Survival and habitat use in translocated and resident greater prairie-chickens

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ABSTRACT

Translocation, or the purposeful movement of organisms from one location to another for conservation, is currently being used to bolster populations of the endangered greater prairie-chicken (*Tympanuchus cupido*). We used radiotelemetry to compare survival between 58 resident birds and 54 newly translocated greater prairie-chickens that were sourced from a location more than 325 km away. Model averaged survival estimates were lower in translocated birds (0.42; 95% CI: 0.17–0.66) than in resident prairie-chickens (0.65; 95% CI: 0.46–0.79) through the breeding season. Habitat, sex and year were each included in at least 1 of the top 4 models, but the model averaged confidence intervals for each parameter encompassed zero. Survival of both resident and translocated prairie-chickens increased throughout the breeding season. Both translocated and resident prairie-chickens selected for core prairie habitat over agriculture, and birds tended to avoid surrounding private grasslands and wooded areas. We suggest that future translocation projects account for reduced survival of translocated birds when determining the appropriate release cohort sizes and sex ratios. We also recommend that future management for greater prairie-chicken habitat focus on the expansion of core protected patches of prairie to promote elevated survival and better chances of conservation success.

Introduction

Translocation, or the movement of individuals from one area to another with the intent of bolstering or establishing wild populations, has served as a conservation tool for more than 100 years (International Union for Conservation of Nature [IUCN] 1987; Kleiman 1989). However, many early translocation projects were poorly documented, and thus few provided information for future programs (Seddon et al. 2007). A growing body of literature about translocation is emerging (Ewen et al. 2012) but many studies consist of qualitative and retrospective analyses (Seddon et al. 2007). As a result, few examples of science-based frameworks are available to facilitate the effective use of translocation as a conservation tool (Kaler et al. 2010; Terhune et al. 2010; Stephenson et al. 2011; Kesler et al. 2012). Without research-based guidelines, future translocations will likely gamble valuable resources and endangered and declining species.

The greater prairie-chicken (*Tympanuchus cupido*) is a grouse native to mid-continent grassland habitats in North America, and populations have declined precipitously from historical numbers (Svedarsky et al. 2000). Translocation has been used to supplement populations in areas with severe declines, and the history of greater prairie-chicken translocation projects reflects the difficulties that many conservation programs have faced due to a limited base of knowledge in translocation biology. In the United States, at least 26 attempts have been made to translocate greater prairie-chickens since 1950 (Toepfer et al. 1990; Mechlin et al. 1999; Snyder et al. 1999). Similar to translocations of other taxa (Griffith et al. 1989; Wolf et al. 1996), few greater prairie-chicken projects were successful at establishing self-sustaining populations (Kruse 1973; Toepfer et al. 1990) and few left documentation about why failures occurred (Snyder et al. 1999). Consequently, basic data are missing about project duration, release methods, release site selection, season of release, and numbers of birds released. These data are needed to identify successful methodologies to improve future translocation projects (Snyder et al. 1999).

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Many translocation projects involving grouse (Kurzejeski and Root 1988; Toepfer 1988; Musil et al. 1993; Kaler et al. 2010) and other taxa (Wilson et al. 1992; McKinstry and Anderson 2002) have documented periods of reduced survival immediately following release. Unfamiliarity with the landscape (Farina and Belgrano 2004), high levels of predation, and poor habitat quality have been proposed as causes of reduced survival in translocated individuals (Van Zant and Wooten 2003; Siano et al. 2006; Moorhouse et al. 2009; Tavecchia et al. 2009). Female survival is sometimes lower than male survival during grouse translocations (Kurzejeski and Root 1988; Toepfer 1988), a pattern that has been attributed to elevated reproductive costs (Svedarsky 1988; Thomson et al. 1998) and more frequent and longer female movements (Maxson 1977; Svedarsky 1988).

The greater prairie-chicken's decline in Missouri has been primarily due to the loss and fragmentation of >99% of the native tallgrass prairie habitat, and fragmentation of remnant prairie patches (Missouri Department of Conservation 1999). Habitat degradation, and the associated forces of habitat loss and fragmentation are primary factors driving the loss of biodiversity (Wilcox and Murphy 1985; Fahrig 1997; Battisti 2003; Lindenmayer and Fisher 2006). The degradation of grassland habitat has occurred rapidly during the last two centuries in North America and impacts were wide-spread throughout the mid-continent. Native grassland habitats (i.e., prairie) suitable for the prairie-chickens and other grassland obligate species once occurred on >6 million ha in Missouri (Christisen 1985), but today <36,437 ha of these grasslands remains and only 8907 ha are in public ownership (Missouri Department of Conservation 1999).

Current landscape management for greater prairie-chickens in Missouri emphasizes a core protected area model for Missouri's remaining grassland bird populations, which includes a core of high quality habitat surrounded by a buffer zone matrix of neutral and non-hostile habitats. Core protected area models and buffer zones are used for a range of conservation applications and they emphasize a large high quality core with surrounding areas of lower quality (e.g. UNESCO Man and Biosphere Reserves; Wells and Brandon 1993; UNESCO 1996; Ebregt and Greve 2000; Oliver and Giovanna 2008). In Missouri, the Partners in Flight Grassland Bird Conservation Area Model includes a core protected area and surrounding buffer zone, and it is used to guide prairie management (PIF model; Fitzgerald et al. 2000; Missouri Department of Conservation 2006). The design includes a landscape for greater prairie-chickens with a large block ($\geq$800 ha) of high quality prairie habitat centered upon one or more leks. Matrix habitats ($\geq$3200 ha) surrounding the core reserve are a mix of quality grassland ($\geq$800 ha) and neutral habitats (e.g., agriculture). Additionally, the PIF model recommends that no more than 5% of the matrix be comprised of woody vegetation, which is considered hostile (Fitzgerald et al. 2000). Core protected area models are applied to prairies based on the rationale that the protected core areas, should promote higher survival and reproduction in prairie-chickens (e.g. Missouri Department of Conservation 2006). Further, the non-hostile surrounding matrix should ameliorate the negative effects of patch-size sensitivity (Fitzgerald et al. 2000; Johnson and Winter 2005) and provide additional land for lekking and mating display, predator escape, roosting, and forage (e.g., ecological patterning; Hamerstrom et al. 1957).

Although core protected area models provide a potentially useful guide for management planning, their utility and appropriateness for the grassland landscape remains unclear (Winter et al. 2001; Johnson and Winter 2005). Much of the research regarding patch size and edge effects, upon which the PIF model was based, was conducted in forested landscapes (Donavan et al. 1995). Results from studies on patch size and edge effects conducted in grassland landscapes vary widely, and suggest that overarching

generalizations may be elusive because of interacting landscape characteristics, species, and habitats (Winter and Faaborg 1999; Winter et al. 2000, 2001; Johnson 2001; Johnson and Igl 2001).

When applied to greater prairie-chickens, core protected area models incorporate the concept that large patches of prairie habitat are critical (Christisen 1981; Burger 1988; Ryan et al. 1998; Fitzgerald et al. 2000), but uncertainty remains about the relationship between survival and the birds' use of matrix, or buffer zone habitats surrounding core areas. Whereas prairie-chickens have been recorded to use the patches of buffer agricultural and non-native grassland habitats for feeding, nesting, and brood rearing activities (Horak 1985; Ryan et al. 1998; Svedarsky et al. 2003; Matthews et al. 2011; McNew et al. 2012), the dangers of the fragmented nature of these habitats might be outweighing benefits. Fence lines and shelterbelts that serve as transit lanes for terrestrial predators (Winter et al. 2000) and provide hunting perches for avian predators are common in fragmented habitats (Bohall and Collopy 1984; Svedarsky and Van Amburg 1996; Wolff et al. 1999; Applegate et al. 2004). Further, predation by avian and mammalian predators, such as raptors and coyotes (Canis latrans), is often a leading cause of mortality for greater prairie-chickens in fragmented habitats (Burger 1988; Toepfer 1988; McNew et al. 2012).

Conservation managers are challenged by the lack of empirical information about survival of resident and translocated greater prairie-chickens and how habitats in a landscape with a core protected area and surrounding non-hostile matrix habitats affect the birds. To address these information gaps, we conducted a study of translocated and resident greater prairie-chickens in landscapes with large central reserves and surrounding matrices of hostile and non-hostile habitats in buffer zones. We tested for differences in survival between translocated and resident greater prairie-chickens, males and females, for differences in survival between core area habitats and buffer zone matrix habitats, and for differences in habitat selection. We anticipated that translocated birds would initially have lower survival than residents, because of the stress of release or unfamiliarity with the area of release (Kurzejeski and Root 1988; Toepfer 1988; Musil et al. 1993; Kaler et al. 2010; McKinstry and Anderson 2002). Further, we predicted that females would have lower survival than males because of greater reproductive costs or greater movement (Svedarsky 1988; Thomson et al. 1998; Kemink and Kesler 2013). Finally, we predicted that birds that entered buffer matrix areas (agriculture and primarily non-native grassland habitat patches) outside the protected core areas would exhibit reduced survival.

Study area

We conducted research between March and August in 2010 and 2011 in a core protected area landscape similar to that prescribed by the PIF model. Research was centered around Taberville Prairie (38°3′ N, 93°58′ E) and Wah'Kon-Tah Prairie (37°54′ N, 93°59′ E) within the Taberville and El Dorado prairie-chicken focus areas (Fig. 1). Both areas contained protected core prairie habitat that was managed and owned by the Missouri Department of Conservation and The Nature Conservancy (Taberville: 578 ha, El Dorado: 1213 ha). Management consisted of a spatio-temporal combination of herbicide treatments for invasive and exotic plants, prairie restoration (with locally collected seed), burning, grazing, and high mowing (L. Gilmore, Missouri Department of Conservation, personal communication). Habitat within the buffer matrix and broader landscape surrounding the core prairie habitats consisted of urban areas (5%), water (3%), agriculture (12%), grassland (50%), and woodland (30%). Matrix habitat was under a variety of management prescriptions that included row and forage crops, idle

Fig. 1. Study site location for the Taberville and El Dorado prairie-chicken focus areas.

or grazed woodland, heavily grazed tall fescue (*Fescue arundinacea*), native prairie, and mixed native prairie-fescue pastures.

Methods

Greater prairie-chickens are a lekking species of grouse that depend on prairie habitat for survival and persistence (Christisen 1981). At the time of our study, there were <200 endangered greater prairie-chickens remaining in the state of Missouri, of which a large portion resided within the Taberville and Wah'Kon-Tah areas (Missouri Department of Conservation, unpublished data). Our study occurred during the third and fourth year of a five-year translocation project that was aimed at reestablishing and bolstering the area's greater prairie-chicken populations with translocations from areas in Kansas (∼325 km north west). Prior to our study, releases had occurred in the spring and summer of 2008, 2009 and 2010 at Wah'Kon-Tah Prairie. Thus, over 90% of our radiotagged population consisted of birds established from previous translocations and the remaining birds presumably fledged in Missouri. We considered all translocated birds that overwintered in Missouri prior to the current study to be resident greater prairie-chickens as they had adequate time to familiarize themselves with the release area.

Capture, radiotagging, and release

We trapped resident greater prairie-chickens at lekking sites in the 2010 field season in Wah'Kon-Tah and Taberville Prairies from 23 March 2010 to 15 April 2010 using modified walk-in traps (Schroeder and Braun 1991). In the 2011 field season we trapped birds from 18 January to 29 January on a soybean (*Glycine max*) field near Wah'Kon-Tah Prairie using corn (*Zea mays*) bait and modified walk-in traps (Schroeder and Braun 1991). We trapped birds for translocation on booming grounds in Ottawa, Saline, Lincoln, McPherson, and Ellsworth counties in the state of Kansas between 23 March 2011 and 12 April 2011. Within 6 hours of capture, birds were banded, evaluated by a certified veterinarian and transported to Wah'Kon-Tah Prairie at El Dorado Springs, Missouri (approx. 325 km) where they were radiotagged and hard-released. We banded all captured birds with custom stamped and serially numbered aluminum butt-end leg bands (size 12; National Band

and Tag, Newport, KY, USA) and pendant-style radiotelemetry tags that transmitted a faster pulsing signal if birds did not move for 12 hours (Advanced Telemetry Systems, Isanti, MN USA; model number A3690; battery life approximately 586 days; 16–18 g). The Institutional Animal Care and Use Committee of the University of Missouri (reference #6597) approved these methods and we were authorized to capture and mark greater prairie-chickens by the Missouri Department of Conservation.

Radiotelemetry

We tracked radiotagged resident greater prairie-chickens from 24 March 2010–23 August 2010 ($n=29$) and 12 March 2011–11 August 2011 ($n=29$), and translocated birds from 23 March 2011–11 August 2011 ($n=54$). We tracked all translocated males ($n=26$) and a randomly selected subset of translocated females ($n=28$). Observers searched the area and obtained locations using hand held telemetry units if birds could not be located from vehicles (Advanced Telemetry Systems; 3-element yagi antenna). We searched for every bird within 7.5 km of Taberville or Wah'Kon-Tah Prairie, each day of the week, and during 1 randomly selected 3-hour search period (0600–0900, 0900–1200, 1200–1500, 1500–1800, 1800–2100, or 2100–2400). The 7.5-km search buffer encompassed the area generally used by birds residing at Wah'Kon-Tah and Taberville prairies (K. Carrlson, unpublished data) and it created an area that we were able to search thoroughly each day. We located birds that were outside of the 7.5-km search buffer once each week. Prairie-chickens that could not be located were classified as missing, and we searched for missing birds with scanning receivers on a daily basis, throughout every tracking session, and both inside and outside the 7.5-km search buffer. We also used occasional helicopter tracking to aid in searches for missing birds.

We used vehicle-mounted null-peak telemetry units equipped with electronic compasses (Cox et al. 2002) and hand-held telemetry receivers to search for birds. We recorded the geographic coordinates of a bird's location if it was flushed during tracking. When tracking from a distance, we recorded 3–6 bearings from surrounding locations, which together constituted a bearing group. First and last bearings of each group were separated by ≤35 minutes. We used bearing groups and LOAS (Location of a Signal; version 4.0; Ecological Software Solutions LLC, Hegymagas, Hungary) software to triangulate bird locations and the associated error ellipses (White and Garrott 1990). We censored bearing groups with non-intersecting vectors and error ellipses >2 ha in size to reduce the potential effects of inaccurate locations (Kesler and Haig 2007; Coulombe et al. 2011). These excluded bearing groups represented <5% of the total data set. Consecutive locations for each bird were separated by ≥8 hours.

We searched for birds when we detected a mortality signal (transmitter mortality signals initiated after 12 hour without movement), and recorded geographic coordinates of dead birds. We recorded bearing groups and used triangulation to estimate 9 mortality locations that occurred on private lands where access was restricted. We reviewed location observations, and assumed that birds were dead on the first day that their telemetry location was at the recorded mortality location. During radio-tracking we incidentally located 2 dead birds in hawk (*Buteo* spp.) nests, and we used the last known live locations as the location of mortality. We determined cause of mortality by the location and state of carcasses upon retrieval, and attributed mortality to predators if carcasses were discovered incidentally in a hawk nest, if the birds appeared to be eaten, or if we observed evidence of ripped tendons or bite marks on bones or radiotags (Wolfe et al. 2007).

Habitat classification

We used ArcGIS 9.3 (Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA) and coverages created by the National Agriculture Imagery Program (Salt Lake City, UT: United States Department of Agriculture Farm Service Imagery, 2009) to delineate habitat boundaries on Wah'Kon-Tah and Taberville prairies, and in surrounding areas. We classified habitat based upon ownership and habitat cover type. Habitat classifications included wooded areas, prairie, urban, water, agriculture, and private grassland. Wooded areas included forested areas as well as trees inside of other habitat types. We classified grassland under direct management by the Missouri Department of Conservation as prairie. We considered prairie, fescue, or prairie-fescue combinations of habitat outside of direct management by the Missouri Department of Conservation to be grasslands. We classified cropland such as soybeans, alfalfa, clover, and corn crops to be agricultural habitats. We ground-truthed the digitized classifications in the summer of 2010 by visually verifying that each habitat patch was classified correctly. We used a simplified version of the 2005 land cover maps (30 × 30 m resolution; Missouri Land Use Land Cover Data, Columbia, MO: Missouri Spatial Data Information Service) to classify habitats for areas that were used infrequently by birds and that were outside of Wah'Kon-Tah and Taberville prairies and their immediate surrounding areas. Classification categories included urban, agriculture, private grassland, wooded areas, water, and other.

Table 1
Ordered ranking of survival analysis for greater prairie-chickens as predicted by residency (R), ordinal date (D), sex (S), year (Y) and habitat (H). For each model, we present the log-likelihood (logL), number of parameters included in the model (K), Akaike Information Criteria corrected for small sample size(AIC_c), and Akaike weight (ω_i; model probability given the set of candidate models). Analyses were based on the fates of 112 birds between 12 March and 23 August 2010–2011 in southwest Missouri.

Model	logL	K	AIC_c	ω_i
R+D	234.86	3	475.72	0.19
R+D+S	234.14	4	476.28	0.15
R+D+H	234.28	4	476.57	0.13
R+D+Y	234.86	4	477.72	0.07
R+D+S+Y	234.14	5	478.28	0.05
R	237.25	2	478.51	0.05
R+D+H+Y	234.27	5	478.55	0.05
D	237.42	2	478.84	0.04
R+S	236.62	3	479.23	0.03
S+D	236.65	3	479.29	0.03
H+R	236.68	3	479.37	0.03
H+D	236.94	3	479.89	0.02
S+D+Y	236.02	4	480.04	0.02
H+D+Y	236.1	4	480.2	0.02
S+D+H	236.19	4	480.39	0.02
S+D+H+Y	235.46	5	480.92	0.01
Y	238.52	2	481.05	0.01
Null	239.56	1	481.12	0.01
R+S+Y	236.56	4	481.13	0.01
H+R+Y	236.59	4	481.17	0.01
S	238.82	2	481.65	0.01
H	239.04	2	482.08	0.01
H+S+Y	237.29	4	482.58	0.01
H+S	238.32	3	482.64	0.01

Statistical analyses

Survival. We assessed the effects of date, habitat, sex, year and residency on the survival of translocated and resident greater prairie-chickens. The continuous variable *date* represented ordinal date and was designed to reflect survival that was not constant throughout the season. The variable *residency* was categorical, and designed to represent differential survival in translocated and resident birds. A variable for *sex* was incorporated to represent differential survival among females and males. The *habitat* variable was used to assess survival of greater prairie-chickens that spent a greater proportion of their time in the matrix (non-hostile and neutral) habitats surrounding the core protected prairie. Additionally, we included a variable *year* to account for differences in survival between the two study years. We divided the number of observed locations outside of the core protected prairie habitat by the total number of observed locations for each bird to derive the habitat proportion variable used for each individual.

We tested a suite of biologically relevant a priori hypotheses incorporating residency, habitat, sex, and date independently and additively (Table 1). We fitted observation data to the models using logistic exposure models within a SAS macro (Shaffer 2004; Shaffer and Thompson 2007). The logistic exposure models allowed for staggered entry and were weighted for different observation interval lengths. We right-censored individuals from the analysis if they were missing or when poor radio transmission strength prevented us from identifying bird locations. Model selection was based on an information theoretic approach (Burnham and Anderson 2002). We used adjusted Akaike's information criteria (AIC_c) to rank competing models. We considered models with $\Delta AIC_c < 2$ to be best supported and we model averaged across the subset if more than one model had $\Delta AIC_c < 2$ (Burnham and Anderson 2002). We considered variables included in the best supported subset to affect survival, and we present model-averaged coefficients ($\hat{\beta}$) and associated unconditional 95% confidence intervals to evaluate effect magnitude and range.

Habitat selection

We tested for differences in the types of habitats used by resident and translocated greater prairie-chickens with the Euclidean distance method (Conner and Plowman 2001; Conner et al. 2003). The method tests whether bird locations differ from locations randomly distributed throughout the available area by comparing distances between bird locations and each habitat type with the distances between randomly placed points and habitats (Conner et al. 2003). The Euclidean distance method is more robust to telemetry error than classification-based methods (Aebischer et al. 1993; Bingham and Brennan 2004), and it lends insight into relationships between bird movements and nearby features (Conner and Plowman 2001; Conner et al. 2003). We examined habitat selection, or the difference in habitat use and availability, at the third-order scale (Johnson 1980), which compares habitats used within a home range to the habitats that were available within the same area. For each bird, we defined home ranges by the minimum convex polygon (MCPs; Mohr 1947) bounding all observed locations. We then generated random locations for each individual using Hawth's Tools (Beyer 2004) in ArcGIS 9.3, such that the number of random locations (N_r) within the home range equaled the number of observed points. We were interested in overall habitat use and not nest site selection, so we censored all but 1 radiotelemetry observation of incubating females. Only birds for which we recorded ≥30 locations (n = 70 prairie-chickens) were included in the analysis to avoid sample size biases (Garton et al. 2001). We tracked 7 resident birds during both 2010 and 2011, and we randomly selected 1 of 2 seasons for these individuals to avoid pseudoreplication (Hurlbert 1984).

We used the NEAR analysis in ArcGIS 9.3 to calculate the Euclidian distance of random and observed points to the nearest prairie, private grassland, agriculture, and wooded area. We averaged the distances of actual locations and random locations to habitats for each bird (i) to create vectors (u_i) and (r_i) respectively. We created a vector of ratios of used to random distances (d_i) with a

mean of (p) by dividing (u_i) by (r_i) for each bird. We characterized selection for a habitat by a value of (p) that was significantly less than 1 and an avoidance of any habitat type by a value of (p) that was significantly greater than 1 (Conner and Plowman 2001; Conner et al. 2003). We tested the mean of the ratio vectors (p) for a difference from a vector of 1's using a multivariate analysis of variance (MANOVA). Observations were pooled for resident birds observed in 2010 and 2011 because we found no differences in p (Wilks' Lambda = 1.00, $F_{4,36}$ = 0.03, P = 1.00). We tested for habitat selection differences between resident and translocated birds, and between male and female greater prairie-chickens. We then used univariate t-tests to obtain an ordered ranking of preference for the habitats (Conner and Plowman 2001). We considered differences statistically significant at $\alpha < 0.05$, and statistically suggestive and potentially biologically significant at $\alpha < 0.10$.

Results

We tracked 29 resident greater prairie-chickens (11 female, 18 male) during the 2010 field season and 29 resident birds (15 female, 14 male) during the 2011 field season. From 23 March 2011 to 12 April 2011, we translocated 77 birds (51 female, 26 male) from Kansas to Missouri and released them at Wah'Kon-Tah Prairie. Throughout the 2011 field season, we tracked all of the translocated males (n = 26) and a randomly selected subset of 28 translocated females.

Adult survival

We observed 7 (24%) resident greater prairie-chicken mortalities (2 females, 5 males) during the 2010 field season, and 10 (34%) resident (8 females, 2 males) and 23 (43%) translocated bird mortalities (12 females, 11 males) during the 2011 field season. We retrieved 80% (32/40) of these birds post-mortem, and determined that 87.5% (28/32) of those mortalities were due to predation because of the condition of the carcasses (tooth marks, plucked feathers). No cause of death could be ascertained for the remaining 4 mortalities, as birds were fully intact. We right-censored 4 individuals in 2010 and 9 in 2011 because of disappearance (n = 10) and radio failure (n = 3). Birds that disappeared may have departed from the study area.

Results indicated model selection uncertainty among four top-ranked ($\Delta AIC_c < 2$) survival models (Table 1). The four best supported models all included residency and ordinal date as predictor variables, and together accounted for 54% of the AIC_c weight within the model set (Table 1). Model averaged parameter estimates from the top set indicated that resident birds had higher survival rates than translocated birds ($\hat{\beta}_{resident}$ = 0.72; 95% CI = 0.06 to 1.38) and birds' survival increased as the season progressed ($\hat{\beta}_{date}$ = 0.01; 95% CI = 0.00 to 0.02; Fig. 2). For example, holding all other variables constant at their average values, results indicated that the survival of resident birds from 12 March to 23 August (n = 165 days) was 0.65 (95% unconditional CI 0.46 to 0.79) whereas that of translocated female birds was 0.42 (95% unconditional CI = 0.17 to 0.66). Model averaged parameter estimates also suggested that females were characterized by lower survival than males ($\hat{\beta}_{female}$ = −0.10; 95% CI = −0.49 to 0.28) and that birds that spent more time in non-hostile matrix habitats had lower survival rates ($\hat{\beta}_{matrix}$ = −0.17; 95% CI = −0.85 to 0.50). However, unconditional confidence intervals for the sex, and habitat parameters overlapped zero, indicating that these factors were likely not as influential as residency and day on survival rates.

Together, model averaged parameters and unconditional confidence intervals indicated that daily survival probabilities (S_d) can

Table 2
Habitat selection for 70 greater prairie-chickens in the 2010 and 2011 field seasons in southwest Missouri calculated using Euclidean distance analysis. We present the difference between 1 and the ratio of distances from bird locations to distances from random locations to the four major habitat types in the study area. Values > 0.0 indicate avoidance (P < 0.05). Habitats sharing any common letter rank were similarly preferred or avoided (P < 0.05).

Habitat	Ratio-1	P-value	Ranks
Agriculture	−0.07	0.2303	A
Grassland	0.73	<0.0001	B
Prairie	−0.36	0.0003	C
Woods	0.87	<0.0001	B

be predicted with the following equation

$$logit(S_d) = 4.0896 + Date(0.0088) + RESIDENT(0.7220)$$
$$+ FEMALE(-0.1039) + Matrix(-0.1730) + YEAR_{2010} \ (0.0051)$$

where *DATE* is the ordinal date, beginning with 12 March; *RESIDENT* is an indicator for resident birds, *FEMALE* is an indicator for female sex, *Matrix* is a quantitative variable representing the proportion of time individuals spent in non-hostile matrix habitats, and *YEAR$_{2010}$* is a categorical variable representing the first year of the study.

Habitat use

We found no difference in habitat selection by resident and translocated greater prairie-chickens (Wilks' Lambda = 0.93, $F_{4,65}$ = 1.20, P = 0.32) and no difference in habitat selection by females and males (Wilks' Lambda = 0.93, $F_{4,65}$ = 1.14, P = 0.34). As a group, translocated and resident greater prairie-chickens actively selected for habitats within home ranges (Wilks' Lambda = 0.63, $F_{4,66}$ = 9.79, $P \le 0.01$). Results of Euclidean distance analyses further indicated that birds were observed closer to prairie (Pr > |t| = 0.0003) and further from private grasslands (Pr > |t| < 0.0001) and wooded (Pr > |t| < 0.0001) areas than random locations. When compared to random locations, birds did not appear to be closer to, or further from, agricultural habitats within home ranges (Pr > |t| = 0.23). Greater prairie-chickens tended to be closer to prairie, followed by agriculture, and further from private grassland and wooded areas than random distributions predicted (Table 2).

Discussion

Limited empirical data exist about survival and habitat use in translocated and resident birds, despite numerous translocation attempts (Kruse 1973; Toepfer et al. 1990; Snyder et al. 1999). Our study provides one of few comparisons of survival and habitat use between resident and translocated birds within the same landscape (but see Toepfer 1988; Terhune et al. 2010; Stephenson et al. 2011; Baxter et al. 2013). Similar to Toepfer (1988) we observed that survival tended to be lower in translocated individuals than in resident birds. We also observed that survival was depressed in both groups at the beginning of the breeding season. Habitat use patterns indicated strong selection for prairie and avoidance of wooded areas.

Seasonal estimates of survival in our study indicated substantial vulnerability during the breeding season for resident and translocated greater prairie-chickens. Similar findings have been documented in other populations of greater (Augustine and Sandercock 2011) and lesser prairie-chickens (Hagen et al. 2007). Model-averaged breeding season survival estimates on our study area for translocated (0.42) and resident (0.65) birds were comparable to recently estimated breeding season survival rates in a population of greater prairie-chickens in northeast Kansas (0.45; Augustine and Sandercock 2011). Similar to Augustine and
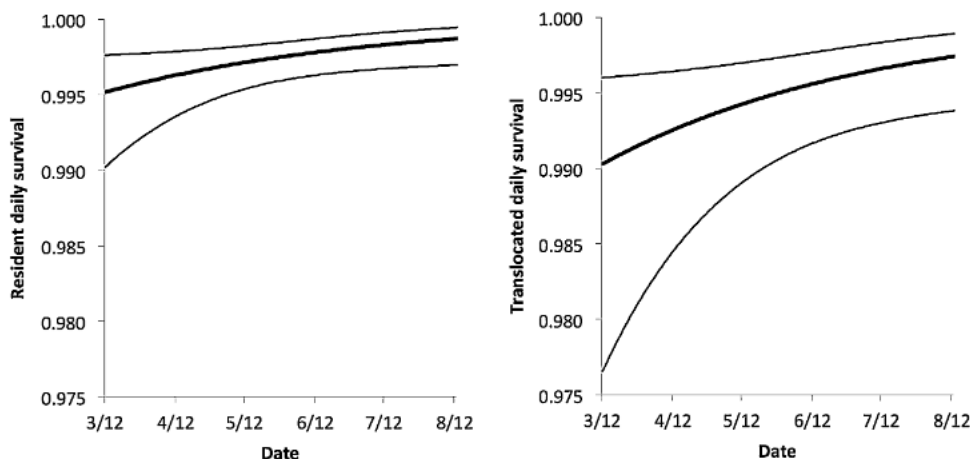
Fig. 2. Model-averaged predictions of daily survival of resident (left) and translocated (right) greater prairie-chickens in southwest Missouri, 2010–2011. Solid black line represents daily survival rates across a period of 165 days during the breeding season. Thin black lines are upper and lower 95% unconditional confidence intervals.

Sandercock (2011), our mortality observations suggested that survival was limited by predation on the Missouri study area, which also aligns with previous studies of greater prairie-chickens in fragmented landscapes (Burger 1988; Toepfer 1988; McNew et al. 2012).

Depressed survival early in the breeding season could be attributed to phenological differences in reproductive behavior or movement patterns. Females expend considerable energy during nesting and incubation periods (Svedarsky 1988; Thomson et al. 1998) and female mortality has been associated with both the nesting and brood rearing period in lesser prairie-chickens (Hagen et al. 2007). Displaying males on leks are exposed to predators such as red-tailed hawks (*Buteo jamaicensis*), and northern harriers (*Circus cyaneus*; Berger et al. 1963; Toepfer 1988; Wolfe et al. 2007). The energetic cost associated with spring lekking might also reduce body condition, making males vulnerable to predators (Vehrencamp et al. 1989, but see Hagen et al. 2005). Both sexes also appear to have higher movement rates during the early portion of the breeding season (Kemink 2012; Kemink and Kesler 2013), and greater movement rates have been linked to depressed survival in other grouse studies (Burger 1988). Some have speculated that this pattern was caused by increased mortality through fence collisions (Wolfe et al. 2007) and heightened exposure to predators (Yoder et al. 2004). Previous studies of grouse translocation also indicated lower survival in translocated females than males (Kurzejeski and Root 1988; Toepfer 1988). Although survival differences between males and females appeared in our top model set, model averaged unconditional confidence intervals suggested that sex was not a strongly-supported parameter. Regardless of sex, however, translocated individuals in our study had significantly lower survival rates than residents.

Predation is one of the most often cited causes of mortality during translocations (McKinstry and Anderson 2002; Van Zant and Wooten 2003; Matson et al. 2004; Siano et al. 2006). Of the birds that we were able to recover, 88% of the mortality in translocated individuals was attributed to predation. Dickens et al. (2010) suggested that translocated birds are more vulnerable to predators than residents because of physiological or psychological stresses associated with translocation. Unfamiliarity with the release area, and an effort to explore, could also elevate predation mortality in translocated birds (Brown et al. 2006; Tavecchia et al. 2009). Frequent movements for orientation within novel habitats are thought to increase vulnerability to predators (Metzgar 1967; Yoder et al. 2004; but see Cox and Kesler 2012), and greater movement rates have been linked to lower survival in previous grouse translocations (Kurzejeski and Root 1988; Cope 1992; Bernardo et al. 2011).

Landscapes fragmented by agriculture often have the most prevalent predator effects (Chalfoun et al. 2002) because of the availability of additional food sources (Andrén 1995; Dijak and Thompson 2000) or the presence of perching and denning sites (Bohall and Collopy 1984; Svedarsky and Van Amburg 1996; Pedlar et al. 1997; Kuehl and Clark 2002; Applegate et al. 2004). Further, predator avoidance strategies that were evolved in prairie habitats, such as cryptic coloration, are likely to be less effective in agricultural or non-native grassland habitats (Braun et al. 1994; Valentine et al. 2007). While the top model set included our habitat parameter, suggesting that birds in our study that spent larger amounts of time in the more fragmented matrix habitats tended to have lower survival rates, model averaged unconditional confidence intervals indicated that, similar to sex, habitat was not a strong predictor of survival.

Despite the poor predictive power of habitat for survival, we still observed strong selection for large and protected patches of prairie by greater prairie-chickens, which aligns with results of previous studies (Christisen 1981; Burger 1988; Ryan et al. 1998; Winter et al. 2006). Indeed, prairie-chickens are believed to be area sensitive (Hamerstrom et al. 1957; Sample and Mossman 1997; Winter and Faaborg 1999) and some even suggest that isolated populations need patches as large as 516,800 hectares to maintain a genetically stable population (Svedarsky et al. 2003). While less studied in grasslands than in forest habitats, features such as fences, trees, and anthropogenic structures found in more fragmented prairie landscapes may decrease habitat suitability. These features often serve as perching sites for avian predators (Bohall and Collopy 1984; Applegate et al. 2004) or transit lanes for mammalian predators (Pedlar et al. 1997; Kuehl and Clark 2002).

Together, results from our investigation elicited patterns similar to those evidenced in the few other greater prairie-chicken translocation studies (Toepfer 1990; Mechlin 1999; Snyder et al. 1999). Low post-release survival of translocated birds indicates that larger release cohorts or multiple years of release might be necessary to buffer against elevated mortality among released birds (Snyder et al. 1999). For example, up to 120 greater prairie-chickens might need to be released to achieve translocated populations entering the fall/winter of 50 ($0.42 \times 120 = 50.4$). Worthwhile avenues for future research would include further examination of the relationship of habitat and sex with greater prairie-chicken survival, as well as the impact of potential predator removal and habitat management and restoration to ameliorate low survival in translocated individuals. Larger sample sizes over multiple years would be needed to uncover these relationships or lack thereof.

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