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LINKING OCCURRENCE AND FITNESS TO PERSISTENCE: HABITAT-BASED APPROACH FOR ENDANGERED GREATER SAGE-GROUSE

CAMERON L. ALDRIDGE[1] AND MARK S. BOYCE

Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9 Canada

Abstract. Detailed empirical models predicting both species occurrence and fitness across a landscape are necessary to understand processes related to population persistence. Failure to consider both occurrence and fitness may result in incorrect assessments of habitat importance leading to inappropriate management strategies. We took a two-stage approach to identifying critical nesting and brood-rearing habitat for the endangered Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta at a landscape scale. First, we used logistic regression to develop spatial models predicting the relative probability of use (occurrence) for Sage-Grouse nests and broods. Secondly, we used Cox proportional hazards survival models to identify the most risky habitats across the landseape. We combined these two approaches to identify Sage-Grouse habitats that pose minimal risk of failure (source habitats) and attractive sink habitats that pose increased risk (ecological traps). Our models showed that Sage-Grouse select for heterogeneons patches of moderate sagebrush cover (quadratic relationship) and avoid anthropogenic edge habitat for nesting. Nests were more successful in heterogeneous habitats, but nest suecess was independent of anthropogenic features. Similarly, broods selected heterogeneous high-productivity habitats with sagebrush while avoiding human developments, cultivated cropland, and high densities of oil wells. Chick mortalities tended to occur in proximity to oil and gas developments and along riparian habitats. For nests and broods, respectively, approximately 10% and 5% of the study area was considered source habitat, whereas 19% and 15% of habitat was attractive sink habitat. Limited source habitats appear to be the main reason for poor nest success (39%) and low chick survival (12%). Our habitat models identify areas of protection priority and areas that require immediate management attention to enhance recruitment to secure the viability of this population. This novel approach to habitat-based population viability modeling has merit for many species of concern.

Key words: Alberta, Canada; Centrocercus urophasianus; *Cox proportional hazard; fitness; Greater Soge-Grouse; habitat; logistic regression; occurrence; persistence; population viability; sagebrush.*

INTRODUCTION

Detailed theoretical and empirical models linking resources to both animal occurrence and fitness measures are necessary to understand the underlying processes determining population persistence. Although numerous local population studies focusing on fine-scale habitat correlations with various species declines have been conducted, landscape-scale habitat models (Franklin et al. 2000, Wisdom et al. 2002*a*, *b*, Akçakaya et al. 2004) or range-wide analyses addressing processes and patterns of persistence have been attempted for relatively few species (see Mattson and Merrill 2002, Laliberte and Ripple 2004). Only a handful of these studies have integrated population dynamics with landscape-level resources (Wiegand et al. 1998, Akçakaya et al. 2004), with even fewer successfully decomposing models to critical life stages and addressing landscape-level drivers of fitness (see Breininger et al. 1998, Franklin et al. 2000, Larson et al. 2004). Links to fitness are a critieal and necessary component for long-term conservation of many species of concern (Donovan and Thompson 2001) that allows biologists and managers to suitably assess population viability (Boyce et al. 1994, Boyce and McDonald 1999).

Ultimately, measures of habitat quality must link fitness (reproduction and survival; Van Horne 1983, Morrison 2001) to resources to accurately assess how resources affect population viability. Occurrence or abundance may not be a good indicator of fitness (Van Horne 1983, Hobbs and Hanley 1990, Morrison 2001, Tyre et al. 2001), particularly in human-dominated landscapes (Remes 2000, Bock and Jones 2004), due to the creation of ecological traps. Thus, assessments should involve the identification of (1) habitats that animals are likely to use (occurrence), in addition to (2) habitats where animals are likely to be successful (fitness). Habitat patches where animals are likely to occur and that also have high reproduction and/or survival measures are source habitats (Pulliam 1988, Breininger et al. 1998), whereas habitats with abundant

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[1] Present address: U.S. Geological Survey, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80526-8118 USA. E-mail: cameron_aldridge@usgs.gov

animals but poor fitness have been referred to as attractive sinks (Delibes et al. 2001, Larson et al. 2004) or ecological traps (Donovan and Thompson 2001, Battin 2004, Bock and Jones 2004). Failnre to differentiate attractive sinks from source habitats may result in incorrect assessments of habitat importance, ultimately leading to inappropriate management. However, the ability to appropriately assess habitat quality is limited by the difficulty in gathering suitable basic life-history information for many speeies (Donovan and Thompson 2001), particularly those that are rare or have low reproductive rates.

Sagebrush-steppe habitats have undergone extensive changes since European settlement. Today, many of these habitats are considered imperiled, facing continuing fragmentation and degradation (Knick et al. 2003, Connelly et al. 2004) due to conversion to agriculture (Connelly et al. 2004), invasion by nonnative species (Knick et al. 2003, Connelly et al. 2004), energy extraction activities and developments (Braun et al. 2002, Lyon and Anderson 2003), intense grazing pressure (Beck and Mitchell 2000, Hayes and Holl 2003, Crawford et al. 2004), and climate change (Neilson et al. 2005). As a result, species dependent on sagebrush-steppe have experienced drastic range contractions and population declines. Sage-Grouse (*Centrocercus* spp.) are a notable example. Currently, Sage-Grouse exist in about half of their historic range (Schroeder et al. 2004), with individual populations declining by 15–90% since the early 1970s (Connelly and Braun 1997, Aldridge and Brigham 2003, Connelly et al. 2004). Many populations are at risk of extirpation, reinforcing the need to appropriately assess habitat relationships for this species.

Although much research has been conducted at fine scales, addressing factors related to nest success (Aldridge and Brigham 2001, Connelly et al. 2004, Holloran et al. 2005) and some related to chick survival (Aldridge and Brigham 2001, Aldridge 2005), research assessing potential landscape features driving habitat selection and fitness is limited. Other than the recently published Greater Sage-Grouse (*Centrocercus urophasianus*) conservation assessment (Connelly et al. 2004), which summarized range-wide habitats and threats, only one study, to our knowledge, used a habitat-based landscape approach to assess Greater Sage-Grouse population persistence within the interior Columbia basin of the western United States (Wisdom et al. 2002*a*, *b*).

Within its current range, the Alberta Greater Sage-Grouse (hereafter Sage-Grouse) population has declined 66–92% since the 1970s (Aldridge and Brigham 2003, Connelly et al. 2004). This population (endangered provincially and within Canada; Aldridge and Brigham 2003) is isolated from other populations and inhabits a heavily fragmented landscape dominated by oil and gas activities (Braun et al. 2002), and has only 400–600 birds remaining (Aldridge 2005). Low productivity limits this population (Aldridge and Brigham 2001, 2002, 2003, Aldridge 2005) and the implementation of long-term habitat management initiatives may be required before increases occur (Crawford et al. 2004).

Our overall objective was to identify nesting and brood-rearing habitats critical to the persistence of Sage-Grouse in Alberta. First, we developed landscape-level occurrence models predicting where Sage-Grouse are likely to nest and raise their young. Secondly, we developed survival models to identify the most risky habitat for Sage-Grouse nests and for chicks. We validated the predictive capacity of these models using independent data sources from prior research in Alberta. We combined these two approaches to identify source habitats where Sage-Grouse are likely to occur and also be successful. Conversely, we identified ecological trap habitats that are attractive to Sage-Grouse, but are habitats where nests are likely to fail, or chicks are likely to die. We used these habitat states to identify areas that require immediate management attention. We discuss our findings within the context of potential reclamations or landscape improvements that could result in the transformation of ecological trap habitats into higher quality source habitats that are likely to sustain the Alberta Greater Sage-Grouse population.

Methods

Study area

Sage-Grouse are found within a 4000 km^2 area of the dry mixed-grass prairie of southern Alberta, Canada (Fig. 1). Our study area (49°24′ N, 110°42′ W, ~900 m elevation) encompasses the core of this range (1110 km^2; Fig. 1). Most lands are grazed by cattle, and roughly one-third of this area is influenced by oil and gas activities. Summer (July–August) temperatures average 19.1°C and annual precipitation is ~358 mm (Onefour Agriculture and Agri-food Canada Research Station [2004], *unpublished weather data*). Silver sagebrush (*Artemisia cana* Pursh) is the dominant shrub, and there are a variety of different forb species, including pasture sage (*A. frigida* Willd.), several species of clover (*Trifolium* spp. and *Melilotus* spp.), vetch (*Astragalus* spp.), and common dandelion (*Taraxacum officinale* Weber ex Wiggers). Needle-and-thread grass (*Hesperostipa comata* Trin. and Rupr.), june grass (*Koeleria macrantha* Ledeb.), blue grama (*Bouteloua gracilis* Willd. ex Kunth), and western wheatgrass (*Pascopyrum smithii* Rydb.) are the dominant grass species (Coupland 1961, Aldridge and Brigham 2003).

Field techniques

Female Sage-Grouse were captured during the breeding season from five of eight known active leks (breeding sites) in southeastern Alberta from 2001 to 2004 and were fitted with a 14-g necklace-style radiotransmitter (RI-2B transmitters, Holohil Systems, Carp, Ontario, Canada). Hens were located every second day so that nesting attempts and nest fate could be assessed. Nest initiation and hatch/failure were estimated as the

midpoint between consecutive (every two days) relocations (Manolis et al. 2000) following Aldridge (2005). From 2001 to 2003, if a nest was successful (i.e., ≥ 1 egg hatched), we captured chicks by hand as soon as possible after hatch and attached 1.6-g microtransmitters (BD-2G transmitters, Holohil Systems, Carp, Ontario, Canada) to two randomly chosen chicks from each brood (see Burkepile et al. 2002, Aldridge 2005). Hens with broods (2001–2004) and chicks (2001–2003) were relocated every two days during the brood-rearing period.

GIS predictor variables

We developed a suite of variables in a GIS that may be important as predictors of Sage-Grouse nest and brood occurrence, as well as survival of nests and chicks. These variables were related to either habitat characteristics or human influences (see Table 1 for a detailed description of each variable and its data source). We used a dry mixed-grass plant community guide based primarily on soil types (Adams et al. 2005) to identify Sage-Grouse ecosite range plant communities (B. W. Adams, *personal communication*). We generated summary statistics calculating the proportion of each habitat class within a 1-km^2 moving window across the landscape. We used a July 2000 Landsat TM Satellite image to generate brightness, greenness, and NDVI (Normalized Difference Vegetation Index) values using a tasselled-cap transformation (Crist and Cicone 1984, Sellers 1985) in the program PCI Geomatica Prime 8.2 (PCI Geomatics 2001). We also estimated the mean and standard deviation (SD) of NDVI values within a 1-km^2 moving window. Higher SD values represent more heterogeneous (variable) habitat patches.

The importance of sagebrush in providing nesting habitat at local scales has been demonstrated (Sveum et al. 1998*b*, Aldridge and Brigham 2002, Holloran et al. 2005), and sagebrush may also be selected at brood-rearing sites (Aldridge and Brigham 2002, Aldridge 2005). We used a digital map of sagebrush developed from aerial photo interpretation to estimate sagebrush cover (the percentage of each landscape polygon that was covered with sagebrush plants; Jones et al. 2005) at the each pixel and 1-km^2 window scales. Sage-Grouse may select for intermediate sagebrush cover (quadratic relationship or concave selection function; Aldridge 2005), because very thick shrub cover can limit herbaceous understory and reduce a bird's ability to detect predators (Wiebe and Martin 1998). Thus, we also assessed selection for sagebrush cover metrics as quadratic functions (Table 1). Finally, we reclassified the sagebrush density distribution defined by Jones et al. (2005) into two measures of "patchy" or heterogeneous sagebrush distribution, estimated per pixel and at the 1-km^2 scale (see Table 1).

Sage-Grouse broods move to mesic habitats with greater forb (Drut et al. 1994*a*, Sveum et al. 1998*a*) and insect (Johnson and Boyce 1991, Drut et al. 1994*b*) abundance later in the summer. We used a soil-moisture index derived from a digital elevation model (DEM; see Evans 2002) called a compound topographic index (CTI), which is correlated with soil moisture and nutrients (Gessler et al. 1995). Similar to our lines of inference for NDVI, we also calculated measures of the mean CTI and the variability (SD) in CTI within a 1-km^2 moving widow (Table 1). In addition, we calculated the distance to the nearest water source (Table 1).

Anthropogenic landscape features included distance measures for roads, trails, oil well sites, crop (cultivated lands), and urban (town, farmstead, energy infrastructure) areas, as well as a density measure for each variable calculated as the linear kilometer per square kilometer for roads and trails, the number of well sites within a 1-km^2 window, and the proportion of area that was either crop or urban within a 1-km^2 window. Noise and human activity associated with road and oil wells may be avoided by (Braun et al. 2002) or may have negative consequences (Lyon and Anderson 2003) for Sage-Grouse. Thus, we also summed the number of pixels classified as either roads or well sites that were visible from any given cell within 250, 500, and 1000 m. To assess how water impoundments (e.g., dams, dugouts, canals, and so on; McNeil and Sawyer 2003) influence habitat selection by Sage-Grouse, we generated distance and density measures for water impoundments (Table 1). The final anthropogenic variables were distance and density measures (proportion of habitat within 1-km^2 window) for human habitat (roads, oil wells, urban), and nonnatural edge habitats (roads, oil wells, urban, and crop). All GIS analyses were conducted using ArcGIS 8.3 (ESRI 2002).

Model development

We conducted univariate analyses for all predictor variables (Hosmer and Lemeshow 2000), using $P < 0.25$ based on a Wald z statistic as a cutoff for inclusion in the full model. We assessed each variable for outliers and nonlinearities (Hosmer and Lemeshow 1999, 2000). If two parameters were correlated ($r > |0.6|$), we retained the variable with the smaller P value. We assessed the full model, dropping the least significant parameter (i.e., largest P value), refitting the reduced model and repeating the process until all remaining parameters were significant at $\alpha = 0.05$ (Hosmer and Lemeshow 1999, 2000). We tested for multicollinearity using variance inflation factors (VIF; Menard 1995), removing variables if VIF scores for individual parameters > 10 or mean model scores > 1 (Chatterjee et al. 2000). All analyses were conducted in STATA 8.2 (STATA 2004), and descriptive results are presented as means $\pm$ SE.

Logistic regression occurrence analyses

We define occurrence as the relative probability of Sage-Grouse resource use based on detections from radiotelemetry. We evaluated third-order habitat selection

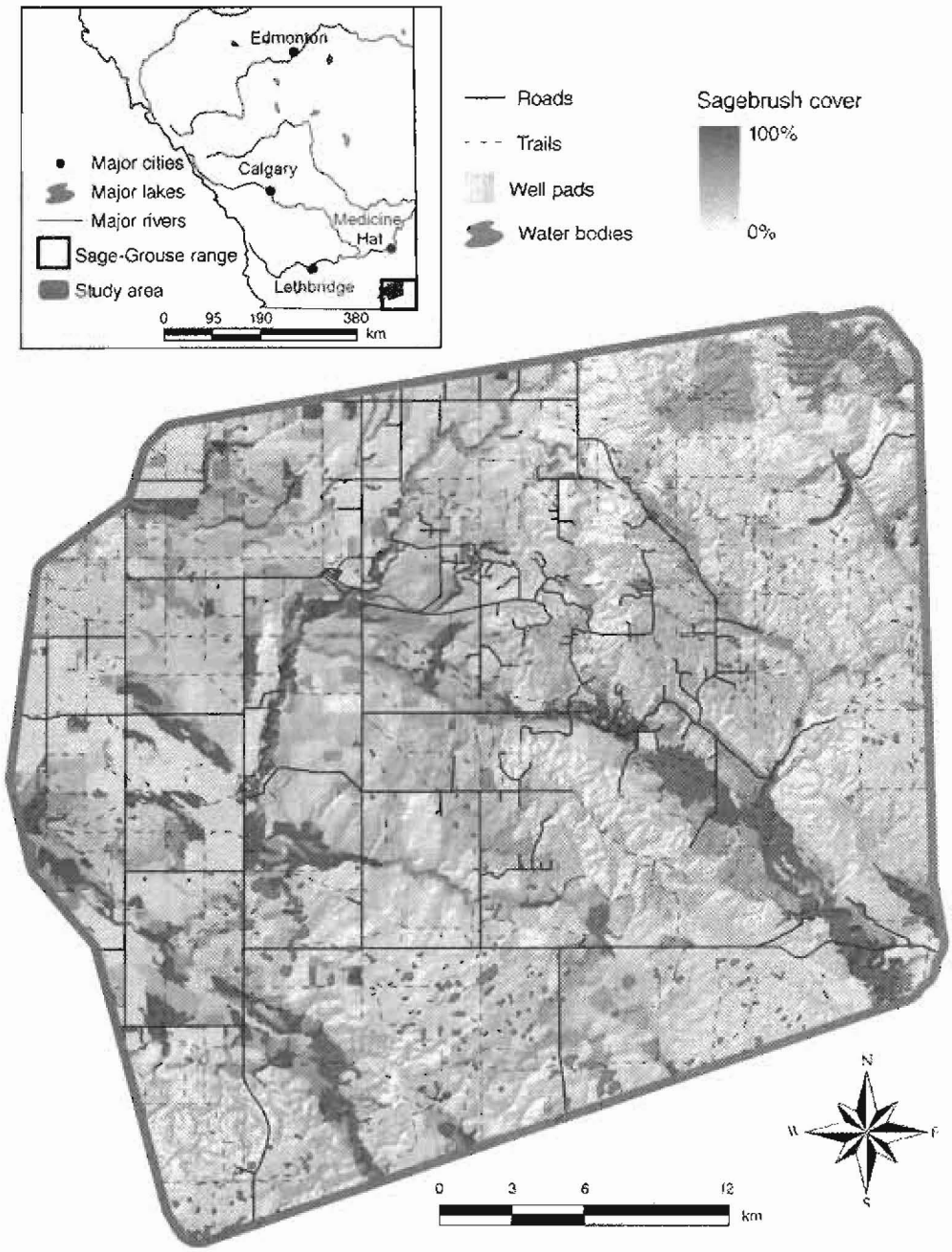

FIG. 1. Alberta Greater Sage-Grouse study area showing sagebrush density along with roads, trails, well pads, and major water bodies. The inset map shows the study area and current range of Sage-Grouse within Alberta, Canada, with major rivers, water bodies, and cities for reference.

(Johnson 1980) using resource selection functions (RSFs; Manly et al. 2002) with a design II approach, following individuals to identify a set of used resources, but assessing availability at the population level (Erickson et al. 2001). The RSF is equivalent to the logistic discriminant contrasting the distributions of used and available resource units (Keating and Cherry 2004, Johnson et al. 2006). Coefficients for RSF models are presented as unstandardized linear estimates and standard errors. We generated 5000 random locations across a 1-km buffer around a 100% minimum convex polygon surrounding all Sage-Grouse nest and brood locations combined (1110 km^2 area), resulting in a sample density of about five available resource units per square kilometer. Due to models being heavily biased toward the larger sample of available (0) resource units, we used an importance weight,

TABLE 1. Explanatory GIS variables used for Sage-Grouse nest and brood/chick occurrence and survival models in southeastern Alberta, Canada.

Variable	Data type	Description
Brit	30 m cont.	brightness generated from a Landsat 7 TM satellite image
Green	30 m cont.	greenness generated from a Landsat 7 TM satellite image
Wet	30 m cont.	wetness generated from a Landsat 7 TM satellite image
NDVI	30 m cont.	NDVI calculated from a TM satellite image
NDVI_avg	30 m cont.	mean NDVI value within a 1-km^2 moving window
NDVI_sd	30 m cont.	standard deviation of NDVI within a 1-km^2 window
CTI	30 m cont.	Compound Topographic Index (high values = increased moisture)
CTI_mean	30 m cont.	mean CTI values within a 1-km^2 moving window
CTI_sd	30 m cont.	standard deviation of CTI values within a 1-km^2 moving window
Well_dist	10 m cont.	distance to nearest standing energy well site
Well_dens	10 m cont.	count of energy well sites within a 1-km^2 moving window
vWell_1km, _500 m, _250 m	30 m cont.	no. visible 30-m pixels that are wells within radius of 1 km, 500 m, or 250 m
Rd_dst	10 m cont.	distance (km) to nearest road (any paved or gravel road)
Rd_dens	10 m cont.	linear km per km^2 of roads
vRd_1km, _500 m, _250 m	30 m cont.	no. visible 30-m pixels that are road within radius of 1 km, 500 m, or 250 m
Tr_dst	10 m cont.	distance (km) to nearest trail (non-paved or gravelled truck trail)
Tr_dens	10 m cont.	linear km per km^2 of trails
Imp_dst	10 m cont.	distance to nearest water impoundment (dam, dugout, canal, combination)
Imp_dens	10 m cont.	count of no. water impoundments within a 1-km^2 moving window
Water_dst	10 m cont.	distance to nearest natural permanent or semipermanent water body
SB	10 m cont.	sagebrush cover (%) as identified from air photo interpretation
SB^2	10 m cont.	squared term for SB
SBmean	10 m cont.	mean sagebrush cover (%) within a 1-km^2 moving window
SBmean^2	10 m cont.	squared term for SBmean
SB_pch1, SB_pch2	10 m cont.	patchy sagebrush distribution 1 (codes 7, 8, 9) or 2 (codes 7, 8, 9, 11) from Jones et al. (2005)
pSB_pch1, pSB_pch2	10 m cont.	proportion of habitat within a 1-km^2 moving window that is SB_pch1 or SB_pch2, respectively
Crop_dst	10 m cont.	distance to nearest cultivated lands
pCrop	10 m cont.	proportion of habitat within a 1-km^2 moving window that is cultivated
pUrban	10 m cont.	proportion of habitat within a 1-km^2 moving window that is urban (town, ranch, energy compressor station, and so on)
Urban_dst	10 m cont.	distance to nearest urban developments
Eco1	10 m cat.	loamy range site with well-drained soils, low sagebrush cover
Eco2	10 m cat.	saline lowlands, swales and depression, sparse low sagebrush
Eco3	10 m cat.	blowout and overflow sites, solonetzic soils: plant community varies, but higher density of sagebrush
Eco4	10 m cat.	loamy upland sites with medium texture soils, fescue and wheat grasses
Eco5	10 m cat.	thin break range sites, soils vary, characterized by greater shrub cover
Eco6	10 m cat.	badlands type habitats with juniper and needle-and-thread-blue grama
Eco7	10 m cat.	broad, wetland and shrubby (willow, rose, snowberry) riparian habitats
Eco8	10 m cat.	all altered habitats (urban, crop, wells and roads); see Hum and Edge
pEco1, pEco2, ... pEco7	10 m cont.	proportion of habitat within a 1-km^2 moving window that is Eco1, Eco2, ... Eco7
Hum_dst	10 m cont.	distance to any human habitat (roads, wells, urban)
pHum	10 m cont.	proportion of habitat within a 1-km^2 moving window that is human habitats
Edge_dst	10 m cont.	distance to habitat that creates nonnatural edge habitats (human above + crop)
pEdge	10 m cont.	proportion of habitat within 1-km^2 moving window that is edge habitats

Notes: All variables were first tested univariately in occurrence (logistic regression) and survival (proportional hazards) models. Candidate variables with $P < 0.25$ were removed, and correlated variables with higher P values were removed. Data type refers to continuous (cont.) or categorical (cat.) variables. All distance measures are in kilometers. NDVI is the Natural Difference Vegetation Index. Data sources are as follows: TM-derived variables were based on a 22 July 2000 Landsat 7 image (Path 39 Row 26); digital elevation models (DEM) were derived from 1:50 000 National Topographic Database Contour Lines; sagebrush, crop, urban, and water base features are from Jones et al. (2005); sagebrush cover is the percentage of the area within each polygon covered by sagebrush (Jones et al. 2005); linear features were based on a 2001 landscape from Alberta Provincial Base features (1:20 000); well locations were provided by Alberta Energy for the study area as of August 2002; water impoundments were mapped based on McNeil and Sawyer (2003); Eco1–Eco7 are dry mixed-grass rangeland ecosite plant community bins after Adams et al. (2005); a viewshed analyses tool for ArcGIS 8.3 (H. L. Beyer, (http://www.spatialecology.com/htools/overview.pbp)), together with a DEM to generate these data, was used to generate density of viable wells and roads. For visibility purposes, we assumed that well sites were 9 m in height and that the average vehicle was 2 m in height.

which gave full weighting to used resource units, but available resource units received a weighting (down) proportional to the ratio of sampled use (1) points to available points (STATA 2004, Users Guide). Weighting effectively adjusts (inflates) the standard errors of the estimates, and allows for traditional inferences about standard errors and P values for coefficient estimates. Given that a shift in brood habitat to more mesic sites at about seven weeks of age (Dunn and Braun 1986, Sveum et al. 1998*a*) does not occur in Alberta (Aldridge and Brigham 2002), we combined locations throughout the brood-rearing period for all analyses.

Proportional hazards survival analyses

We used the Cox proportional hazards regression model (Cox 1972) to assess how landscape variables affect nest survival or success and chick survival. The Cox model allows for left- and right-censoring of data (Andersen and Gill 1982, Cleves et al. 2004) and estimates the hazard rate. We present coefficients for all survival models as hazard ratios ($\exp[\beta_i]$) and standard errors. For chick survival models, we estimated a shared frailty Cox proportional hazards model to account for lack of independenee of chicks within broods (Cleves et al. 2004, Wintrebert et al. 2005). We used the Breslow estimation of the continuous-time likelihood calculation (Cleves et al. 2004) to partition deaths with tied failure times. We assessed the proportional hazards assumption (Winterstein et al. 2001) for our models by testing for nonzero slopes of Schoenfeld residuals (Schoenfeld 1982) and by inspecting logarithm plots of the estimated cumulated hazard functions[21] (Cleves et al. 2004).

Model assessment and validation

We used a χ^2 statistic (Hosmer and Lemeshow 2000) to asses the fit of all final models, except for the chick shared frailty model, for which we used a Wald χ^2 statistic (Hosmer and Lemeshow 1999). We estimated the cumulative daily relative risk of failure for top survival models as the sum of the predicted relative hazard for each individual nest or chick divided by exposure days. We used these predietions to assess the predictive accuracy based on receiver operator characteristic (ROC) estimates (Fielding and Bell 1997). High model accuracy results in ROC estimates above 0.9, good model accuracy between 0.7 to 0.9, and values below 0.7 indicate low model accuracy (Swets 1988, Manel et al. 2001). We used the percentage correctly classified (PCC) at the optimal cutoff (where the absolute value of the difference between sensitivity and specificity is minimized; Liu et al. 2005) to estimate of the predictive capacity of the top occurrence models. We considered PCC $\geq$ 80% as excellent model prediction and PCC $\geq$ 70% was reasonable prediction (Nielsen et al. 2004). We also validated our nest survival model by predicting it to an independent sample of 38 nests with known fate produced by 31 different females from 1998 to 2000 (Aldridge and Brigham 2002). We assessed fit and prediction as previously described for model training data. We did not have independent chick survival data for validation, and limited sample sizes (41 chicks) prevented us from folding our data for cross-validation purposes (Boyce et al. 2002). Thus, for both chiek and nest survival models, we took the predieted daily hazard and tested for differences in the rate of failures or deaths (nest or chick) compared to those that survived. If the model was predietive, failed chicks or nests should have been exposed to greater daily hazards. We used a one-tailed t test with unequal variances to test for differences in daily relative hazard rates.

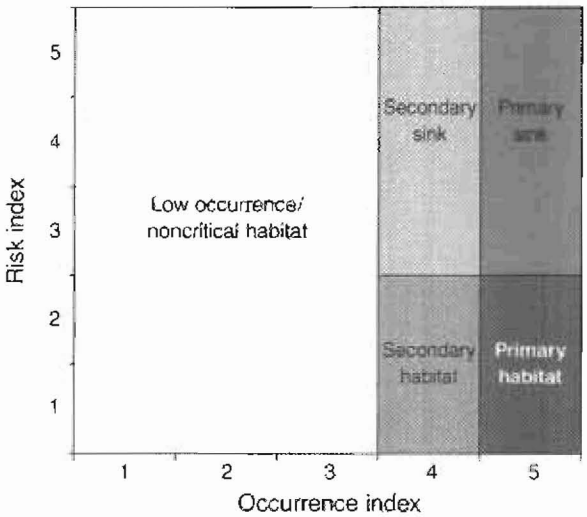

FIG. 2. A graphic representation of nesting and brood-rearing habitat states for Greater Sage-Grouse in southeastern Alberta. States include noncritical (low occurrence) habitat, primary habitat (high occurrence and low-to-moderate risk), secondary habitat (good occurrence and low-to-moderate risk), primary sink (high occurrence and moderate-to-extreme risk), and secondary sink (high occurrence and moderate-to-extreme risk). The figure is developed from the approach of Nielsen et al. (2006).

For RSF models, it is inappropriate to assess model accuracy and predictive capacity using ROCs and PCC (Boyce et al. 2002). Thus, we predicted the RSF to generate relative index-of-occurrence scores, ranking habitat pixels into five quantile bins; bin 1 was the lowest rank. For each model, we initially grouped the landscape into 10 quantile bins, each with an equal proportion of the landseape (see Boyce et al. 2002). In most cases though, some bins contained no training or validation data points, forcing us to lump bins to avoid null cells. We adjusted for availability of habitat (amount of area) within each bin as suggested by Boyce et al. (2002). We used a Spearman rank correlation to test for a correlation between frequency (area-adjusted) of use locations within increasing bin ranks (Boyce et al. 2002). Again, we validated both occurrence models using training data sets (2001 to 2004), and performed out-of-sample validation (1998 to 2000) using an independent sample of 40 nest locations produced by 33 different females, and 151 brood locations from 16 different broods (Aldridge and Brigham 2002, Aldridge 2005).

Development of habitat states

We defined the five ranked bins for nest and brood occurrence models as (1) poor, (2) low, (3) moderate, (4) good, and (5) high occurrence, with good-to-high bins indicating that Sage-Grouse were likely to occur there. Similarly, we applied survival models, ranking the predicted relative risk of failure (nest or chick) for the survival models, into five quantile risk bins: (1) minimal,

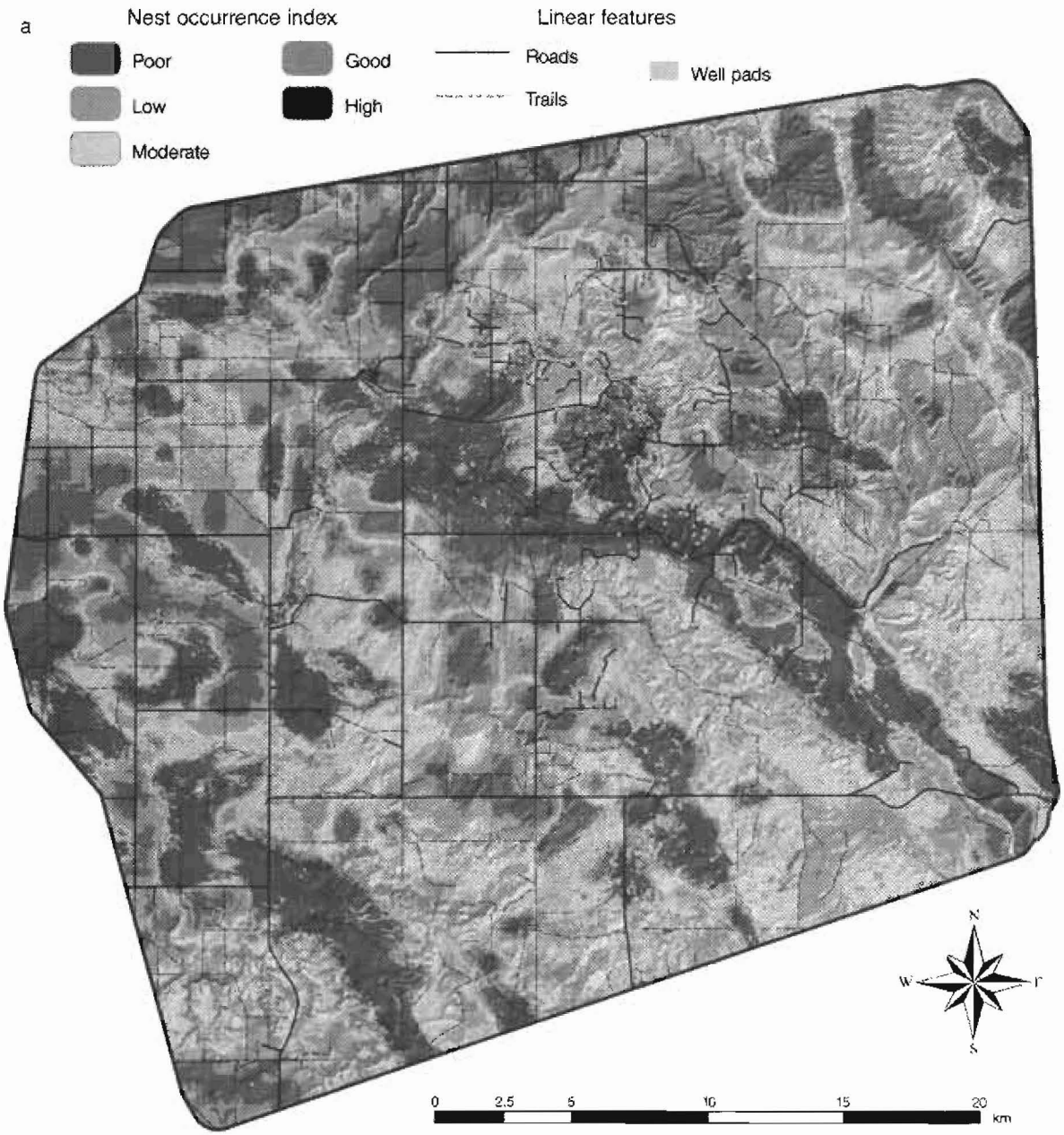

FIG. 3. Relative index of Sage-Grouse (a) nest and (b) brood occurrence in southeastern Alberta, as determined by logistic-regression occnrrence models. Good and high index values indicate that Sage-Grouse are likely to use these habitats for nests or brood-rearing, respectively.

(2) low, (3) moderate, (4) high, and (5) extreme risk of failure. We used these occurrence and risk indices to identify five different habitat states, similar to the methods of Nielsen et al. (2006). Firstly, occurrence bins ranking from poor to moderate (1–3) were classified as overall low use, and it was assumed that Sage-Grouse would be unlikely to occur in those habitats, although we tested this with validation data. We refer to bin 5 as primary habitat and bin 4 as secondary habitat, based on the relative probability of use of resource units in these bins. We overlaid the respective nest or chick survival model predictions on the occurrence maps in our GIS to identify the habitat states. Primary and secondary occurrence habitats falling in areas of moderate-to-extreme risk (bins 3–5) were classified as attractive sink habitats, broken into primary and secondary sinks, respectively. Similarly, habitats with low risk (bins 1–2) but high occurreuce (occurrence bins

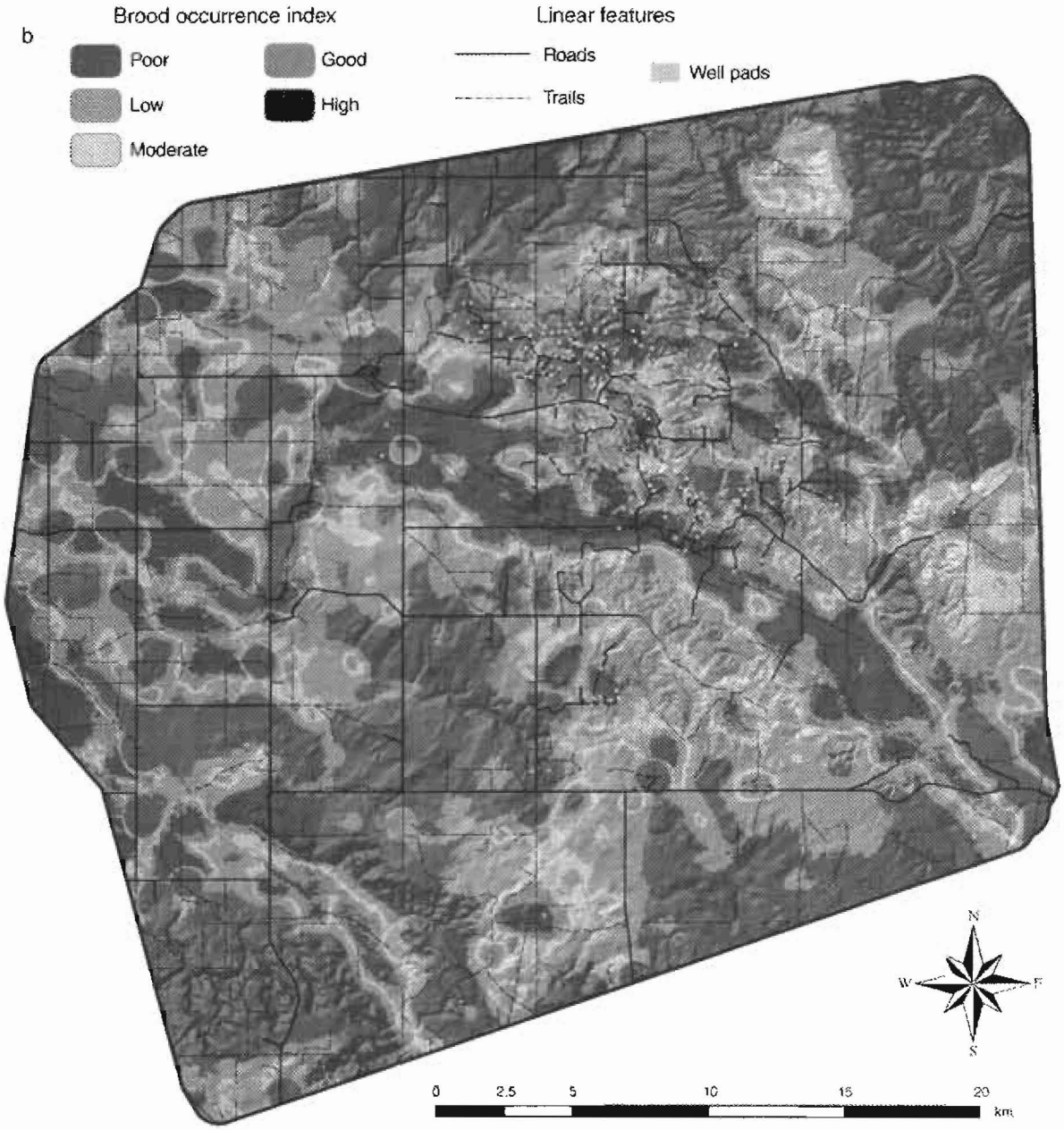

FIG. 3. Continued.

5 and 4) were considered primary or secondary source habitat. We graphically illustrate these conceptual habitat classes in Fig. 2 and develop maps depicting these habitat states for nesting and brood-rearing habitats within each habitat state.

RESULTS

From 2001 to 2004, we located 113 Sage-Grouse nests for occurrence modeling (two nests were from unmarked females). Nest survival/success over the 28 day incubation period was 39.4% ± 4.84% for 111 nests produced by 61 radio-marked females (all values reported as mean ± SE). With only five of 111 nests produced by yearlings, we were precluded from testing for age effects. There was no difference in nest survival among years of our study (log rank $\chi^2_3 = 5.50$, $P = 0.14$) and there was no difference in survival between initial (40.2% ± 5.7%, $n = 77$) and second nesting attempts (37.5% ± 9.0%, $n = 34$; log rank $\chi^2_1 = 0.07$, $P = 0.79$), allowing us to combine all nests when modeling survival.

From 2001 to 2004, we identified a total of 669 brood locations from 35 Sage-Grouse broods (19.11 ± 0.60 locations/brood), which we used to model brood occurrence. From 2001 to 2003, we radio-marked 41

TABLE 2. Estimated coefficients (β_i) and standard errors for the final nest occurrence model for 113 Sage-Grouse nests in southeastern Alberta from 2001 to 2004.

Variable	β_i	SE	P
Brit	−0.0215	0.0082	0.009
SBmean	0.1025	0.0401	0.011
SBmean^2	−0.0014	0.0007	0.047
pSB_pch2	1.5251	0.7602	0.045
pEco6	−3.0573	0.9654	0.002
pEdge	−2.8002	1.3531	0.038

Notes: To characterize habitat availability, 5000 random points were used; these points were weighted using importance weights such that the available sample was effectively 113 points. P values indicate the significance of the coefficients using a Wald z statistic.

chicks from 22 different broods. Chick survival to 56 days using the shared frailty proportional hazards model was 12.3% and there was significant correlation (at $\alpha = 0.10$) in the fate of chicks within broods ($\theta = 0.96$, $P = 0.086$).

Nest occurrence

Our stepwise modeling approach resulted in a final nest occurrence model that contained six parameters (Table 2); no interactions were significant. This model had good fit (likelihood ratio $\chi^2_6 = 53.62$, $P < 0.0001$). Sage-Grouse showed strong avoidance of badland habitats ($\beta_{pEco6} = -3.0573$), areas with a high proportion of anthropogenic edge habitats ($\beta_{pEdge} = -2.8002$), and areas with greater brightness values ($\beta_{Brit} = -0.0212$). Conversely, Sage-Grouse selected nesting habitat that contained large patches (1 km^2) of moderate sagebrush cover (quadratic or concave relationship; $\beta_{SBmean} = 0.1025 + \beta^2_{SBmean} = -0.0014$), but where the distribution of sagebrush within these patches was heterogeneous ($\beta_{pSB_patch2} = 1.5251$; Table 2).

When we applied this model to the study area (Fig. 3a) and mapped the five habitat bins, only 30% of the landscape was considered to have a good-to-high likelihood of Sage-Grouse nesting there. However, the majority of nests (72% of training nests and 65% of validation nests) occurred within the good-to-high habitat bins, indicating that lower ranked habitat bins were used less frequently. Both the nests ($n = 113$ nests) that we used to build the model (years 2001–2004) and the validation sample (years 1998–2000, $n = 40$ nests) showed an increasing frequency (area-adjusted) of occurrence within the predicted nest index bin (training data: $r_S = 1.00$, $P < 0.0001$; testing data: $r_S = 1.00$, $P < 0.0001$), suggesting that the RSF for nest occurrence was approximately proportional to probability of use.

Brood occurrence

After stepwise removal of variables, the final brood occurrence model contained 15 significant variables with no interaction terms. This model had good fit (likelihood ratio $\chi^2_{15} = 583.32$, $P < 0.0001$). Similar to the nest occurrence model, hens with broods selected for large patches (1 km^2) of moderate sagebrush cover (quadratic; $\beta_{SBmean} = 0.10445 + \beta^2_{SBmean} = -0.0010$) that contained a patchy distribution of sagebrush ($\beta_{pSB_patch2} = 1.7924$; Table 3). Selection was strong for mesic habitats, selecting for higher wetness values ($\beta_{Wet} = 0.0217$) and higher mean CTI scores ($\beta_{CTImean} = 0.4835$), while avoiding high brightness values ($\beta_{Brit} = -0.0076$; Table 3). Broods avoided habitats associated with a high density of urban developments ($\beta_{pUrban} = -64.9741$), areas close to cultivated cropland ($\beta_{Crop_dist} = 0.1525$), and habitats composed largely of ecosite plant community types in bins 4 (loamy upland sites), 5 (thin break sites), and 6 (badland sites; Table 3). Sage-Grouse broods tended to occur in areas with a greater density of trails ($\beta_{Tr_dens} = 0.2336$) and were closer to water impoundments than random ($\beta_{Imp_dist} = -0.6305$; Table 3). Broods tended to be closer to well sites ($\beta_{Well_dist} = -0.4087$), but at the same time, they avoided areas with a greater density of visible well sites within 1 km ($\beta_{vWell_1km} = -0.2016$; Table 3).

We applied this 15-parameter brood occurrence model to the study area (Fig. 3b), binning habitats from poor to high occurrence. Only 20% of habitat fell within good-to-high habitat occurrence, but the majority of brood locations (77% of training points and 71% of testing points) fell within the good-to-high habitat, suggesting that our relative bin ranks capture brood occurrence across the landscape. The brood occurrence model was predictive, with the area-adjusted frequency of occurrence increasing with increasing bin rank; for 669 model training locations, $r_S = 1.00$, $P < 0.0001$; for 151 validation brood locations, $r_S = 1.00$, $P < 0.0001$.

Nest survival

The final nest survival model contained three variables (Table 4). Nest failure was independent of human-

TABLE 3. Estimated coefficients (β_i) and standard errors (SE) for the final brood occurrence model for 669 Sage-Grouse brood locations in southeastern Alberta from 2001 to 2004.

Variable	β_i	SE	P
Brit	−0.0076	0.0032	0.018
Wet	0.0217	0.0088	0.013
CTI_mean	0.4835	0.0872	<0.001
Well_dist	−0.4087	0.0446	<0.001
vWell_1km	−0.2016	0.0591	0.001
Tr_dens	0.2336	0.0887	0.008
Imp_dist	−0.6305	0.2134	0.003
SBmean	0.1044	0.0175	<0.001
SBmean^2	−0.0010	0.0003	<0.001
pSB_pch2	1.7924	0.3703	<0.001
Crop_dist	0.1525	0.0339	<0.001
pUrban	−64.9741	18.2819	<0.001
pEco4	−1.2791	0.3625	<0.001
pEco5	−2.1208	0.3368	<0.001
pEco6	−1.8744	0.4931	<0.001

Notes: To characterise habitat availability, 5000 random points were used; these points were weighted using importance weights such that the available sample was effectively 669 points. P values indicate the significance of the coefficients using a Wald z statistic.

TABLE 4. Estimated hazard ratios (exponentiated coefficients, $\exp[\beta_i]$) and standard errors for the final proportional hazards nest survival model using 111 Sage-Grouse nest sites in southeastern Alberta from 2001 to 2004.

Variable	β_i	SE	P
NDVI_sd	10.9×10^{-8}	9.44	0.034
SB	1.0138	0.0052	0.007
pSBpch1	0.2862	0.1784	0.045

Note: P values indicate the significance of the coefficients using a Wald z statistic.

use features. Nest failure was greatly reduced in habitats that contained a heterogeneous mix of sagebrush cover ($\beta_{SBpch1} = 0.2862$; Table 4). However, there was a slight increase in risk as sagebrush cover in the immediate vicinity of the nest site increased ($\beta_{SB} = 1.0138$; Table 4). As the variability in NDVI increased (NDVI_sd), risk of failure decreased significantly ($\beta_{NDVI_sd} = 10.9 \times 10^{-8}$; Table 4).

Although the final nest survival model had good fit (likelihood ratio $\chi^2_3 = 12.94$, $P < 0.005$), it had moderate-to-low predictive accuracy ($ROC_{train} = 0.67$; $ROC_{test} = 0.59$) and low predictive capacity ($PCC_{train} = 60.4\%$; $PCC_{test} = 55.3\%$). Using the cumulative daily relative hazard, however, failed nests were exposed to more risky habitats for training data set ($t_{102.05} = 3.52$, $P < 0.001$), but this model had difficulty detecting failures using the independent sample of 40 nests (22 failures; $t_{24.50} = 0.82$, $P = 0.21$). When we applied this final nest survival model to the landscape, ~60% of habitat occurred within the moderate-to-extreme risk categories, in which we predict Sage-Grouse nests are likely to fail (Fig. 4a).

Chick survival

For the chick survival model, no variables were significant ($\alpha = 0.05$) after sequential removal. However, the last two variables removed were significant at $\alpha = 0.10$ ($\beta_{CTI} = 1.1883$; $\beta_{vWell_1km} = 1.5219$; Table 5) and we used these in the final model, given small chick sample size (24 failures of 41 chicks). Based on these parameters, chick failure increased in habitats with a higher visible well site density within 1 km, and surprisingly, risk was also greater in habitats with higher CTI values. Model fit was moderate (Wald $\chi^2_2 = 5.74$, $P < 0.057$), predictive accuracy ($ROC_{train} = 0.67$) was low, but classification accuracy ($PCC_{train} = 70.7\%$) was good. Using only these two parameters, our model accurately identified chicks that failed as being exposed to more risky habitats, having higher cumulative daily relative hazard rates ($t_{38.39} = 3.03$, $P = 0.002$), but we had no independent sample for validation. When we applied this model to the landscape (Fig. 4b), areas with greater oil and gas activities fell into the extreme risk category, but the majority of the riparian areas (linear sections with high CTI values) were also identified as risky habitats. About 60% of habitat was identified as risky for Sage-Grouse chicks.

Nest habitat states

Of the 30% of the landscape that we identified as having a good-to-high likelihood of being used as nesting habitat, over half of this habitat (19% of the landscape) occurs in high-risk areas, with 11.6% of habitat classified as a primary sink and 7.4% classified as secondary sink nesting habitat (Fig. 5a). Only a small portion of the landscape is primary nesting habitat (8.4%), with just 2.6% of habitat considered secondary habitat. Primary nesting habitat averaged 5.83 ± 0.12 km (mean ± SE) from active leks in Alberta, and secondary habitat was 6.77 ± 0.22 km. The cumulative percentage of source nesting habitat increases linearly up to about 10 km, where it asymptotes and a threshold is reached, encompassing about 90% of all source habitats (Fig. 6a).

Brood habitat states

Our brood occurrence maps indicated that there is limited habitat available (20% good-to-high occurrence class) for Sage-Grouse brood-rearing. In addition, three-quarters of available habitat (15% of the landscape) is high risk and classified as habitat sinks (Fig. 5b); only 5% is source brood-rearing habitat (primary plus secondary habitat; Fig. 5b). Primary and secondary brood-rearing habitats averaged 4.52 ± 0.16 km, and 6.21 ± 0.17 km from the nearest active lek, respectively. Similar to nesting habitat, ~90% of all source brood-rearing habitats occur within ~10 km of all active lek sites (Fig. 6b).

DISCUSSION

Our landscape-scale models indicate a limited supply of habitats selected by Sage-Grouse (good-to-high occurrence bins), with about 30% of the habitat likely to be used for nesting (Fig. 3a) and 20% for brood-rearing (Fig. 3b). Over half of that 30% identified as attractive nesting habitat (19% of the landscape) is considered risky (moderate-to-extreme risk; Fig. 5a) causing an ecological trap (Delibes et al. 2001, Kristan 2003). Therefore, more than half of the nesting habitat used by Sage-Grouse will not result in successful nesting attempts (Fig. 5a), even though Sage-Grouse still occupy those habitat patches. An even greater threat to recruitment and population persistence may be the brood habitat ecological trap, with three-quarters of

TABLE 5. Estimated hazard ratios (exponentiated coefficients, $\exp[\beta_i]$) and standard errors (SE) for the shared frailty final proportional hazards chick survival model using 41 Sage-Grouse chicks from 22 different broods in southeastern Alberta from 2001 to 2003.

Variable	β_i	SE	P
CTI	1.1883	0.1145	0.073
vWell_1km	1.5219	0.3437	0.063

Notes: P values indicate the significance of the coefficients using a Wald z statistic. The shared frailty variance estimate is 0 = 0.96, $P = 0.086$.

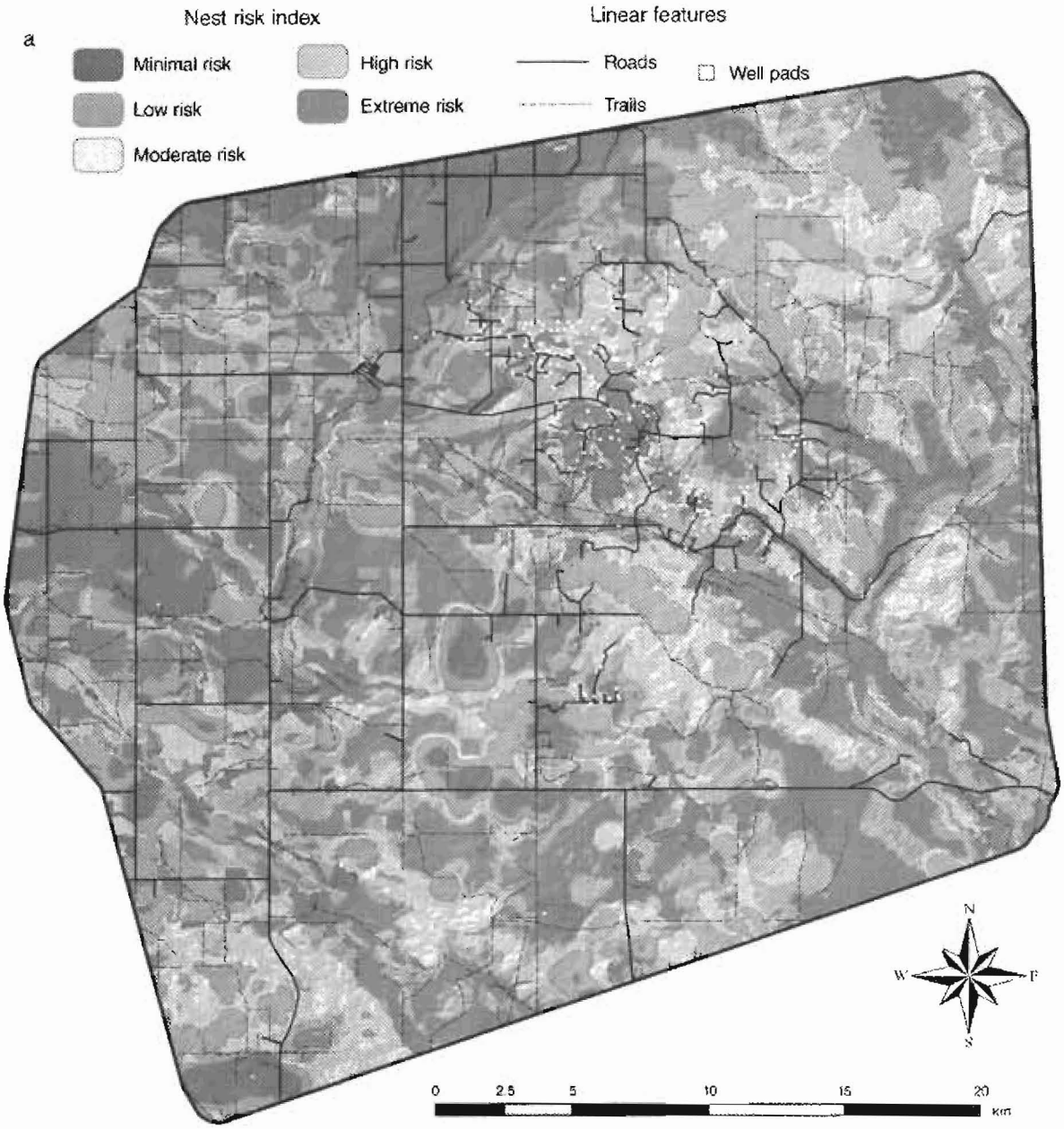

FIG. 4. Relative index of risk for Sage-Grouse (a) nest failure and (b) chick failure in southeastern Alberta, as determined by Cox proportional hazards modeling of survival. High and extreme risk values indicate that a nest is likely to fail or a chick is likely to die if it occurs in these habitats.

the attractive brood habitat (15% of the landscape out of the 20% considered attractive) likely to result in chick failure (Fig. 4b). Low nest success (39%; Sage-Grouse range 15–86%; Schroeder et al. [1999]), and poor chick survival (12%) are driven by an abundance of attractive sink habitats where Sage-Grouse have poor recruitment. Our approaches not only spatially identify habitats with poor fitness, which ultimately drive population dynamics (Van Horne 1983, Morrison 2001), but also address mechanisms driving declines.

Nesting habitat

Consistent with our predictions for nest occurrence and previous research at finer scales (Aldridge 2005), nests were more abundant in habitat patches (within a 1 km^2 area) with moderate sagebrush cover. Selection was also strong for large patches (1 km^2) that contained a heterogeneous distribution of sagebrush cover, with continuous and sparsely distributed sagebrush habitats used less than expected by chance. Sage-Grouse select locally for greater herbaceous understory cover and our

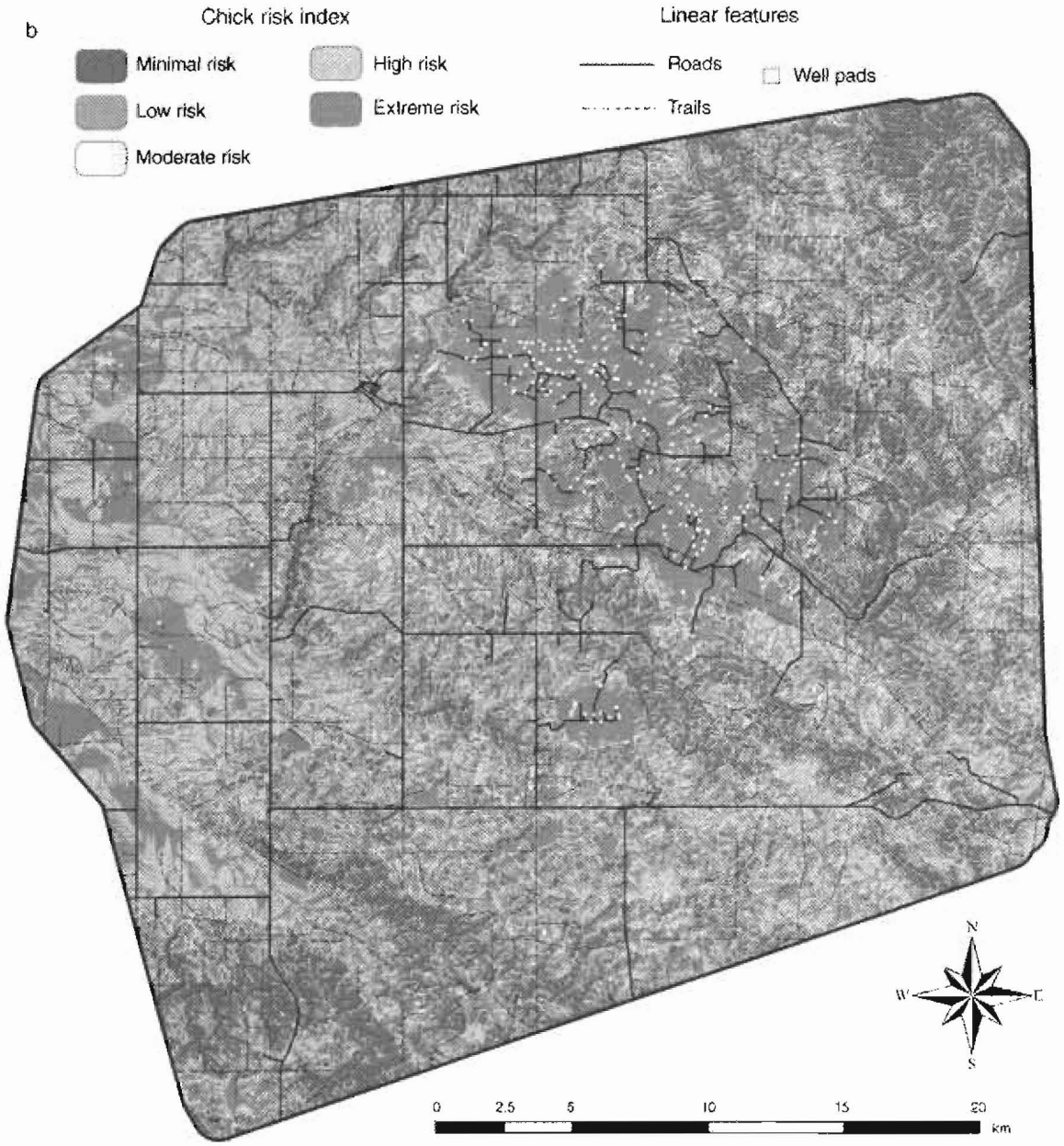

FIG. 4. Continued.

landscape models identified coarse-scale correlates for habitat that lack this understory cover. Moderate cover and patchy distributions are likely to provide suitable overstory shrub cover while allowing for the lateral herbaceous cover reqnired to conceal nests from predators (Wallestad and Pyrah 1974, Wiebe and Martin 1998, Aldridge and Brigham 2002). Nest abundance was lower in habitats with high brightness values, suggesting that habitats with increased bare ground were avoided. This idea is reinforced by the apparent avoidance of less productive badland habitats that contain steep and dry, exposed soils (Adams et al. 2005).

As predicted, nest failure was lower in habitats that contained a heterogeneous mix of sagebrush cover ($\beta_{SBpch1} = 0.2862$), with limited or continuous dense cover resulting in nest failure (Table 4). Conceivably, this may explain the slight increase in risk with increasing sagebrush cover in the immediate vicinity of the nest (linear increase; $\beta_{SB} = 1.0138$; Table 4). Risk also was significantly reduced for increasing NDVI_sd measures. The NDVI index values were small, ranging from 0.012 to 0.099. Taking the natural logarithm of the unexponentiated β coefficient ($\beta_{NDVI_sd} = -18.33$) times an increase in the NDVI_sd index values of 0.01 (~10%

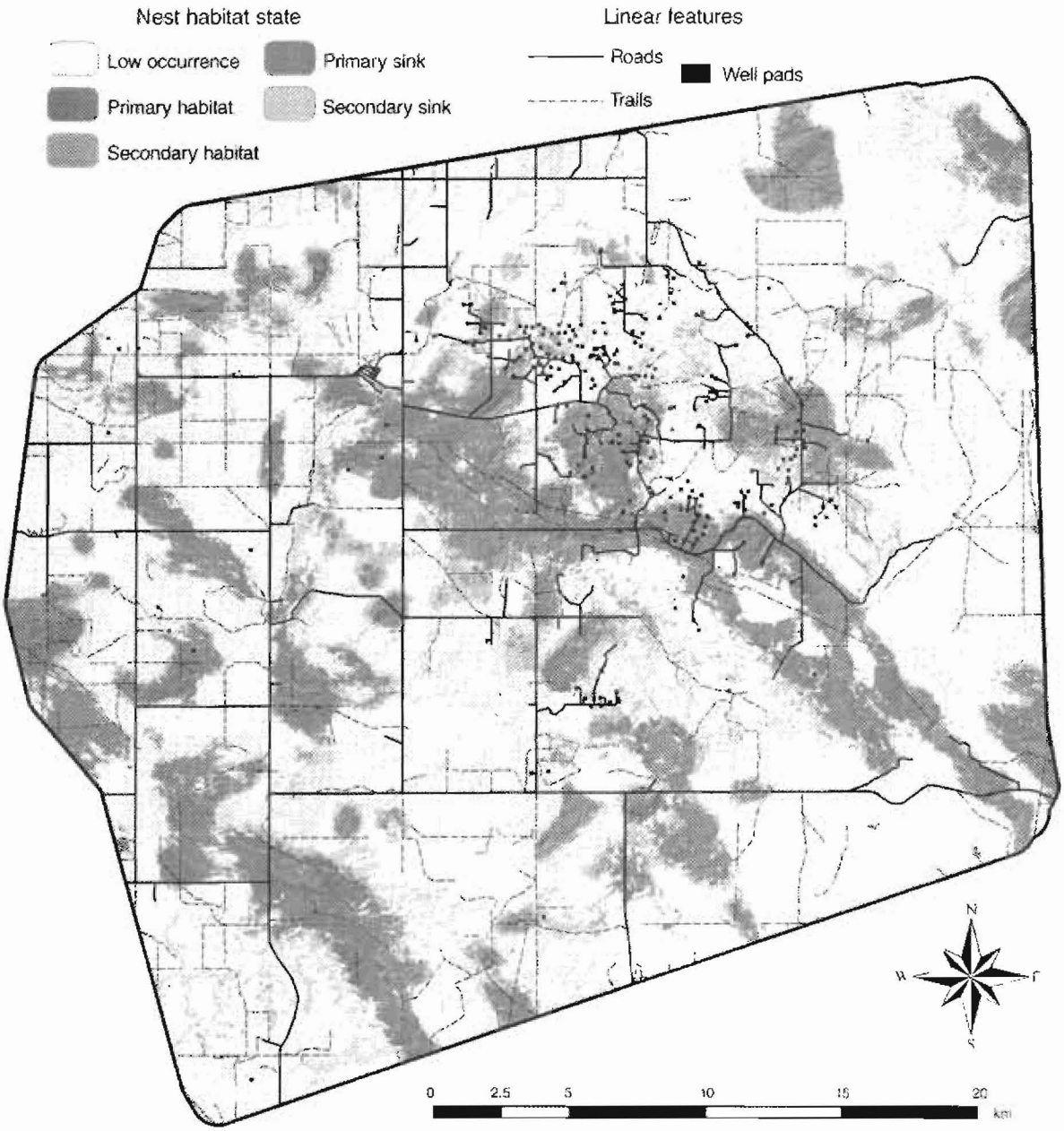

FIG. 5. Habitat states for Sage-Grouse (a) nest and (b) brood habitat in southeastern Alberta. Noncritical habitat indicates that Sage-Grouse are not likely to occur there. "Primary" and "secondary" indicate high and good likelihood of occurrence, respectively. "Habitats" are areas with minimal-to-low risk of failure, whereas "sinks" are areas with moderate-to-extreme risk. For example, primary habitat indicates areas where nests or broods are likely to occur (high occurrence values) and to be successful or survive (minimal-to-low risk values). Primary sink indicates high occurrence, where nests or broods are likely to fail or die (moderate-to-extreme risk values).

of value range) indicates that nest survival would increase by ~17% (exp[−18.33 × 0.01] = 0.833). Thus, more diverse, heterogeneous habitats reduced the risk of nest failure, as indicated by the small hazard ratio for the NDVI variability measure (Table 4).

Although the proportion of human-use features did not enter into our final nest occurrence model, when roads, well sites, urban habitats, and cropland were combined into one parameter (pEdge), Sage-Grouse strongly avoided nesting in these edge-habitat dominated landscapes. Hens may be responding to increased predator densities associated with edge-type habitats (Andrén and Angelstam 1988, Herkert et al. 2003) and agricultural landscapes (Andrén 1992, Kurki et al. 2000, Fuhlendorf et al. 2002, Manzer and Hannon 2005). However, like others (Pasitschniak-Arts and Messier

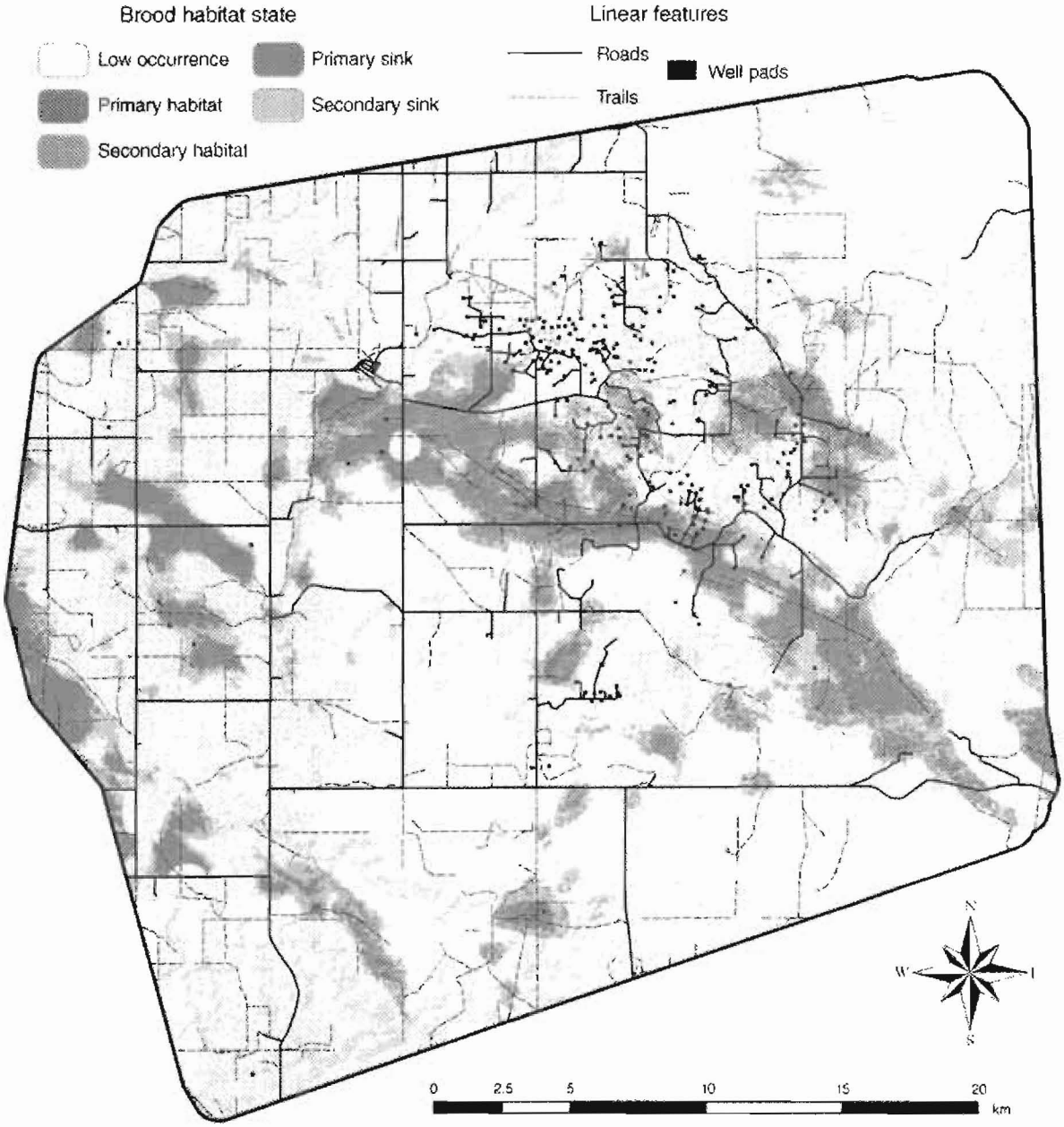

FIG. 5. Continued.

1995, Svobodova et al. 2004), we found no effect of edge habitats, or other human features, on Sage-Grouse nest success (Table 4). Nest placement for Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) in Kansas, USA was farther from paved roads than at random (Pitman 2003). In the same area, proximity to human structures greatly reduced habitat suitability, whereas roads had no obvious effect (Hagen 2003). Recent work on Sage Grouse in Wyoming, USA (Lyon and Anderson 2003, Holloran 2005) suggests that oil and gas activities within 5 km of lek sites results in sharp declines in male attendance, and avoidance by nesting females. However, Lyon and Anderson (2003) found no difference in nest success between disturbed and control leks. In our study, the mean percentage of edge habitat within a 1-km^2 window around nest sites was 2.9% ± 0.7%, compared to a mean of 10.1% ± 0.3% (mean ± SE) across the landscape. Females' strong avoidance of edge habitats ($\beta_{pEdge} = -2.80$) probably prevented us from being able to detect differences in nest success relative to these features.

Ecological traps tend to be more prevalent in human-dominated landscapes (Remes 2000, Bock and Jones 2004), where birds fail to recognize risks with which they

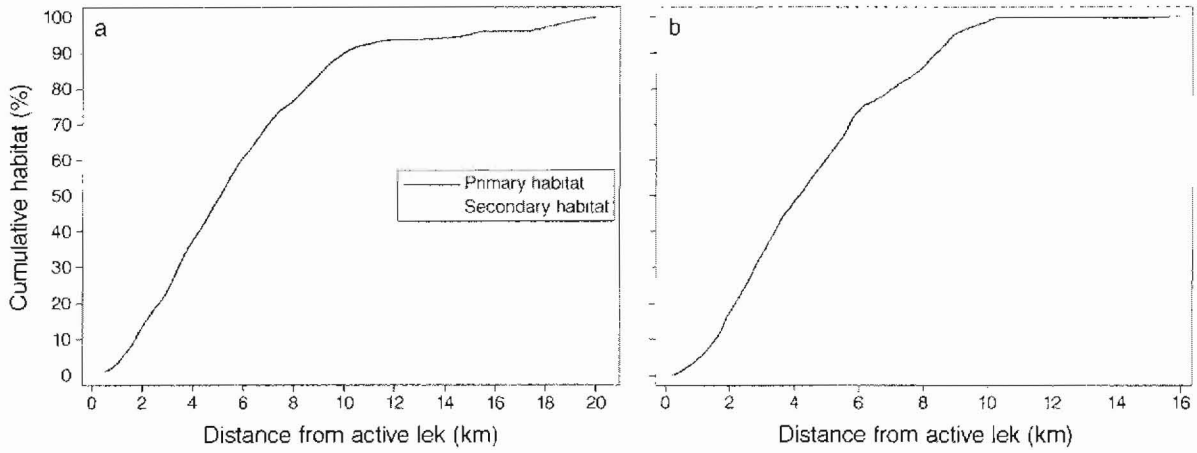

FIG. 6. Primary and secondary source (a) nest and (b) brood habitat for Sage-Grouse in southeastern Alberta, shown as a function of the distance from an active lek.

did not evolve. Sage-Grouse, however, might recognize some of these habitats as risky, avoiding potential ecological traps created in human-dominated habitat patches; at least when selecting nesting habitat. This does not mean that human features have no ill effects on nesting Sage-Grouse. Avoidance of human features removes that habitat pateh from use by Sage-Grouse, and effectively removes habitat within a 1 km^2 area (functional habitat loss). This zonal-habitat influence may be greater, but we did not test the effect of edge habitat density in windows > 1 km^2. Even though Sage-Grouse might recognize and avoid these anthropogenic threats, half of all high-use nesting (good-to-high rank) habitats is considered attractive sinks (Fig. 5a), ecological traps driven by habitat features. We suggest that our habitat maps be used to identify risky nesting habitats and that managers should focus efforts at improving nest success by enhancing sagebrush cover above the currently available 5–10% cover, following recommended habitat guidelines (Connelly et al. 2000), while establishing a heterogeneous mix of sagebrush patches. Management of local range conditions (Crawford et al. 2004; see Aldridge 2005) aimed at enhancing grass and forb understory that improves visual obstruction cover in these risky nesting areas probably will be required to convert sinks into source-type habitats. Range conditions should be assessed locally and grazing could be used to adaptively manage and enhance these habitats (Aldridge et al. 2004). For instance, removing cattle or reducing grazing intensity in some areas may result in increased shrub cover and/or plant species diversity (Manier and Hobbs 2006).

Brood habitat

As predicted, Sage-Grouse also selected for moderate ranges of sagebrush cover at brood-rearing sites. Brood occurrence was greater in more heterogeneous sagebrush stands, where patchy cover reduces predator efficiency (Wiebe and Martin 1998) but still affords necessary forb resources. Sage-Grouse are more abundant in patchy habitats containing a mix of mesic, forb-rich foraging areas interspersed within suitable sagebrush escape cover (Boyce 1981).

Brooding hens appeared to avoid areas closer to cultivated cropland or with a greater proportion of urban developments. Although Sage-Grouse may forage regularly on alfalfa (Patterson 1952), or occasionally on insects found in other cereal crops, they typically do not occur in cultivated lands or landscapes heavily dominated by agriculture. Cultivation directly removes habitats and is correlated with Sage-Grouse population declines in Idaho, USA (Leonard et al. 2000).

In some cases, Sage-Grouse broods occurred close to well sites, but not often in areas with high well densities (Fig. 3b). This relationship may partially be due to the static 2002 distribution of well sites for our GIS landscape, as energy developments have increased slightly over time. However, Holloran (2005) similarly found that nest sites occurred closer to well sites in areas of lower well density. Disturbed habitats, such as trails and well pads, tend to harbor succulent invasive species such as dandelions (*Taraxacum officinale*), important forage to which Sage-Grouse are attracted. Despite this attraction, our chick survival model predicts a 1.5 times increase in risk for each additional oil well that is visible within 1 km of brood locations (see Fig. 4a). As a result, a significant portion of frequently used brood habitat is classified as attractive sink habitats (see Fig. 5b), suggesting that Sage-Grouse may only partially recognize some ecological cues related to anthropogenic features. Birds are run over by vehicles accessing these wells (C. L. Aldridge, *unpublished data*), and are killed by raptorial predators, such as Golden Eagles (*Aquila chrysaetos*) and Great Horned Owls (*Bubo virginianus*), that perch on the power lines leading to well sites. Regardless of the mechanism, chicks have a low

probability of survival, which is further reduced when energy extraction activities dominate the landscape.

Sage-Grouse broods also avoided the less productive and more exposed badland range plant community habitats (pEco6), as well as thin-break range sites (pEco5) and the loamy upland sites (pEco4; Table 3). The thin-break sites are similar to badland habitats, but contain greater sagebrush cover, and the loamy upland sites are more productive range sites, but are dominated by various grasses, resulting in a lack of shrubs and forbs (Adams et al. 2005). Although these two sites might provide added cover from either sagebrush or dense grass cover, they lack the forb component required by Sage-Grouse broods.

More mesic habitats were selected by broods, with occurrence being associated with lower brightness values and higher mean CTI and wetness values (Table 3). These habitats are probably required for birds to meet dietary requirements, because forb (Drut et al. 1994*a*, Sveum et al. 1998*a*) and insect (Johnson and Boyce 1991, Drut et al. 1994*b*) abundance is higher. Hens also chose to be closer to water impoundments. The effect of altered water hydrology on the vegetation productivity, composition, and distribution within this xeric ecosystem is unknown. Removing some of these impoundments may allow water to recharge former mesic sites, rather than retain water behind a dam or within a dugout.

Although mesic habitats were selected, higher CTI values resulted in increased chick failure. Excluding the high-risk values associated with greater well-site densities (Fig. 4b), the majority of other high-CTI risky habitats occurred in riparian habitats along creeks and streams. These habitats are not frequently used by Sage-Grouse broods (see Fig. 3b), but there may be increased risk associated with these shrubby riparian corridors, which often contain a greater concentration of predators (Wilcove 1985). Aldridge (2005) showed that, at local scales, mesic, forb-rich habitats preferred by Sage-Grouse broods tend occur in more risky open habitats. Sage-Grouse may be making trade-offs between habitats that provide protective escape cover and risky open, mesic habitats that provide necessary forage resources. Recent droughts resulting in reduced cover could have made these habitats even more risky for Sage-Grouse chicks, particularly if livestock grazing intensities were not subsequently reduced. Relationships among water impoundments, drought conditions, and the availability of mesic brood habitats are poorly understood (Crawford et al. 2004) and need to be investigated within a long-term adaptive management framework (Aldridge et al. 2004).

Conclusions

For most prairie grouse species, the lek is often thought of as the focal point for year-round activities. Much research has focused on maintaining required habitats surrounding leks and attempting to identify links between habitat alterations and lek dynamics (Wakkinen et al. 1992, Niemuth 2000, Fuhlendorf et al. 2002, Niemuth and Boyce 2004). However, our approach of modeling and mapping high-quality nesting and brood-rearing habitats suggests that such a heavy focus on habitat protection around lek sites may not be suitable to ensure the viability of Sage-Grouse populations. Both nest and brood source habitats, on average, are ~6 km from active leks, but the curvilinear relationship (Fig. 6) suggests that a threshold occurs at ~10 km from leks, within which the majority (~90%) of all source habitats occur. Thus, using a fixed buffer distance around leks of <10 km to protect Sage-Grouse habitat may not suitably protect important nesting and brood-rearing habitats. Wakkinen et al. (1992) suggested that the originally recommended 3.2-km buffer around leks (Braun et al. 1977) may not be large enough to protect nesting habitats, and Connelly et al. (2000) suggested that polygons of 5 km and 18 km may be required to protect breeding habitats for nonmigratory and migratory populations, respectively. The province of Alberta uses a 1-km protection buffer around lek sites (see Alberta Provincial Government web site, *available online*).[2] Complete protection of all areas within this buffer would protect <5% of the available source nesting and brood-rearing habitat identified by our models, which is unlikely to sustain this population. The buffer approach to habitat management and protection could easily result in important habitats being left unprotected and noncritical habitats being protected.

We see our empirically based modeling approach as a framework for identifying and protecting important source nesting and brood-rearing habitats for Sage-Grouse. We identify key sink habitats, which provide managers with the ideal opportunity to evaluate management alternatives aimed at increasing productivity through habitat management following an adaptive management framework (Aldridge et al. 2004), using these models as the baseline habitat accounting system for assessments and future monitoring for Sage-Grouse in Alberta. Careful attention still needs to be given to managing for other seasonal habitat requirements, such as lekking, summer, and winter habitat, and connectivity between habitats. We see great utility in applying our habitat states modeling approach to population viability assessments for many species across different ecological systems.

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[2] (http://www.srd.gov.ab.ca/fw/landuse/pdf/GrasslandParkland.pdf)

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