Habitat Selection and Brood Survival of Greater Prairie-Chickens

Ty W. Matthews, Andrew J. Tyre, J. Scott Taylor, Jeffery J. Lusk, and Larkin A. Powell

Abstract. The Greater Prairie-Chicken (Tympanuchus cupido pinnatus) is a species that may benefit from conversion of crop ground to grassland through the Conservation Reserve Program (CRP). CRP grasslands could provide nesting and brood-rearing habitat, an important component of population persistence. Managers and policymakers currently lack evidence of CRP’s relative contribution to populations of Greater Prairie-Chicken. We used radiotelemetry to mark females (n = 100) in southeast Nebraska, in a landscape which had >15% of land area enrolled in CRP. We examined macrohabitat and microhabitat selection of brood-rearing females (n = 36) using discrete choice models, and examined the variability in brood survival using logistic exposure models. Brood-rearing females selected locations inside cool-season CRP grasslands at higher rates than rangeland, but did not select cropland. At a vegetation level, brood-rearing locations had more bare ground and forb cover than random points. However, landcover and vegetation did not affect survival rates of broods; variation in daily brood survival was best explained by temporal effects such as hatch date and brood age. Our results suggest that CRP grasslands provide acceptable brood-rearing habitat, and managers should encourage land owners to create habitat with high forb content and an open understory. Broods in our study had low survival rates to 21 days (0.59; 95% CI: 0.41, 0.77), which may explain the low juvenile/adult ratio observed in hunter-killed birds in the region. Disturbance of CRP fields to increase bare ground and forb cover may improve their value to Greater Prairie-Chicken broods.

Key Words: brood, Conservation Reserve Program, grassland habitat, radiotelemetry, Tympanuchus cupido.


Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*; hereafter prairie chicken) populations in southeast Nebraska appear to have been benefited by conversion of cropland to grassland through the U.S. Department of Agriculture’s (USDA) Conservation Reserve Program (CRP). Through CRP, land owners receive an annual rental payment to remove highly erodable farm ground from production and into grassland cover. Prairie chicken populations in southeast Nebraska comprise the northernmost extension of the Flint Hills population (Vodehnal 1999, Johns g ard 2000). Unlike the Flint Hills in Kansas, southeast Nebraska’s landscape was dominated by agricultural row crops. Post-settlement conversion of grasslands to croplands by European settlers caused this prairie chicken population to decline to low levels (Johnsgard 1983, Schroeder and Robb 1993). However, the population appeared to increase in the 1990s after approximately 15% of the landscape was converted to grassland through CRP (Taylor 2000). Our goal was to understand the mechanisms behind the increase in population size of prairie chickens.

The Nebraska Game and Parks Commission’s (NGPC) long-term management for prairie chickens in southeast Nebraska is planned with the realization that CRP grasslands could rapidly disappear if the program was removed from the Farm Bill or if profit margins caused land owners to favor crop production over participation in CRP. Svedarsky (1988) and Westemeier et al. (1999) found that prairie chickens used grasslands similar to the low-diversity, brome-dominated CRP fields found in southeast Nebraska. However, studies of brood success in these habitats are needed to assess the ability of CRP fields to provide sufficient brood-rearing habitat needed to sustain a population.

Juvenile survival is a key demographic parameter for prairie chickens and other grouse species (Wisdom and Mills 1997, Sandercock et al. 2005, Hannon and Martin 2006), and lack of quality habitat for nesting and brood-rearing is often a limiting factor (Hamerstrom et al. 1957, Bergerud 1988). Brood habitat should provide sufficient bare ground to facilitate chick movement, adequate overhead cover to protect chicks from predators, and it should be close to nesting cover (Vodehnal and Haufler 2007). When left undisturbed for 3–4 years, CRP land can accumulate a substantial amount of vegetative litter and may lack the bare ground needed by prairie chicken chicks (McCoy et al. 2001). Prairie chicken chicks also require an abundance of arthropods, the chicks’ main food source during the first two weeks (Jones 1963). CRP fields may lack these essential invertebrates if vegetation diversity is low. Problems associated with low arthropod abundance may be alleviated when forb and legume species are incorporated into CRP plantings or when high-diversity grasslands are in close proximity to nesting cover.

Other types of landcover may act as important predictors of brood-rearing habitat for prairie chickens in southeast Nebraska. Pasturelands are grasslands once used for row-crop production and subsequently seeded with native or non-native grasses, whereas unplowed rangelands are native grasslands used for cattle grazing. Both habitats are thought to be used by brood-rearing females (Horak 1985, Burger et al. 1989). However, it is unclear whether short vegetation typically found in CRP provides adequate concealment from predators or protection from adverse weather to successfully produce broods.

Our goal was to examine prairie chicken use of habitat for brood-rearing in southeast Nebraska, with specific interest in habitats provided by CRP. Our objectives were to (1) examine brood habitat selection at the two scales of macrohabitat (landscape composition) and microhabitat (vegetation structure and local composition), and (2) assess the consequences of habitat use on daily survival of prairie chicken broods. Demographic information related to brood survival will be used to inform changes in land-use policy and to inform management decisions needed to support prairie chicken populations in southeast Nebraska.

**METHODS**

**Study Area**

Our study was conducted in Johnson and Pawnee counties in the tallgrass ecoregion of southeast Nebraska. The landscape consisted of rolling uplands produced mainly from glacial till and loess accumulation. Soil types in these counties were characterized by Wymore–Pawnee soil association (USDA 1986). Average annual precipitation was 84 cm, with the majority falling between the
months of May and August. Average monthly temperature maximum and minimum were 32°C and
–12°C, occurring in July and January, respectively. Our focus area was dominated by production
corn, soybean, and grazed grasslands, with millet and sorghum in lesser quantities. In 2007,
163.3 km² (ca. 17%) of Johnson County and 172.1 km² (ca. 15%) of Pawnee County had been
enrolled in CRP (Farm Service Agency, USDA).

Trapping and Monitoring

We used walk-in traps to capture female prairie
chickens from 20 March to 19 April in 2007–2008
(Schroeder and Braun 1991). We trapped birds at
13 different leks during 2007 (7 leks) and 2008
(10 leks). Male attendance ranged from 15 to
70 individuals per lek. At first capture, we fitted
each female with a necklace-type radio transmitt-
er (<20 g, Model #A3960, Advanced Telemetry
Systems, Inc., Isanti, MN) and released each
efemale immediately at the capture location.
Animal capture and handling protocols were
approved by the University of Nebraska–Lincoln
Institutional Animal Care and Use Committee
(Protocol #05-02-007).

We recorded locations of each female
5–10 times per week from time of capture to
1 August using a vehicle mounted with a null-
peak dual antenna-receiver with an electronic
compass (Gilsdorf et al. 2008). We randomly
chose the order of fields in which we tracked
the females to avoid temporal biases. We took
at least three bearings within a 10-minute period
for each location to minimize error caused by
movements. Additional bearings were taken until
we received an error polygon of less than 0.1 ha
(ca. 18-m radius). All UTM coordinates and asso-
ciated error polygons were calculated in the field
via an onboard computer and software [Location
of a Signal (LOAS), Ecological Software Solutions,
Urnäsch, Switzerland, version 4.0]. We visually
confirmed nest locations by approaching females
with a handheld antenna and receiver, and
flushed females to record the number of eggs in
the nest within the first week of incubation. Once
daily locations indicated the female had stopped
incubating (i.e., 2–3 locations off nest), we visu-
ally inspected the nest to determine nest fate and
the number of eggs that hatched. We used daily
telemetry observations to locate females with
broods for 21 days after hatch. We used nocturnal
two-flush counts on days 10 and 21 post-hatch to
determine if a brood was successful (=1 chick at
flush). We assigned failed brood fates to females
flushed long distances without returning and we performed systematic ground searches to
confirm total brood failure. We used two subse-
quent flushes of such females to verify this clas-
sification of fate.

Landscape and Vegetation Sampling

We evaluated landscape composition by creating
a year-specific, vector-based GIS by landcover
layer (ArcGIS 9.0, ESRI, Redlands, CA). We
used aerial photographs and extensive ground-
truthing through visual inspection to classify
each land cover into one of five landcover types:
cropland (row crops, alfalfa), grassland, wood-
land, wetland, and anthropogenic (farmsteads,
utility facilities). Grassland cover types were
further divided in four subtypes: (1) warm-
season CRP fields (predominantly switchgrass,
Panicum virgatum; big bluestem, Andropogon
gerardii; little bluestem, Schizachyrium
scoparium; Indian grass, Sorghastrum nutans; or
sideoats grama, Bouteloua curtipendula), (2) cool-
season CRP fields (predominantly smooth
brome, Bromus inermus; and orchard grass,
Dactylis glomerata), (3) rangeland (unplowed
native grasslands), and (4) pastureland
(pastures previously plowed).

At every third brood location, we estimated
percent canopy cover for cool-season grasses
(COOL), warm-season grasses (WARM), forbs
(FORB), standing litter (SL) and bare ground
(BARE) using a 1-m diameter sampling hoop
(modified from Daubenmire 1959) and a visual
obstruction reading (VOR) to the nearest 0.25 dm
(Robel et al. 1970). BARE was the percent ground
that was not covered by residual vegetation below
the vegetation canopy. We took the sample from a
random location within the 0.1-ha error polygon.
We also assessed the vegetation composition and
VOR at five random points in the same field and
habitat type. All random points were created with
Hawth’s Analysis Tools for ArcGIS (Beyer 2004),
and we used a handheld GPS receiver to find the
point in the field. Last, we classified each used
brood location and random point into three topo-
logical categories (TOPO; upper, middle, or lower)
relative to the maximum and minimum elevation
in that particular field, using a digital elevation
TABLE 13.1

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>Log(L)</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landcover + distance to cropland</td>
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<td>-1,355.8</td>
<td>2,726.62</td>
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<td>0.61</td>
</tr>
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<td>2,727.98</td>
<td>1.84</td>
<td>0.31</td>
</tr>
<tr>
<td>Landcover + distance to cropland + distance to edge</td>
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<td>-1,355.8</td>
<td>2,731.24</td>
<td>5.43</td>
<td>0.06</td>
</tr>
<tr>
<td>Landcover + distance to woodland + distance to cropland + distance to edge</td>
<td>8</td>
<td>-1,354.2</td>
<td>2,733.54</td>
<td>8.59</td>
<td>0.02</td>
</tr>
</tbody>
</table>

NOTE: Models are ranked by AICc, Akaike’s Information Criterion adjusted for small sample size; K is the number of parameters (note that discrete choice models have no intercept); log(L) is the log likelihood of the model; ΔAICc is the difference of each model’s AICc value from that of the minimum AICc model (row one); and wi is the Akaike weight (sum of all weights = 1.00). Landcover includes five strata (cool-season CRP, warm-season CRP, pasture, rangeland, and other habitats). Twelve models with wi < 0.02 are not shown.

model (DEM, UNL School of Natural Resources). All sampling was done within two days of locating brood.

Analysis and Model Selection

Discrete choice models calculate the probability of an individual selecting a resource as a function of the attributes of that resource and all other resources within the individual’s available habitat (Cooper and Millspaugh 1999, McDonald et al. 2006). Discrete choice analyses estimate the probability of selection of categorical variables relative to a reference, and we used rangeland as the reference for landcover. We estimated the area of available habitat in two steps. First, we calculated the maximum displacement distance between locations collected on consecutive days for each brood. Second, we calculated available habitat as the circular area around each location with a radius equal to the minimum of these maximum displacement distances. We used Cox proportional hazards regression function (COXPH) in the survival package (Therneau and Lumley 2009) of Program R (R Development Core Team 2009) to develop our macro- and microhabitat discrete choice models. For each set of models, a correlation matrix was created to avoid any within-scale correlation.

We assessed selection of brood macrohabitat using discrete choice analysis of 16 biologically reasonable a priori models including a null model (Cooper and Millspaugh 1999, McDonald et al. 2006). Our macrohabitat models considered the effect of landcover type on habitat selection. We created a set of covariates for landcover (Landcover, Table 13.1) based on our classification of five habitats in our study area: cool-season CRP, warm-season CRP, pasture, rangeland, and other habitats (largely anthropogenic and water). Because woodlands and edges are known to support larger numbers of mammalian and avian predators and may be avoided by brooding prairie chicken females (Svedarsky et al. 2003), we also created covariates for linear distance to woodland (Distance to woodland) and edge (Distance to edge, Table 13.1). We defined an edge as any transition in vegetation such as fence rows, tree lines, roads, change in dominant vegetation type, or other boundaries that delineated habitat types. Finally, we created a covariate for distance to any crop field (Distance to cropland, Table 13.1), as crop fields may be an important food source for females (Svedarsky and Van Amburg 1996); brooding females could be attracted to grasslands near crop fields. We generated 20 random locations per brood location within the habitat defined as available to compare against the used locations. We used 20 random locations rather than the five suggested by McFadden (1978) to decrease the variance in covariate coefficients (Baasch 2008). We replaced any random locations that were <18 m of our brood location estimate, to match the size of our maximum allowable error polygon.
Our microhabitat analysis consisted of eight biologically reasonable a priori models using combinations of the following groups of covariates: vegetation composition (% Cover; WARM, COOL, FORB, SL), a quadratic model of vegetation structure (VOR + VOR^2 + Bare), and topographic position (TOPO). The seven models with covariates were compared to a null model with no covariates. We hypothesized that vegetation composition could be a key component of habitat selection for brooding prairie chicken females (Jones 1963, Kobriger 1965). We considered a non-linear effect of vegetation structure (VOR) because brooding females generally select areas less dense than nest sites (Jones 1963). Last, we hypothesized that prairie chicken females may prefer locations where topography allows better detection of potential predators or faster escape flights during predation attempts. We compared the microhabitat at brood locations with the random points taken within the field containing the nest.

We estimated daily brood survival and assessed the contribution of individual covariates in a set of eight biologically reasonable a priori models in a logistic-exposure structure (Shaffer 2004) using program R and logexp package (Post van der Burg 2005). Our monitoring intervals were usually 10–11 days in length, as we flushed broods at day 10 and day 21 post-hatch. We flushed at 10 days post-hatch to assess survival before any chicks had fledged. At day 21, all chicks should have fledged. Our models considered landcover (Landcover, % of observations during interval spent in: cool-season CRP, warm-season CRP, rangeland, pastureland, cropland), time (Julian day of hatch and brood age), and climate (average daily temperature during monitoring interval and average daily precipitation). We compared models with covariates to a null model. Flanders-Wanner et al. (2004) found that high temperature and precipitation events negatively impacted production of Sharp-tailed Grouse (Tympanuchus phasianellus). Temporal covariates, such as hatch date and brood age, have been found to affect brood survival in other galliform species (Riley et al. 1998, Fields et al. 2006, Hannon and Martin 2006). We used age as a categorical variable (1–10 or 11–21 days old) because we flushed broods in discrete time intervals to avoid negative impacts of survival. We used female location and movement patterns to estimate date of hatch. Ten-day and 11-day period survival estimates were calculated as daily survival rates for first 10 days post-hatch \( (S_{10} = DS_{10}^{10-10}S_{11}) \); 21-day period survival estimates were calculated as \( S_{21} = S_{10}S_{11} \). Variances for \( S_{10}, S_{11} \) and \( S_{12} \) were approximated using the delta method (Powell 2007).

We performed model selection using an information-theoretic approach to evaluate a priori models for brood habitat selection and survival. We ranked each model from most to least support given the data, using Akaike’s Information Criterion corrected for small sample size \( (AIC_c; \) Burnham and Anderson 2002). For brood survival, we used effective sample size \( (n = \text{total number of days the broods survived} + \text{number of intervals that ended in failure}) \) for the calculation of \( AIC_c \) (Rotella et al. 2004). We computed Akaike weights \( (\omega_i) \) for each model, where \( \omega_i \) represents the probability a model being the best approximating model of those considered given the data. For each analysis, we considered a confidence set of all models with a combined model weight of \( \geq 90\% \). We selected the top model if it was the most parsimonious of the confidence set. When the highest-ranked model was not the most parsimonious, we used conditional model averaging over the 90% confidence set to predict the covariates and associated standard errors (Burnham and Anderson 2002:152–153). We limited model-averaged predictions from continuous data to the range of data we observed.

RESULTS

We captured, radio-tagged, and monitored 100 prairie chicken females (2007: 38, 2008: 62). We monitored 36 females with broods from successful nests (2007: 11; 2008: 25). Eighteen broods (50%) survived to 10 days after hatching (2007: 2; 2008: 16). A total of 17 of 18 (95%) broods that were active at 10 days after hatching survived to day 21.

We obtained 455 locations of brooding females, which were distributed among cool-season CRP (29%), rangeland (27%), pastureland (20%), warm-season CRP (11%), cropland (7%), and other (6%) landcover classes.
Each of our females traveled >500 m at least once during a 24-hr time period while attending young. Thus, we established 500-m radii around each brood location as the available habitat for subsequent analyses. Within-scale correlations for each model set were reasonable ($r < 0.40$).

The top macrohabitat-level selection model included effects of landcover type and distance to crop field (Table 13.1). The relative probability of a brooding female selecting a location for her brood in a cool-season CRP field was 1.39 (95% CI: 1.03–1.88) times higher than rangeland (Table 13.2). A female’s probability of selecting a location in a crop field for brooding is 2.64 (95% CI: 1.87–3.73) times lower than the chance of selecting rangeland. Each increase in distance of 100 m from cropland predicted a 10% decrease in the relative probability of selection, holding all other variables constant (Fig. 13.1). Selection probabilities among rangeland, pastureland, and warm-season CRP were similar.

The minimum AICc microhabitat-level selection model included all effects (global model)
and had an $\omega_i$ of 1.0. Prairie chicken females with a brood selected areas with mid-level topography 11.3 (95% CI: 1.6–79.8) and 21.7 (95% CI: 3.0–153) times more than bottom- or high-level topography, respectively (Table 13.3). Relative probability of selection increased as percent cover of forbs increased, with mean use of 33.6% (SE = 25.4, range: 0–85%). Selection also increased with an increase in bare ground, with a mean use of 24.8% (SE = 29.9, range: 0–100%). Probability of selection peaked at approximately 3 dm for VOR and decreased as VOR deviated from this point (Fig. 13.2). Average VOR at use points was 2.4 dm (SE = 0.8, range: 1–5 dm).

Brood survival was a function of time (brood age and Julian day of hatch; Table 13.4). Daily brood survival decreased as nests hatched later in the breeding season and increased as broods aged (Fig. 13.3). No habitat or landscape characteristics we studied accounted for variation in daily brood survival. The mean daily survival probability of a brood in the 1–10 day old age-class was 0.95 (95% CI: 0.95–0.96), and 0.99 (95% CI: 0.96–1.00) in the 11–21 day class. The mean probability of a brood surviving to day 21 was 0.59 (95% CI: 0.41–0.77). The average number of chicks per brood surviving to day 21 was 4.50 (SE = 0.71) in 2007 ($n = 2$ broods) and 3.13 (SE = 2.50) in 2008 ($n = 15$ broods).

**DISCUSSION**

Brooding prairie chicken females in southeastern Nebraska selected cool-season CRP fields over any other landcover. Cool-season CRP fields provide large expanses of undisturbed grassland in Nebraska, but our finding is contrary to previous studies, which found brooding females selected disturbed areas such as cultivated pastures, recently burned grasslands, and native prairie hay fields (Jones 1963, Svedarsky 1979, Burger et al. 1989, Westemeier et al. 1995). Rangelands and pastures represented disturbed habitats in our study area, and the lower selection ratio for disturbed grassland may be related to the vertical structure of these grasslands. Large quantities of rangeland and pastureland in our study area may not have been suitable for brood-rearing due to excessive

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Coefficient</th>
<th>SE</th>
<th>Selection Ratio</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Cool-season grass</td>
<td>0.054</td>
<td>0.030</td>
<td>1.056</td>
<td>0.996</td>
<td>1.120</td>
</tr>
<tr>
<td>% Warm-season grass</td>
<td>0.091</td>
<td>0.104</td>
<td>1.096</td>
<td>0.894</td>
<td>1.343</td>
</tr>
<tr>
<td>% Forb</td>
<td>0.145</td>
<td>0.041</td>
<td>1.156</td>
<td>1.067</td>
<td>1.252</td>
</tr>
<tr>
<td>% Standing litter</td>
<td>-0.053</td>
<td>0.042</td>
<td>0.949</td>
<td>0.874</td>
<td>1.037</td>
</tr>
<tr>
<td>% Bare ground</td>
<td>0.072</td>
<td>0.027</td>
<td>1.074</td>
<td>1.018</td>
<td>1.136</td>
</tr>
<tr>
<td>VOR</td>
<td>5.857</td>
<td>1.908</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>VOR$^2$</td>
<td>-1.212</td>
<td>0.351</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Topography</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bottom</td>
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<td>1.082</td>
<td>0.521</td>
<td>0.063</td>
<td>4.341</td>
</tr>
<tr>
<td>Middle</td>
<td>2.424</td>
<td>0.998</td>
<td>11.285</td>
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<td>79.832</td>
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<tr>
<td>Upper</td>
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<td>—</td>
<td>1.000</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

**TABLE 13.3**

Coefficients ($\beta$), standard errors, selection ratios [exp($\beta$)], and associated 95% confidence intervals for variables in the top model predicting microhabitat selection for Greater Prairie-Chicken females with broods in southeast Nebraska, 2007–2008.

<table>
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<tr>
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<tr>
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<td>1.074</td>
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<td>VOR</td>
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<td>—</td>
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<tr>
<td>VOR$^2$</td>
<td>-1.212</td>
<td>0.351</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

**NOTE:** Upper-level topography was set as the baseline topographic level. Selection ratios were not calculated for variables involved in quadratic effects due to the dependence on values of other variables.
grazing by cattle. Both landcover types were generally grazed year after year and provided little vegetative concealment. In contrast, grazed pastures in the Nebraska Sandhills, which is in the north-central part of the state, serve as the main brood-rearing habitat for prairie chickens (Vodehnal 1999). These grasslands are generally stocked at lower rates and are usually grazed in rotational systems, giving brooding females better overhead concealment from predators and adverse weather.

We observed that the pastures and rangelands that were used by broods were either lightly grazed grasslands or idle grasslands with no disturbance, which contrasted with the majority of available pastures and rangelands on the landscape. Brooding females also selected areas near crop fields in all landcover types, although crop fields themselves were avoided. Grassland–cropland edges may provide favorable complexes of bare ground and structurally appropriate vegetation consistent with our observations of microhabitat preferences. Females may also forage in these agricultural fields, even though there is little food for their young. Rumble et al. (1988) found that a large portion of the diets of prairie chickens in the Sheyenne National Grasslands consisted of agricultural crops, mainly corn and alfalfa. We would expect crops to be even more important to prairie chicken diets in southeastern Nebraska, because the landscape is dominated by crop fields, which increases availability and use (Horak 1985). An increase of forb and legume components, such as alfalfa and sweet clover, in grasslands may decrease dependence of crop fields by brood-rearing females (Svedarsky et al. 2003).

Within selected fields, female prairie-chickens with broods selected vegetation that was high in forb content and bare ground (Fig. 13.2). Our results are consistent with previous research (Westemeier et al. 1995, Norton 2005), and seem reasonable considering that primary brood behavior during the day consists of foraging for insects and mid-day loafing. Greater forb cover provides a higher abundance of insects, which are the primary food source of prairie chicken chicks during the critical first two weeks after hatching (Jones 1963, Schroeder and Braun 1992, Svedarsky et al. 2003). Bare ground and forb cover cannot be simultaneously maximized (Fig. 13.2), but our data suggest that habitat with a high proportion of forbs and bare ground will be preferred over brooding habitat without these features. Brooding females in our study also selected sites with intermediate topography, probably related to the vegetation densities and composition associated with each topographic strata. Newell et al. (1988) reported that broods in the Sheyenne National Grasslands in South Dakota used lowlands and midlands more than uplands due to the sparse vegetation in upland habitats. The converse may also be true in our study, with the majority of the vegetation in the lowlands.
being too tall and dense. Our results provide support for this assertion since broods selected sites with mid-range visual obstruction readings (1.75 to 3 dm; Fig. 13.2).

We observed low brood survival in Nebraska, especially in 2007 (21-day success: 18%) but also in 2008 (21-day success: 60%), and low chicks per brood at 21 days. Mortality resulted in a 21-day chick survival of only 14.4% for both years combined, which is less than the 37% chick survival to 24 days post-hatch reported by Newell et al. (1988) and 65% chick survival to 21 days post-hatch found by Norton (2005). Thus, it appears that low brood survival is responsible for the low juvenile:adult ratios in hunter wing surveys (J. Lusk, unpubl. data). Since hunting resumed in 1999 in southeastern Nebraska, the average juvenile:adult ratio has been 0.91, compared to 1.77 for Nebraska’s Sandhills region over the eight-year period (J. Lusk, unpubl. data).

Prairie chicken females with broods selected cool-season CRP fields. However, our survival analyses suggest that either landcover as we measured it is not an important factor in brood survival, or perhaps all the habitats used by monitored broods were equally poor. Instead, age of brood and hatch date were the only predictors of survival (Table 13.4, Fig. 13.3). One would expect selection patterns to optimize brood survival, but our data shows no evidence of a survival advantage to cool-season CRP fields despite their preferential use. It is possible that the high rate of mortality,

TABLE 13.4

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>Log(L)</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
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<tbody>
<tr>
<td>Timea</td>
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<td>49.87</td>
<td>0.00</td>
<td>0.55</td>
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<tr>
<td>Time + climateb</td>
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<td>-23.99</td>
<td>51.75</td>
<td>1.88</td>
<td>0.21</td>
</tr>
<tr>
<td>Landcoverc + time + climate</td>
<td>9</td>
<td>-20.32</td>
<td>51.76</td>
<td>1.89</td>
<td>0.21</td>
</tr>
<tr>
<td>Landcover + time</td>
<td>7</td>
<td>-23.26</td>
<td>55.75</td>
<td>5.88</td>
<td>0.03</td>
</tr>
</tbody>
</table>

NOTE: See Table 13.1 for metrics of model selection.

a Includes additive effects of Julian day of hatch and brood age.

b Includes additive effects of temperature and precipitation.

c Includes effects of proportion of time spent in cool-season CRP, warm-season CRP, rangeland, pastureland, and cropland.
especially in 2007, swamped any effects of habitat on brood survival. It is also possible that prairie chickens on our study site are responding to an ecological miscue associated with invasive brome in cool-season CRP (Misenhelter and Rotenberry 2000, Schlaepfer et al. 2002). Regardless, given the population growth observed on our study area since inception of the CRP program, CRP grasslands may benefit nest and/or adult survival to a degree that makes its effect on chick survival relatively unimportant to population persistence.

The relationship of brood survival with age has been well documented by Newell et al. (1988) and Norton (2005). Older chicks have greater ability to make short flights, as well as better development of thermoregulation, which decreases the need of regular brooding by the female (Svedarsky and Van Amburg 1996). Daily brood survival decreased the later in the breeding season that hatching occurred (Fig. 13.3), possibly due to declining female condition as the season progressed (Thogmartin and Johnson 1999). Svedarsky et al. (2003) suggested that prairie chickens are similar to waterfowl in that chicks have an increased survival rate when hatched by females with large fat reserves. Fields et al. (2006) also found declining brood survival in Lesser Prairie-Chickens (Tympanuchus pallidicinctus) with later hatch date but attributed it to confounding weather variables and insect production. Broods hatching later in the breeding season in our study may have experienced lower insect availability due to higher temperatures and lower precipitation. Higher temperature may also directly affect brood survival by inducing heat stress and water loss (Fields et al. 2006), especially when chicks are unable to thermoregulate on their own. Temperature may indirectly affect brood survival by reducing foraging time. Alhborn (1980) found that Lesser Prairie-Chickens seek shade and reduce foraging activity during periods of high temperatures. We averaged daily temperatures and precipitation during each brood’s monitoring period, which tended to suppress extreme highs and lows that may cause mortality. Our monitoring intervals were set at 10 and 21 days to avoid observer bias on survival and habitat use; future studies may wish to weigh these potential biases with the need to investigate effects of short-term weather variability.

The low brood survival observed during our study was due to high levels of predation (Schote et al., this volume, chapter 18), which may be attributed to lack and distribution of quality habitat (Schroeder and Baydack 2001). Schole et al. (this volume, chapter 18) found 87% of radio-marked prairie chicken chicks died due to predation in southeastern Nebraska during our 2008 field season. The landscape was dissected with tree lines, roads, and power lines, with generally small (< 32 ha) tracts of grasslands interspersed through agricultural fields. Habitat fragmentation has been linked to an increase in predation by increasing travel time in poor habitat and increasing diversity and density of predators (Schroeder and Baydack 2001). Similarly, Ryan et al. (1998) demonstrated that prairie chicken broods have smaller home ranges and higher survival in large contiguous grasslands than in a prairie–mosaic landscape.

Grasslands in our study area may have vegetative characteristics that also induce high levels of predation. CRP fields in that area are generally monocultures of brome or switchgrass with few patches of diverse vegetation and high litter accumulation from >10 years of undisturbed growth. Brooding females in CRP fields would have to make longer movements more often in search of suitable habitat, making them and their chicks more vulnerable to predation. The accumulation of litter has also been linked to an increase in small mammals, and has been suggested as attracting mammalian predators in the area (Westemeier 1988). Doxon (2005) found that an accumulation of litter impedes movement of gamebird chicks, and this may affect chicks’ ability to escape predators. Undisturbed landcovers like CRP fields in this area may need to be managed by rotational grazing, burning, or mowing to maintain proper height, density, and species composition (Svedarsky et al. 2003). Additionally, pastures and rangelands are commonly intensively grazed with no years of deferred grazing, which results in large expanses of areas with little to no overhead canopy cover, giving no protection from predators. Pastureland and rangeland in our area were also commonly invaded by woody vegetation, providing perches for avian predators. Frederickson (1996) stated that range conditions needed for satisfactory brood survival may be restricted by intense grazing. For optimal benefit to prairie chickens, grazed grasslands may need to adopt lower stocking rates or rotational grazing similar to the Sandhills region of north-central Nebraska.
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