta, Canada. This population is experiencing low recruitment, so we assess resource use during the brood-rearing period to identify management priorities. First, we develop logistic regression occurrence models fitted with habitat covariates. Second, we use proportional hazard survival analysis to assess chick survival (fitness component) associated with habitat and climatic covariates. Sage-grouse show strong selection for sagebrush cover at both patch (smaller) and area (larger) spatial scales, and weak selection for forbs at the patch scale only. Drought conditions based on an index combining growing degree days and spring precipitation strongly reduced chick survival. While hens selected for taller grass and more sagebrush cover, only taller grass cover also enhanced chick survival. We show that sage-grouse may not recognize all ecological cues that enhance chick survival. Management activities targeted at providing habitats that sage-grouse are likely to use in addition to those that enhance survival are most likely to ensure the long-term viability of this population. Our techniques account for both occurrence and fitness in habitat quality assessments and, in general, the approach should be applicable to other species or ecosystems.

Keywords: fitness, greater sage-grouse, habitat, occurrence, persistence, sagebrush, selection, survival

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INTRODUCTION

Species–habitat relationships have become a priority in conservation biology (Boyce and McDonald, 1999; Morrison, 2001; Brotons et al., 2004). Simply predicting the occurrence of animals across habitats is useful, but becomes much more valuable and informative if occurrence (or abundance) is related to fitness (Tyre et al., 2001; Breininger and Carter, 2003; Bock and Jones, 2004; Aldridge and Boyce, 2007). Understanding spatial variation in fitness is critical to the conservation of many species of concern (Donovan and Thompson, 2001), allowing for population viability assessment (Boyce et al., 1994; Boyce and McDonald, 1999) and identifying appropriate management objectives. High-quality habitats should be defined as those where animals are likely to occur and achieve high levels of fitness (reproduction and survival; Van Horne, 1983; Morrison, 2001; Aldridge and Boyce, 2007). However, density dependence resulting in individuals sorting themselves according to the ideal free distribution could in turn result in higher density in selected habitats without apparent fitness variation (Fretwell and Lucas, 1969). Regardless, conservation of wildlife populations must make this crucial link between resources and fitness (Franklin et al., 2000; Morrison, 2001; Bock and Jones, 2004; Larson et al., 2004; Nielsen et al., 2005).

We illustrate the importance of considering both occurrence and fitness metrics when assessing habitat requirements for the endangered greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) in Alberta, Canada. Sage-grouse inhabit shrub-steppe ecosystems that once covered a large portion (1.2 million km^2; Schroeder et al., 2004) of the northwestern United States and small southern portions of three western provinces of Canada. During the last century, these ecosystems have been transformed by agricultural activities (Connelly et al., 2004), invasion by non-native plant species (Knick et al., 2003; Connelly et al., 2004), energy-extraction activities and developments (Braun et al., 2002; Lyon and Anderson, 2003), intense grazing pressures (Beck and Mitchell, 2000; Hayes and Holl, 2003; Crawford et al., 2004), and climate change (Neilson et al., 2005), resulting in direct loss of nearly half of those habitats and the degradation and fragmentation of that which remains. All sage-grouse populations have declined by approximately 2% per year since 1965 (Connelly et al., 2004), and low reproductive success (Connelly and Braun, 1997; Braun, 1998; Crawford et al., 2004) resulting from poor nesting success (Crawford and Lutz, 1985; Aldridge and Brigham, 2001; Connelly et al., 2004) and chick survival (Aldridge and Brigham, 2001; Burkepile et al., 2002) has been identified as a potential driver of these declines. The Alberta sage-grouse population inhabits the northern fringe of the species' range and has declined by 66–92% since 1965 (Aldridge and Brigham, 2003).

Chick survival is one of the demographic parameters most limiting for prairie grouse (Johnson and Braun, 1999; Aldridge and Brigham, 2002, 2003; Connelly et al., 2004; Hagen et al., 2004) and has been identified as a priority in most conservation and recovery strategies for sage-grouse throughout their range (Harris et al., 2000; Connelly et al., 2004; Crawford et al., 2004). Thus, when identifying habitat requirements for chicks, assessing habitat selection (occurrence) alone may result in insufficient assessments of

habitat quality (Van Horne, 1983; Morrison, 2001), potentially leading to inappropriate management (but see Bock and Jones, 2004). The exception might occur if density dependence forces sage-grouse to use sub-optimal habitats. However, sound management strategies should assess how resources affect fitness parameters such as chick survival as well as habitat selection if sage-grouse are to persist (Aldridge, 2005; Aldridge and Boyce, 2007).

Herein, we focus on habitats selected for brood-rearing at two spatial scales, while simultaneously assessing how these habitats influence chick survival for sage-grouse in Alberta, Canada. We first use logistic regression occurrence models to identify habitat characteristics selected by females with broods. We then link habitat covariates to survival using a shared frailty Cox proportional hazards model to assess chick survival relative to habitat and climatic covariates. We hypothesize that sage-grouse select sagebrush and herbaceous habitat components, as has been previously demonstrated (see Hagen et al., 2007, for a review). Similarly, we predict that vegetation components such as increased herbaceous cover (food) and structural cover afforded by shrubs will enhance chick survival, whereas conditions associated with drier climate periods resulting in reduced cover and abundance of mesic habitats containing forbs and insects (Crawford et al., 2004) will adversely affect chick survival. However, habitat selection and survival may not necessarily be related, particularly if sage-grouse fail to recognize ecological factors linked to habitat quality. We then use these models to suggest minimum habitat-quality thresholds that could be used by managers to maintain viable sage-grouse populations.

STUDY AREA

The study area is located in the dry, mixed-grass prairie of southeastern Alberta, Canada (49°24′N, 110°42′W, ca. 900 m elevation). Daily summer (July–August) temperatures average 19.1 °C and annual precipitation is ca. 358 mm (AAFC–AAC 2004 unpublished weather data). The area is characterized by many coulee draws and creeks with gentle slopes. The dominant shrub species is silver sagebrush (*Artemisia cana*) and the dominant forb species include pasture sage (*A. frigida*), several species of clover (*Trifolium* spp. and *Melilotus* spp.), vetch (*Astragalus* spp.), and common dandelion (*Taraxacum officinale*). Needle-and-thread grass (*Stipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Pascopyrum smithii*) are the dominant grass species (Coupland, 1961; Aldridge and Brigham, 2003).

Whereas agricultural expansion in the 1970s apparently isolated Alberta sage-grouse from more southern populations (Schroeder et al., 2004), there has been little conversion to cropland within the study region and grazing is the dominant land-use practice (Adams et al., 2004). The landscape, however, is heavily fragmented by infrastructure associated with oil and gas development, including roads and power lines (Braun et al., 2002; Aldridge and Boyce, 2007). An increased frequency of extended drought conditions (Aldridge and Brigham, 2002) and the introduction of West Nile virus (Naugle et al., 2004) also adversely affect this sage-grouse population.

MATERIALS AND METHODS

FIELD TECHNIQUES

Chick captures and relocations

　　Chicks of radiocollared females were captured by hand as soon as possible after hatch by flushing the hen from her brood (May–July, 2001–2003). Chicks averaged 2.5 days of age (range 0–8 days) at capture. From each brood we randomly selected two chicks and attached radio transmitters to them with two sutures (similar to the technique described by Burkepile et al. (2002; but see Aldridge, 2005). Transmitters weighed 1.6 g and had a battery life of 10–12 weeks (BD-2G transmitters; Holohil Systems Ltd., Carp, ON Canada). Chicks were returned to the point of capture and remotely monitored via telemetry until the hen returned (usually within minutes).

　　Using standard telemetry techniques, radiomarked chicks were relocated every two days following Aldridge and Boyce (2007). When both telemetry and flush methods failed to detect the presence of chicks, we continued to monitor the hen every two days to confirm brood status. Chicks were monitored through 8 weeks of age, the age at which chicks can survive independent of the hen (Schroeder, 1997; Schroeder et al., 1999).

Habitat measurements

　　We assessed vegetation characteristics at one brood use location per week for each brood tracked—typically two days after the brood was located at the site. Behaviors were not assessed at use locations, preventing us from separating different types of use (i.e., foraging, roosting, dispersing). We estimated the percent cover and height of vegetation classes according to methods outlined in Aldridge and Brigham (2002; see Table 1 for a complete list of variables). A 1-m^2 quadrat was placed at the identified use site. To identify the scale at which habitat characteristics might be selected, we took measurements at 8 additional quadrats placed 7.5 and 15 m (two in each of the 4 cardinal directions) away from the use site. The areas enclosed within the 7.5-m "patch" (the center quadrat and the 4 quadrats 7.5 m from the center quadrat) and the 15-m "area" (all 9 quadrats) scales were 177 and 707 m^2, respectively. To obtain a potentially more accurate estimate of percent sagebrush canopy cover (hereafter cover) we measured the line intercept (1-cm increments) of live green sagebrush along 4–15-m line transects radiating from the use site in each cardinal direction (Canfield, 1941). Measurements were recorded separately for the first 0–7.5 m (patch scale) and the entire 0–15 m (area scale) transect. We recorded the same measurements at a (dependent) random location within 100–500 m of each use site, using a random azimuth and distance from the use site. From 1998–2000, Aldridge and Brigham (2002) made these same habitat assessments at a (independent) sample of brood locations, which we use to evaluate our occurrence models. Additional variables measured only in our study from 2001–2003 included residual grass and percent litter cover in quadrats, and we used Robel pole (Robel et al., 1970) measurements of vertical obstruction cover at 2.5-m intervals along all 4 line-intercept transects (Table 1).

Table 1

Explanatory habitat variables, means, and standard errors (in parentheses) of values used to assess brood occurrence and chick survival for 139 brood sites and 139 paired random locations at "patch" (177 m^2) and "area" (707 m^2) scales in southeastern Alberta, 2001–2003. ForbOth was not used in survival models. When grass was absent, grass height values were considered zero. Initially, models for brood occurrence were fit with parameters above the dashed line, evaluated using an independent dataset collected from 1998–2000, and then additional parameters measured only from 2001–2003 (below dashed line) were added to the top model. No independent data were available for evaluating the final chick survival model

Variable code	Description	177-m^2 patch scale		707-m^2 area scale	
		Brood site	Random site	Brood Site	Random site
SBint	Sagebrush cover (%) estimated using line intercept	6.12 (0.52)	1.76 (0.22)	5.12 (0.42)	1.94 (0.22)
SB	Sagebrush cover (%) estimated with 1-m^2 quadrats	8.85 (0.67)	2.79 (0.34)	7.05 (0.49)	2.95 (0.30)
Bush	Cover (%) of all shrubs (including sagebrush) estimated with 1-m^2 quadrats	11.65 (0.77)	4.82 (0.56)	10.02 (0.65)	5.06 (0.53)
Gr	Grass cover (%) estimated with 1-m^2 quadrats	21.20 (1.15)	20.27 (1.30)	21.69 (1.14)	20.65 (0.28)
GrHgt	Mean maximum grass height (cm) within each 1-m^2 quadrat	35.82 (1.20)	30.50 (1.20)	35.38 (13.40)	30.66 (1.15)
Forb	Forb cover (%) estimated with 1-m^2 quadrats	8.88 (0.77)	8.07 (0.72)	8.69 (0.70)	8.01 (0.72)
ForbOth	Unpalatable (other) forb cover (%) estimated with 1-m^2 quadrats	0.60 (0.10)	0.94 (0.12)	0.62 (0.08)	0.94 (0.11)
Robel	Visual obstruction reading (height in cm) measured at 2 m from pole	10.30 (0.58)	4.95 (0.48)	9.16 (0.46)	5.20 (0.47)
Resid	Residual grass cover (%) estimated using 1-m^2 quadrats	3.61 (0.38)	3.62 (0.38)	3.63 (0.37)	3.65 (0.37)
Litter	Estimate of the cover (%) of litter (dead organic matter) using 1-m^2 quadrats	21.20 (1.02)	16.86 (0.92)	21.22 (0.99)	17.27 (0.87)

Chick survival

Date of death for a radiomarked chick was estimated as the date we failed to detect the chick with the hen and no brooding behaviors were observed (see Aldridge and Boyce, 2007). Chicks were recorded as having died on the date they were no longer located with the hen.

DATA ANALYSES

We used a design IV approach (Erickson et al., 2001) to evaluate 4th-order (Johnson, 1980) sage-grouse brood habitat selection and chick survival. Our dependent locations represented a random sample of unused control sites and were compared to used sites (brood locations) for occurrence modeling using a case-control logistic regression. Sage-grouse were not observed at any unused control sites and, given the low population density, the proportion of control sites actually "used" by sage-grouse was low over the course of our study (i.e., low contamination rate; Keating and Cherry, 2004). Thus, we generated a resource selection function (RSF) contrasting used and control locations, which is proportional to the probability of use (Manly et al., 2002; Keating and Cherry, 2004).

Survival analyses were based solely on used locations, comparing sage-grouse chicks that survived (0) to those that died (1) over a particular interval. We assessed brood occurrence and chick survival at both measured scales (7.5-m patch and 15-m area) surrounding the identified use and paired random locations. All analyses were conducted in STATA 8.2 (STATA 2004).

Model development

A priori candidate brood occurrence models were developed using habitat data collected from 2001–2003. These models were consistent with data collected from 1998–2000 (Aldridge and Brigham, 2002). Additional parameters (Robel, obstruction cover; Resid, residual grass cover; and Litter, dead fallen matter) were then added in an attempt to improve model fit (Table 1).

Candidate chick survival models included all habitat variables as well as climate covariates (Onefour Agriculture and Agri-food Canada Research Station, AAFC–AAC 2004 unpublished weather data). Small sample size limited the number of parameters we were able to model for survival. Consequently, before testing a set of combined models based on top models within the three groups, we chose to evaluate relative support for candidate models within three general hypotheses describing chick survival: (1) climate, (2) herbaceous cover and structure, and (3) sagebrush and shrub cover. We calculated several climate variables used for survival models. Growing degree days (GDD) were estimated as the number of degrees above 5º C for each mean daily temperature (Ball et al., 2004), summed over the growing season (beginning 1 March and ending with the tracking date of that year). We also developed a dryness index, which was the GDD for that year divided by the cumulative spring precipitation since the 1 March beginning of the growing season. We assessed all models for outliers and non-linearities (Hosmer and Lemeshow, 1999, 2000), tested for colinearity between parameters ($|r| > 0.7$), and assessed multicollinearity using variance inflation factors (Menard, 1995).

Matched case-control occurrence analyses

We estimated an RSF for paired observations using a case-control logistic regression and present coefficients for occurrence models as unstandardized linear estimates and standard errors. This 1-to-1 matched case-control design (Hosmer and Lemeshow 2000: 223; Manly et al., 2002:150) constrains availability temporally and spatially within similar range ecosite communities, controlling for factors that might otherwise lead to incorrect null models or biases in habitat selection (Compton et al., 2002). We used the Huber–White sandwich variance estimator to account for the lack of independence of repeated habitat samples for the same brood (Pendergast et al., 1996).

Proportional hazards survival analyses

On average, chicks were relocated every 2.3 ± 0.09 days, allowing us to estimate daily survival rates using a Kaplan–Meier (KM) product limit estimator (Kaplan and Meier, 1958) with a staggered-entry design (Pollock et al., 1989; Winterstein et al., 2001). To assess the effect of various habitat and climate covariates on chick survival, we used the Cox proportional hazards regression model (Cox, 1972), which accommodates left and right censoring (Andersen and Gill, 1982; Cleves et al., 2004). We used a shared frailty model, which incorporates a latent random effect (Burnham and White, 2002) for each brood (cluster) accounting for non-independence of chicks within broods (Cleves et al., 2004; Wintrebert et al., 2005). We present coefficients for all survival models as hazard ratios ($\exp[\beta_i]$) and standard errors.

We compared the basic KM chick survival function to the baseline cumulative survival function without fitting any covariates, but we did fit a latent random effect for chicks within broods. This method accounts for the lack of independence among siblings and determines whether a shared frailty model is necessary. We developed Cox proportional hazards models for each a priori candidate model using habitat (time varying) and climatic (some time varying and some fixed) covariates. Because we did not measure habitat characteristics at every relocation, we carried forward habitat covariates across intervals, assuming exposure was constant until the subsequent weekly habitat measurement location. Independent climate variables were used for each interval (see results section).

Deaths with known "failure" times were partitioned using the Breslow estimation of the continuous-time likelihood calculation (Cleves et al., 2004). We assessed the proportional hazards assumption (Winterstein et al., 2001) for each candidate model (effects of the covariates on survival do not change over time, except for ways in which the model is already parameterized, Cleves et al., 2004). Models violating this assumption were removed. We report survival estimates as means ± standard errors.

Model selection, assessment, and evaluation

We used an information-theoretic approach to model selection using Akaike's Information Criteria (AIC) with a correction for small sample size (AIC_c). We used the differences in AIC_c scores (Δ_i) to identify the best approximating occurrence or survival model within the candidate set and AIC_c weights (w_i) to assess the probability that a given model was the best within the set of candidate models (Burnham and Anderson, 2002).

We used the Wald χ^2 statistic (Hosmer and Lemeshow, 2000) to asses the fit of each survival or occurrence model and estimated the variance explained by calculating the reduction in log-likelihood for the given model from the null model (deviance explained). For survival models, we compared the "relative" deviance estimates between survival models within the same set of candidate models, as outlined by Hosmer and Lemeshow (1999).

We used estimates of the receiver operating characteristic (ROC) area under the curve (Fielding and Bell, 1997) to assess the predictive accuracy of top AIC_c-selected occurrence models (Swets, 1988; Manel et al., 2001). The percent of correctly classified (PCC) observations at the optimal cut-off was used to estimate the predictive capacity of the top occurrence models (Nielsen et al., 2004). Predicted probabilities above the optimal probability cut-off point (point that maximized both the sensitivity and specificity curves; Swets, 1988; Nielsen et al., 2004; Liu et al., 2005) were classified as presence and those below the cutoff point were classified as absence. Prior to adding the Robel, Resid, and Litter variables, we evaluated the top models developed with training data (2001–2003) using an independent sample of 113 brood locations collected from 1998–2000 for 17 different broods (see Aldridge and Brigham, 2002).

To assess the fit of the top combined AIC_c-selected chick survival models, we predicted cumulative hazard using the top model at each scale and tested for differences in daily relative hazard for chicks that died (1) compared to those that survived (0) using a *t*-test with unequal variances. Finally, we developed predictive survival curves for top combination models to assess risk of chick mortality across the 90th percentile of the range of availability for that parameter, while holding all other parameters at their mean values. This allowed us to generate dose-response curves and suggest threshold levels for the risk of chick mortality in relation to each parameter of interest based on the asymptote of the curve. We could not generate similar curves for occurrence models due to the conditional nature of the case-control analyses.

RESULTS

We tracked 24 broods from 2001–2003 and assessed vegetation characteristics at 139 brood sites: 42 sites from 8 broods in 2001, 15 sites from 3 broods in 2002, and 82 sites from 13 broods in 2003. Habitat characteristics were measured at an average of 5.8 ± 0.86 sites for each brood. We captured a total of 130 chicks from 23 of the 24 tracked broods, and radiomarked 41 chicks from 22 different broods. We obtained an average of 11.0 (range 1–43) relocations per chick. One chick death was research related, two chicks died from exposure (i.e., drowned in a spring rain storm), and two chicks moved onto lands for which we could not obtain permission to access. Data on all individuals were right censored on their last location date.

CANDIDATE MODELS

Sagebrush cover estimated by either the quadrat method (SB) or Canfield line intercept method (SBint) was positively correlated at both spatial scales (r ≥ 0.87). Thus, only one measure of sagebrush cover could be included in a given model. Grass height was

the only measure of vegetation height that was not correlated with its respective measure of cover. All other correlated height variables were less predictive than cover estimates, based on deviance explained in univariate models, and were not included in a priori candidate models. Variable means at use and random locations are shown in Table 1.

Occurrence candidate models

Hypothesizing that selection for shrub cover might not be linear, we fit both linear and quadratic relationships for each shrub variable. The six different shrub component variables were combined with six different combinations of herbaceous variables, resulting in 36 different a priori candidate models for sage-grouse brood occurrence (Table 2). We present results only for occurrence models that represent the 90% confidence set ($\sum w_i > 0.90$). Additional parameters measured in 2001–2003 (visual obstruction cover [Robel], residual grass cover [Resid], and litter ground cover [Litter]) were added to the top model at each scale, resulting in six additional model combinations (Table 2c).

Survival candidate models

We examined seven different univariate climate models (Table 3), consisting of various GDD and precipitation measures. The GDD model by itself violated the proportional hazards assumption and was dropped from further analyses. The same six shrub variables used for the brood occurrence analyses were used for chick survival models. We used 13 different 1- and 2-parameter herbaceous component models (Table 4), which we assessed both as stand-alone models and in combination with the shrub variables. Model 12 violated the proportional hazards assumption and was dropped from our set of candidate models.

Conditional fixed-effects occurrence analyses

Tabular details for occurrence model results are shown in the Appendix. The top brood occurrence models at both scales had weak support ($w_i < 0.90$; Table A1), but coefficient (β_i) estimates were stable across all candidate models. When the additional parameters were added to the top models at both spatial scales, they only marginally increased predictive capacity and original models still had the most support ($w_i = 0.364$ and 0.234, area and patch scales, respectively). We restricted our inferences about brood site selection to the most parsimonious models, Model 10 and Model 28 (patch and area scale, respectively).

Patch-scale brood occurrence

All ten highest ranked candidate models ($\sum w_i > 0.90$) contained sagebrush cover estimated with the quadrat sampling method (SB), and the two best models included the quadratic term. All models were highly predictive, explaining about 50% of the variation (deviance explained) in brood occurrence (Table A1). Model #10 was the top AIC_c-selected brood occurrence model and had good fit (Wald $\chi^2_4 = 43.96$, $p < 0.0001$) but weak support ($w_i = 0.16$) within our set of candidate models. This model, however, had great accuracy when predicted on both the training and testing data sets (ROC_{train} =

Table 2

(a) Shrub and herbaceous component models used to generate a priori candidate brood occurrence models based on 139 brood sites and 139 paired random locations in southeastern Alberta from 2001–2003 at the patch (177 m^2) and area (707 m^2) scales. (b) Each of the six shrub and herbaceous component models were combined into 36 different initial candidate models. (c) The model structure of the top AIC$_c$-selected model when the additional parameters were added

(a)

Shrub component variables	Herbaceous component variables
A = SB	g = Gr
B = SB + SB^2	h = Gr + GrHgt
C = Bush	i = Gr + Forb
D = Bush + Bush^2	j = Gr + GrHgt + Forb
E = SBint	k = Forb + GrHgt
F = SBint + SBint^2	l = Gr + GrHgt + Forb + ForbOth

(b)

#	Sagebrush quadrat models	#	Bush models	#	Sagebrush intercept models
1	A + g	13	C + g	25	E + g
2	B + g	14	D + g	26	F + g
3	A + h	15	C + h	27	E + h
4	B + h	16	D + h	28	F + h
5	A + i	17	C + i	29	E + i
6	B + i	18	D + i	30	F + i
7	A + j	19	C + j	31	E + j
8	B + j	20	D + j	32	F + j
9	A + k	21	C + k	33	E + k
10	B + k	22	D + k	34	F + k
11	A + l	23	C + l	35	E + l
12	B + l	24	D + l	36	F + l

(c)

Model #	Additional parameter models
Top model	(Top AIC$_c$-selected model for a given scale)
1	(Top model) + Robel
2	(Top model) + Resid
3	(Top model) + Litter
4	(Top model) + Robel + Resid
5	(Top model) + Robel + Litter
6	(Top model) + Resid + Litter
7	(Top model) + Robel + Resid + Litter

0.992, ROC$_{test}$ = 0.841) and excellent (84.1%) and good prediction (77.0%), respectively (Table A2).

Table 3

Explanatory climate variables and models used to assess chick survival for 41 radiomarked chicks from 22 different broods in southeastern Alberta, 2001–2003. Variables were generated for each year that chicks were followed. Due to small sample sizes, a priori climate models consisted of single parameters only

Model #	Variable code	Description
1[a]	GDD[b]	Cumulative growing degree days (above 5 ºC) from 1 March to the chick location date
2	Sp_PPT_Cumm	Cumulative growing season (since 1 March) precipitation
3	Dry_Index	An overall dryness index, calculated as the GDD (above) divided by Sp_PPT_Cumm (above)
4	Sp_PPT_Prior	Total spring (April through June) precipitation for the prior spring
5	Sp-Su_PPT_Prior	Total spring and summer precipitation (April though August) of the prior year
6	Tot_PPT_Prior	Total precipitation for the prior full calendar year
7	GDD_Prior	Total growing degree days (above 5 ºC) from March through August for the prior year

[a]The GDD model was dropped due to violations of the proportional hazards assumption.
[b]All weather data were provided by Onefour Agriculture and Agri-food Canada Research Station, located in the study area (Onefour, Alberta, Canada).

Inferences based on this top model indicate strong positive but decreasing selection for sagebrush cover (concave function; Table A3). Hens selected strongly for taller grass at brood sites, and weakly for greater percent forb cover (Table A3).

Area-scale brood occurrence

Of the 12 models at the area scale within the 90% confidence set (Table A1), 8 contained the SBint variable as either a linear or quadratic term, and all contained the GrHgt variable. All models explained >41.0% of the variation in brood habitat selection, with the top model (Model 28) explaining 44.1%. Similar to that of the patch-scale model, this model had weak support ($w_i = 0.18$) as the top candidate model, but it had good fit (Wald $\chi^2_4 = 56.42$, $p < 0.0001$) and good model accuracy for both training and testing datasets ($ROC_{train} = 0.900$, $ROC_{test} = 0.802$, Table A2). Model 28 also had good prediction (79%) for the training dataset and reasonable prediction on the independent testing dataset (71%, Table A2). Inference based on Model 28 at the area scale again indicated strong positive but decreasing selection for sagebrush cover (concave function; Table A3). Broods were found in areas with taller grass but avoided areas with greater grass cover.

PROPORTIONAL HAZARDS SURVIVAL ANALYSES

Using a basic Kaplan Meier (KM) curve, chick survival to 8 weeks (56 days) was estimated at 0.296 ± 0.081 (Fig. 1). There were no between-year differences in survival

Table 4
Candidate models used to identify the shrub and herbaceous models that best predicted sage-grouse chick survival for 41 radiomarked chicks from 22 different broods in southeastern Alberta, 2001–2003. We did not have an independent testing dataset for candidate models containing "additional" parameters (Resid, Robel, and Litter)

Shrub Model #	Shrub component variables	Herbaceous model #	Herbaceous component variables
1	SB	1	Forb
2	$SB + SB^2$	2	Forb + Gr
3	Bush	3	Forb + Robel
4	$Bush + Bush^2$	4	Forb + Resid
5	SBint	5	Robel
6	$SBint + SBint^2$	6	Robel + GrHgt
		7	Robel + Resid
		8	Gr + GrHgt
		9	Resid + GrHgt
		10	Litter
		11	Litter + Forb
		12^a	Litter + Robel
		13	Litter + GrHgt

[a]Herbaceous model #12 was dropped due to violations of the proportional hazards assumption.

(log rank $\chi^2_2 = 2.86$, $p = 0.24$) nor between first (n = 33) and second (n = 8; log rank $\chi^2_1 = 2.32$, $p = 0.13$) nesting attempts, allowing us to pool data for further survival analyses.

The baseline hazard chick survival model using the shared frailty produced lower survival estimates to 56 days (0.123) than the KM estimate, and was outside the 95% CI for the KM model (range 0.151 to 0.497, Fig. 1). The estimate of the frailty variance, theta ($\theta = 0.96$), was large and significant at $\alpha = 0.10$ (likelihood ratio $\chi^2_1 = 1.87$, $p = 0.086$). Therefore we fit a shared frailty model for all candidate models.

Climate chick survival models

Of the six climate models tested, Model 3 (dryness index only) was the top AIC_c-selected model. This model had only moderate support ($w_i = 0.34$), but it had reasonable fit (Wald $\chi^2_1 = 3.48$, $p = 0.06$). By itself, the dryness index explained more than twice as much variation in chick survival as any other individual climate variable (10.97%). Climate Model 3 (Dry_Index) was selected for use in our combined models.

Shrub chick survival models

Tabular details for survival model results are shown in the Appendix. At the patch scale, the top AIC_c-selected chick proportional hazards shrub model contained the SB variable, suggesting a linear relationship with chick survival (Table A4). This model (#1) had only moderate support ($w_i = 0.44$), but the Akaike weight was more than double the second best model (SBint). The model had significant fit (Wald $\chi^2_1 = 6.13$, $p = 0.01$),
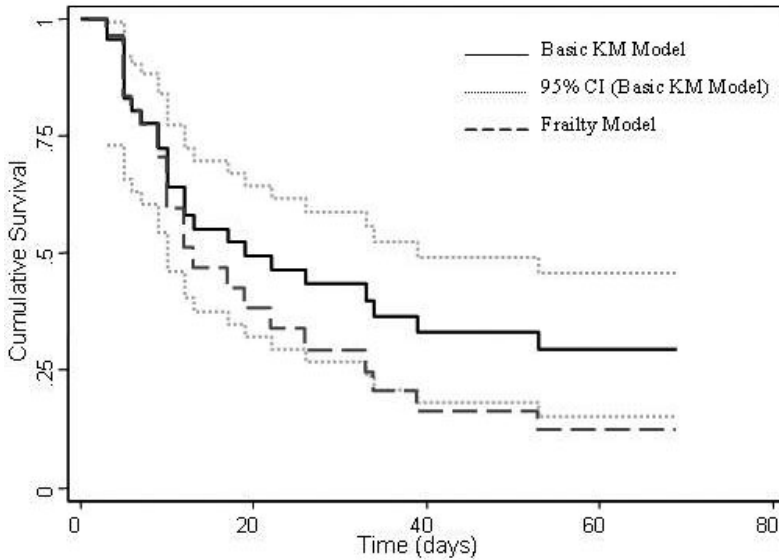
Fig. 1. Kaplan Meier (KM) cumulative chick survival curves for 41 radiomarked sage-grouse chicks from 22 different broods in southeastern Alberta, 2001–2003. The basic KM curve (solid line) does not take into account the correlation of marked chicks within the same brood, whereas the frailty model (dashed line) represents the baseline Cox proportional hazard survival (i.e., no covariates) and accounts for lack of independence of siblings within the same brood. We could not generate 95% confidence intervals for the frailty model due to the conditional nature of the Cox model on covariates within the model.

explained 14.22% of the variation, and was used for combined model building at the patch scale.

At the area scale, the top AIC_c-selected chick proportional hazards model contained the quadratic for sagebrush estimated with the line intercept method (SBint + SBint^2; Table A4). This model had moderate support ($w_i = 0.34$) and the Akaike weight was about twice that of the next best model. This model had good fit (Wald $\chi^2_1 = 6.09$, $p < 0.05$) and explained the most variation within the candidate set at this scale (22.56% deviance explained, Table A4). We used shrub Model 6 (SBint + SBint^2) for combined candidate models at the area scale.

Herbaceous chick survival models

At both the patch and area scales, Model 8 (Gr + GrHgt) was the top AIC_c-selected herbaceous survival model (Table A5). At the patch scale this model had weak support

($w_i = 0.30$) and moderate fit (Wald $\chi^2_1 = 4.76$, $p = 0.09$), but explained the greatest deviance (18.53%) of all herbaceous models. Similarly, at the area scale, Model 8 had a poor fit (Wald $\chi^2_1 = 3.70$, $p = 0.16$) and weak support ($w_i = 0.20$), but explained the greatest deviance (14.35%; Table A5). We retained Model 8 as the herbaceous model for combined survival models at both scales.

Combination chick survival models

Using the top shrub and herbaceous models for each spatial scale, and the top climate model, we developed seven candidate models for each scale. The candidate model set consisted of the top models from each group and all possible combinations of these models (Table A6). The patch scale combination model SB + Dry_Index failed to converge and was removed.

Model 5, which contained a climate and herbaceous component, was the top AIC_c-selected model at the patch scale (Table A7). This model had good fit (Wald $\chi^2_1 = 12.12$, $p = 0.007$), moderate support ($w_i = 0.65$), and explained 42.68% of the variation in survival. Risk of chick mortality increased as the drought index increased, was strongly reduced with increased grass cover, but increased with grass height (Table A8). Threshold response curves suggested a significant reduction in risk to sage-grouse chicks if grass cover was greater than about 20–25% (Fig. 2a). Although risk increased with increasing grass height, this risk is realized only when grass height is greater than ca. 40 cm (Fig. 2b). The model also demonstrates that the moderate-to-high dryness index values dramatically increase the risk of chick death (Fig. 2c).

At the area scale, Model 6 was the top AIC_c-selected survival model (Table A7). This model had good fit (Wald $\chi^2_1 = 16.74$, $p = 0.005$), strong support as the top candidate model ($w_i = 0.91$), and explained considerably more variation in chick survival (58.27%) than any other model. Risk of death again increased with the dryness index, and was positive but decreasing with sagebrush cover (Table A8), suggesting higher chick survival in less dense sagebrush habitats. Risk of chick death was slightly reduced with increased grass cover but increased with grass height (Table A8). Threshold response curves indicate that the relative risk of chick death increased with greater sagebrush cover, and tailed off in denser sagebrush habitats (Fig. 3a). Risk was higher above about 3% sagebrush cover (line-intercept) but was reduced if cover was greater than ~9%. Similar to the patch-level threshold curves (Fig. 3a), risk was reduced with increased grass cover at the area scale, but the threshold was lower (>5% cover, Fig. 3b). Risk also increased with increasing grass height at the area scale, but only when grass was taller than about 30–35 cm (Fig. 3c). Again, the area-level-threshold model also illustrates that hot and dry growing seasons (high dryness index values) reduce chick survival (Fig. 3d).

Both the patch- and area-scale models validated well on the within-sample training dataset. The mean daily hazard was significantly greater for chicks that died within the 56-day monitoring period compared to those that survived or were censored (patch scale: $t_{37.2} = 4.17$, $p < 0.001$; area scale: $t_{31.9} = 3.73$, $p < 0.001$). Based on model covariates, chicks that died were exposed to more hazardous or risky conditions.
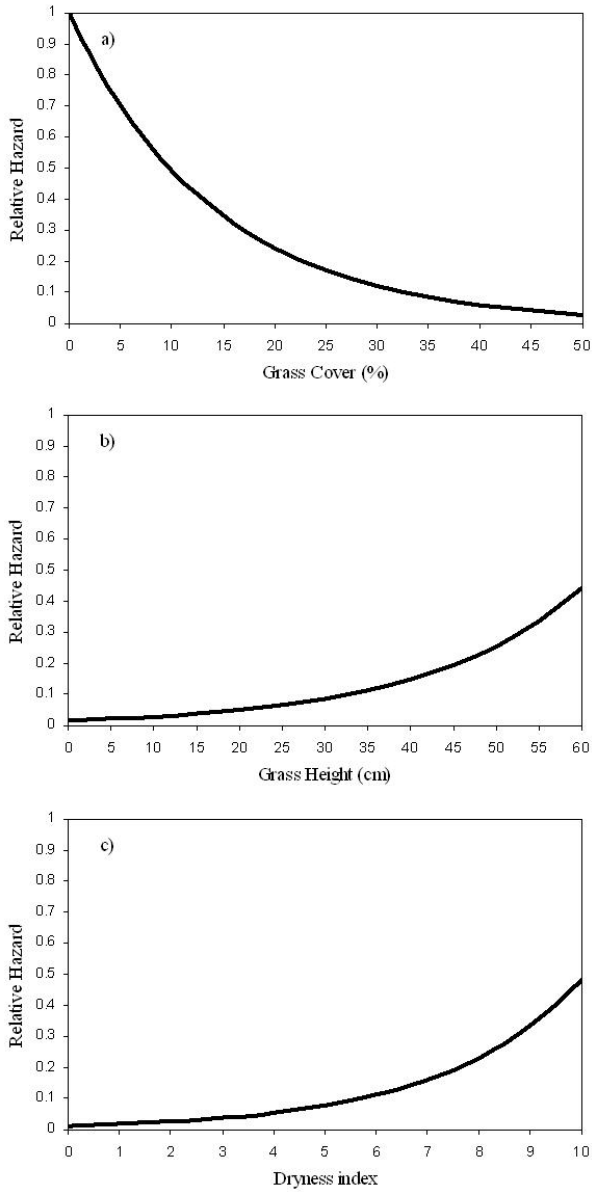
Fig. 2. Threshold response curves for the top AIC_c-selected model (combined Model #5) at the patch scale (177 m²) for relative risk (hazard) for sage-grouse chicks in southeastern Alberta, from 2001–2003. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values.

Fig. 3. Threshold response curves for the top AIC$_c$-selected model (combined Model #6) at the area scale (707 m^2) for relative risk (hazard) for sage-grouse chicks in southeastern Alberta, from 2001–2003. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values.
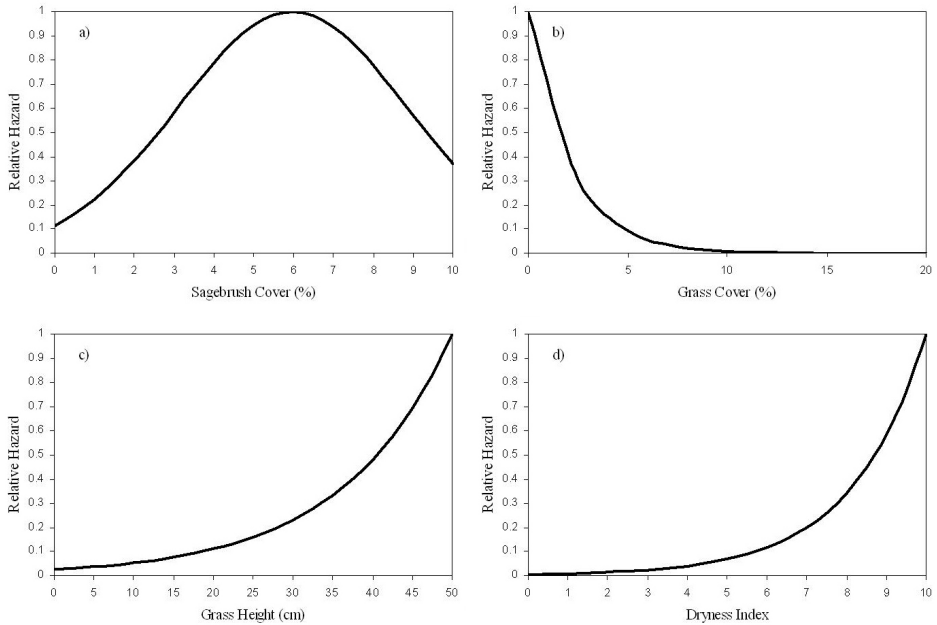

DISCUSSION

Our results highlight the importance of accounting for fitness components when assessing wildlife–habitat relationships (Van Horne, 1983; Morrison, 2001; Aldridge and Boyce, 2007). Sage-grouse may not always select for habitat characteristics (e.g., high selection for dense sagebrush cover and tall grasses) that enhance fitness measured by chick survival (e.g., increased chick mortality in dense sagebrush and in sites with tall [>35 cm] grasses). Thus, management efforts should strive to maintain and enhance habitats that are likely to increase survival, in addition to those selected by the birds. For this population, defining brood habitat requirements as those that enhance juvenile survival, and ultimately recruitment, are necessary to appropriately identify management needs for the species (Aldridge and Brigham, 2001; Crawford et al., 2004).

Overall, we were able to explain 44–50% of sage-grouse brood habitat selection and chick survival using only climatic and habitat covariates. Dose-response curves from survival models allowed us to generate threshold levels for habitat variables such as sagebrush cover, grass cover, and grass height, which will allow for enhanced chick survival. These thresholds provide initial targets for managing sage-grouse brood-rearing habitat in Alberta.

Similar to previous studies, we conclude that the lack of forb-rich habitats that exist in this study likely contributed to the observed selection of sagebrush throughout the brood-rearing period (Aldridge and Brigham, 2002). Although we detected selection for forbs at the patch scale, a similar pattern was not evident at the area scale. Some of the herbaceous survival models that contained forbs had reasonable deviance explained (Table A5), yet none of the patch- or area-scale chick survival models containing forbs were selected as the most predictive model. However, as suggested (but not assessed) in other studies (Peterson, 1970; Schoenberg, 1982; Drut et al., 1994a; Sveum et al., 1998; Aldridge and Brigham, 2002), the risk of chick death in our study was reduced with greater forb cover, but the effect was weak (95% CI overlapped 1). The uniformly low availability of forbs in southeastern Alberta may limit our ability to detect differences in selection and survival relative to forb availability. If forbs are important for survival but abundance is low everywhere, survival rates may be uniformly low relative to forb cover, limiting variation in survival and our ability to detect trends. More than 50 marked individuals (41 in our study) might also be required to generate robust survival estimates (Winterstein et al., 2001).

The scale of habitat measurement appeared to play a minor role in chick survival and habitat selection. Chick mortalities were predicted by grass cover and height at both the patch and area scales. Taller grass at both spatial scales appeared to have negative consequences for chick survival, but threshold models illustrate that habitats are not risky until grass is taller than 35–40 cm (Figs. 2b,3c). Hens appear to recognize this, selecting only moderately for tall grass at both scales. Conversely, patches containing grass cover beyond 20–25% (Fig. 2a) greatly reduced the risk of chick mortality.

However, hens appear not to recognize fitness ties to greater grass cover, showing strong avoidance of dense grass cover. While dense grass cover may reduce the risk of chick mortality, hens may be forced to make a trade-off between these less risky grass-dominated habitats and foraging on forbs and insects in mesic habitats that are open and thus, more risky (less grass and structural cover). The low availability of mesic forb-rich habitats in Alberta may force hens to spend more time meeting dietary requirements, which may put their chicks, and possibly themselves, at greater risk of predation—an ecological trap (Delibes et al., 2001; Breininger and Carter, 2003). In Alberta, management strategies that enhance cover of grass and increase the abundance of mesic habitats to elevate forb abundance would enhance habitat quality and population viability for sage-grouse. Further research is required to understand these relationships, possibly in larger populations with more variability in forb abundance and where larger sample sizes could be obtained.

Our results suggest that precipitation and climate (dryness index) play a pivotal role in sage-grouse chick survival. Spring precipitation has long been suggested to correlate with sage-grouse productivity (June, 1963; Gill, 1966; Schroeder et al., 1999), but until now quantitative studies addressing its effects have not been conducted. Warm years with high amounts of precipitation in the growing season likely result in greater structural growth and protective cover. This may enhance nesting success (June, 1963; Aldridge and Brigham, 2002) and can elevate chick survival. Precipitation prevents forb desiccation and enhances insect abundance, both of which are important food resources

for sage-grouse chicks (Klebenow and Gray, 1968; Dunn and Braun, 1986; Johnson and Boyce, 1990; Drut et al., 1994b).

Although we cannot manage climate to benefit sage-grouse populations, it is important to recognize that weather patterns are highly variable and will affect chick survival. To ensure that populations remain viable when subjected to stochastic events, such as extreme weather or disease outbreaks, it would be important for managers to ensure the availability of high-quality brood-rearing habitats that encourage sage-grouse use and maximize survival (and reproduction) when using those habitats. Ensuring these habitats are in proximity to high-quality nesting habitats within a landscape context (Aldridge and Boyce, 2007) will increase the probability that hens will use these habitats and successfully fledge chicks.

An obvious and interesting difference in factors affecting chick survival was evident between models at patch and area scales. While sagebrush cover was an important component of the area-scale model, no sagebrush or shrub variables entered into the top model at the patch scale. This lack of relationship with sagebrush cover and survival at the patch scale was surprising, given that brood occurrence models indicated that brood hens select strongly for moderate ranges of sagebrush cover. Previous research has shown that sage-grouse select for sagebrush cover early in the brood-rearing cycle, prior to moving away from sagebrush uplands (Patterson, 1952; Dunn and Braun, 1986) and into forb-rich mesic habitats containing 14–40% forb cover (Peterson, 1970; Schoenberg, 1982; Drut et al., 1994a). However, avoidance of dense sagebrush during brood-rearing has also been detected in Washington (Sveum et al., 1998). While hens move their chicks into sagebrush habitats, it appears to compromise chick survival and might be maladaptive, again resulting in an ecological trap (Delibes et al., 2001; Donovan and Thompson, 2001; Bock and Jones, 2004). This is significant, given that reproduction and juvenile survival drive population dynamics for sage-grouse (Johnson and Braun, 1999).

We strongly suggest that future studies assessing wildlife–habitat relationships consider both processes that determine habitat quality for a given species: occurrence and fitness (Van Horne, 1983; Morrison, 2001; Aldridge and Boyce, 2007). Selection by individuals for certain resources may not result in fitness enhancements. Thus, management objectives developed based on occurrence information alone may result in misguided conservation efforts, as we have demonstrated for sage-grouse in Alberta. Whereas fitness data often are more difficult and costly to gather, we encourage further research into occurrence–fitness relationships, across local and landscape scales (Aldridge and Boyce, 2007). The techniques we used here for linking occurrence and survival, although limited in wildlife and conservation fields, offer a proven and promising approach for accurately assessing habitat quality and developing habitat-based population viability assessments for a variety of species (Boyce et al., 1994; Boyce and McDonald, 1999; Aldridge and Boyce, 2007).

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APPENDIX

Table A1

Rankings by Akaike's information criterion corrected for small sample size (AIC_c) for brood occurrence models, difference in AIC_c value between the ith and top-ranked model (Δ_i), and Akaike weights (w_i) for all models within a cumulative summed AIC_c weight ($\sum w_i$) of 0.90 for 139 brood locations at the patch (177 m^2) and area (707 m^2) scale for greater sage-grouse in Alberta, 2001–2003. All model Wald χ^2 tests were significant at $p < 0.0001$. Percent deviance explained (Dev. exp.) indicates the reduction in the log-likelihood from the null model

	Model #	Model structure	AIC_c	Δ_i	w_i	$\sum w_i$	Model Wald χ^2	% Dev. exp.
Patch	10	SB + SB^2 + Forb + GrHgt	104.803	0.000	0.163	0.163	43.96	49.92
	4	SB + SB^2 + Gr + GrHgt	104.925	0.121	0.153	0.316	43.97	49.86
	3	SB + Gr + GrHgt	105.270	0.467	0.129	0.446	39.40	48.58
	9	SB + Forb + GrHgt	105.400	0.597	0.121	0.567	39.41	48.51
	8	SB + SB^2 + Gr + GrHgt + Forb	105.501	0.698	0.115	0.682	49.15	50.67
	7	SB + Gr + GrHgt + Forb	106.007	1.204	0.089	0.771	44.33	49.29
	12	SB + SB^2 + Gr + GrHgt + Forb + ForbOth	107.574	2.770	0.041	0.812	59.42	50.73
	6	SB + SB2 + Gr + Forb	107.739	2.936	0.038	0.849	43.98	48.39
	11	SB + Gr + GrHgt + Forb + ForbOth	108.043	3.240	0.032	0.882	55.28	49.35
	5	SB + Gr + Forb	108.846	4.043	0.022	0.903	35.23	46.72
Area	28	SBint + SBint^2 + Gr + GrHgt	116.021	0.000	0.182	0.182	56.42	44.10
	27	SBint + Gr + GrHgt	116.876	0.855	0.119	0.301	53.00	42.55
	36	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth	117.212	1.192	0.100	0.401	81.46	45.73
	32	SBint + SBint^2 + Gr + GrHgt + Forb	117.394	1.374	0.092	0.493	62.47	44.50
	35	SBint + Gr + GrHgt + Forb + ForbOth	117.395	1.374	0.092	0.584	73.14	44.50
	31	SBint + Gr + GrHgt + Forb	118.150	2.129	0.063	0.647	56.97	42.99
	4	SB + SB^2 + Gr + GrHgt	118.435	2.414	0.054	0.701	46.33	42.84
	34	SBint + SBint^2 + Forb + GrHgt	118.504	2.484	0.053	0.754	40.43	42.81
	10	SB + SB^2 + Forb + GrHgt	118.838	2.817	0.044	0.798	44.66	42.64
	33	SBint + Forb + GrHgt	119.044	3.023	0.040	0.839	32.95	41.43
	3	SB + Gr + GrHgt	119.220	3.199	0.037	0.875	47.98	41.34
	9	SB + Forb + GrHgt	119.233	3.212	0.037	0.912	39318	41.33

Table A2

Comparison of top AIC_c-selected brood occurrence models, metrics for overall model significance, model fit, and classification accuracy for both training (139 brood sites from 2001–2003) and testing data (113 brood sites from 1998–2000) across different scales for greater sage-grouse in Alberta. All model Wald χ^2 tests were significant at $p < 0.0001$. Percent deviance explained (Dev. exp.) indicates the reduction in the log-likelihood from the null model. The area under the receiver operating characteristic curves (ROC [SE]) and the percent correctly classified (PCC) observations based on the training dataset's optimal cutoff point were used to assess model classification accuracy

Scale	Model #	AIC_c-selected model	AIC_c	Model Wald χ^2	% Dev. exp.	Optimal cutoff	Training data		Testing data	
							ROC	PCC	ROC	PCC
177-m²-patch scale	10	SB + SB² + Forb + GrHgt	104.803	43.96	49.92	0.5012	0.992 (0.015)	84.17	84.09 (0.027)	76.99
707-m²-area scale	28	SBint + SBint² + Gr + GrHgt	116.021	56.42	44.10	0.5014	0.900 (0.017)	79.14	0.8024 (0.029)	70.80

Table A3

Estimated coefficients (β_i), standard errors (shown in parentheses), and 95% confidence intervals for top AIC_c-selected candidate brood occurrence models for greater sage-grouse in southeastern Alberta. Models were developed on 139 brood sites and 139 paired random locations collected from 2001–2003

Variable	Patch scale Model #10	Confidence intervals		Area scale Model #28	Confidence intervals	
		Lower	Upper		Lower	Upper
SB	0.460 (0.083)	0.296	0.623			
SB^2	–0.007 (0.001)	–0.009	–0.004			
SBint				0.757 (0.170)	0.425	1.090
SBint^2				–0.024 (0.008)	–0.039	–0.009
Gr				–0.040 (0.011)	–0.062	–0.017
GrHgt	0.058 (0.025)	0.010	0.107	0.115 (0.028)	0.060	0.170
Forb	0.038 (0.021)	–0.004	0.080			

Table A4

AIC_c-selected shrub variable proportional hazards chick survival models and Akaike weights (w_i) for all models at the 177-m^2-patch and 707-m^2-area scales for 41 chicks in southeastern Alberta, 2001–2003. The Wald χ^2 indicates the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (theta). Theta is the estimate of the shared frailty variance and the p-value for the likelihood ratio tests (LR) for the significance of the correlation. Percent deviance explained (Dev. exp.) indicates the reduction in the log-likelihood from the null model

Model #	Shrub model structure	Theta estimate	LR p-value	Log-likelihood	K	AIC_c	$\Delta_i AIC_c$	w_i	Model Wald χ^2	Model χ^2 p-value	Dev. exp. (%)
177-m^2-patch scale											
1	SB	<0.001	0.437	72.022	2	148.616	0.000	0.441	6.13	0.013	14.22
5	SBint	0.052	0.483	72.854	2	150.279	1.663	0.192	3.96	0.047	8.07
2	SB + SB2	<0.001	0.500	71.974	3	151.149	2.532	0.124	5.91	0.052	14.56
3	Bush	0.777	0.158	73.363	2	151.298	2.682	0.115	1.08	0.30	4.08
4	Bush + Bush2	0.805	0.169	72.522	3	152.244	3.628	0.072	2.60	0.272	10.57
6	SBint + SBint2	<0.001	0.466	72.777	3	152.755	4.138	0.056	4.25	0.120	8.65
707-m^2-area scale											
6	SBint + SBint2	0.348	0.342	70.795	3	148.790	0.000	0.346	6.09	0.048	22.56
4	Bush + Bush2	0.805	0.154	71.455	3	149.924	1.134	0.196	4.34	0.114	9.42
1	SB	0.059	0.475	72.676	2	150.111	1.321	0.179	4.30	0.038	18.18
2	SB + SB2	0.109	0.455	72.034	3	151.046	2.257	0.112	4.65	0.098	5.08
5	SBint	0.326	0.351	73.237	2	151.267	2.478	0.100	2.02	0.155	14.14
3	Bush	0.871	0.125	73.759	2	152.089	3.300	0.066	0.22	0.636	0.86

Table A5

AIC$_c$-selected herbaceous variable proportional hazards chick survival models and Akaike weights (w_i) for all models at the patch (177 m²) and area (707 m²) scale for 41 chicks in southeastern Alberta, 2001–2003. The Wald χ^2 indicates the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (theta). Theta is the estimate of the shared frailty variance and the p-value for the likelihood ratio tests (LR) for the significance of the correlation. Percent deviance explained (Dev. exp.) indicates the reduction in the log-likelihood from the null model

	Model #	Model structure	Theta estimate	LR p-value	K	AIC$_c$	Δ$_i$ AIC$_c$	w_i	Model Wald χ^2	Model χ^2 p-value	Dev. exp. (%)
Patch	8	Gr + GrHgt	0.215	0.352	3	150.007	0.000	0.300	4.76	0.093	18.53
	2	Forb + Gr	<0.001	0.500	3	151.412	1.405	0.149	4.83	0.089	13.62
	1	Forb	0.798	0.110	2	151.696	1.689	0.129	0.60	0.439	2.47
	5	Robel	0.923	0.091	2	152.234	2.227	0.098	0.06	0.801	0.26
	10	Litter	0.939	0.099	2	152.290	2.283	0.096	0.01	0.930	0.03
	4	Forb + Resid	0.403	0.351	3	153.998	3.991	0.041	1.35	0.509	3.79
	11	Litter + Forb	0.800	0.115	3	154.324	4.318	0.035	0.60	0.742	2.48
	3	Forb + Robel	0.798	0.110	3	154.325	4.318	0.035	0.60	0.741	2.47
	6	Robel + GrHgt	0.909	0.100	3	154.494	4.487	0.032	0.43	0.808	1.78
	9	Resid + GrHgt	0.789	0.170	3	154.590	4.583	0.030	0.37	0.832	1.39
	7	Robel + Resid	0.723	0.190	3	154.706	4.700	0.029	0.29	0.867	0.91
	13	Litter + GrHgt	0.976	0.096	3	154.759	4.752	0.028	0.17	0.920	0.69
Area	8	Gr + GrHgt	0.296	0.307	3	151.208	0.000	0.202	3.70	0.157	14.35
	1	Forb	0.779	0.117	2	151.920	0.713	0.142	0.40	0.529	1.56
	5	Robel	0.878	0.099	2	151.995	0.787	0.136	0.30	0.583	1.25
	2	Forb + Gr	0.034	0.483	3	152.119	0.911	0.128	4.02	0.134	11.04
	10	Litter	0.995	0.083	2	152.248	1.040	0.120	0.05	0.822	0.21
	4	Forb + Resid	0.201	0.444	3	154.248	3.040	0.044	1.61	0.448	2.79
	6	Robel + GrHgt	0.843	0.115	3	154.289	3.081	0.043	0.62	0.734	2.62
	3	Forb + Robel	0.779	0.118	3	154.439	3.231	0.040	0.50	0.777	2.01
	11	Litter + Forb	0.805	0.114	3	154.490	3.282	0.039	0.45	0.800	1.80
	7	Robel + Resid	0.745	0.204	3	154.584	3.376	0.037	0.39	0.822	1.41
	13	Litter + GrHgt	1.016	0.083	3	154.814	3.606	0.033	0.11	0.944	0.47
	9	Resid + GrHgt	0.802	0.188	3	154.817	3.610	0.033	0.14	0.933	0.45

Table A6

Overall combined candidate proportional hazards chick survival models for 41 radiomarked chicks from 22 different broods at the patch (177 m²) and area (707 m²) scales in southeastern Alberta, 2001–2003. The top climate (Climate), shrub (Shrub), and herbaceous (Herb) models were used at each scale for combination models. The top within each group was also considered as candidate models within this set. The patch-scale model with the combination of sagebrush and the dryness index (SB + Dry _Index) would not converge on a Maximum Likelihood estimate and was therefore not estimated

	Model #	Patch scale combination models		Model #	Area scale combination models
1st Shrub	1-	SB	1st Shrub	1-	SBint + SBint²
1st Herb	2-	Gr + GrHgt	1st Herb	2-	Gr + GrHgt
1st Climate	3-	Dry_Index	1st Climate	3-	Dry_Index
	4-	SB + Gr + GrHgt		4-	SBint + SBint² + Gr + GrHgt
	5-	Gr + GrHgt + Dry_Index		5-	Gr + GrHgt Dry_Index
	6-	SB + Dry_Index + Gr + GrHgt		6-	SBint + SBint² + Dry_Index + Gr + GrHgt

Table A7

AIC$_c$-selected combined proportional hazards chick survival models and Akaike weights (w_i) for all models at the patch (177 m²) and area (707 m²) scales for 41 chicks in southeastern Alberta, 2001–2003. The Wald χ^2 indicates the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (theta). Theta is the estimate of the shared frailty variance and the p-value for the likelihood ratio tests (LR) for the significance of the correlation is presented. Percent deviance explained (Dev. exp.) indicates the reduction in the log-likelihood from the null model

Model #	Combined model structure	Theta estimate	LR p-value	Log-Likelihood	K	AIC$_c$	Δ_iAIC$_c$	w_i	Model Wald χ^2	Model χ^2 p-value	Dev. exp. (%)
177-m²-patch scale											
5	Dry_Index + Gr + GrHgt	<0.001	0.500	67.184	4	144.474	0.000	0.650	12.12	0.007	42.68
6	SB + Dry_Index + Gr + GrHgt	<0.001	0.500	67.053	5	147.440	2.966	0.148	13.11	0.011	43.30
1	SB	<0.001	0.437	72.022	2	148.616	4.142	0.082	6.13	0.013	14.22
3	Dry_Index	<0.314	0.283	72.468	2	149.508	5.034	0.052	3.48	0.062	10.97
2	Gr + GrHgt	0.215	0.352	71.403	3	150.007	5.533	0.041	4.76	0.093	18.53
4	SB + Gr + GrHgt	0.001	0.500	70.362	4	150.829	6.355	0.027	8.18	0.042	25.31
707-m²-area scale											
6	SBint + SBint² + Dry_Index + Gr + GrHgt	0.314	0.283	63.377	5	140.087	0.000	0.905	16.74	0.005	58.27
1	SBint + SBint²	0.348	0.342	70.795	2	146.161	6.074	0.043	6.09	0.048	22.56
5	Dry_Index + Gr + GrHgt	0.034	0.483	68.299	4	146.704	6.617	0.033	10.55	0.014	37.10
3	Dry_Index	0.779	0.117	72.468	2	149.508	9.421	0.008	3.48	0.062	10.97
4	SB + Gr + GrHgt	0.878	0.099	69.893	4	149.892	9.805	0.007	7.49	0.112	28.17
2	Gr + GrHgt	0.296	0.307	72.003	3	151.208	11.121	0.003	3.70	0.157	14.35

Table A8

Estimated hazard ratios (exponentiated coefficients—exp[β_i]), standard errors (shown in parentheses), and confidence intervals for top AIC$_c$-selected candidate proportional hazards chick survival combined models for 41 chicks from 22 different broods in southeastern Alberta, 2001–2003. The top combined model at both scales had the Dry_Index, the Gr + GrHgt herbaceous component model, and a sagebrush component

Variable	Patch scale model # 5	Confidence intervals		Area scale model # 6	Confidence intervals	
		Lower	Upper		Lower	Upper
Dry_Index	1.441 (0.183)	1.123	1.850	1.707 (0.268)	1.256	2.321
SBint				2.068 (0.549)	1.230	3.479
SBint^2				0.941 (0.022)	0.898	0.985
Gr	0.932 (0.026)	0.882	0.985	0.953 (0.031)	0.894	1.017
GrHgt	1.056 (0.021)	1.015	1.098	1.076 (0.027)	1.025	1.130