

Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape

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Abstract

Context Conservation of grassland vertebrates requires a mechanistic understanding of the effects of landscape heterogeneity on habitat selection and demographic performance.

Objectives Our goal was to investigate the effects of rangeland management on resource selection and nest survival of upland sandpipers (*Bartramia longicauda*).

Methods We conducted our project at Konza Prairie, a Long-Term Ecological Research site. The station has 60 experimental units with replicated grazing and fire treatments that create a heterogeneous landscape of different habitat patches. We radio-tracked sandpipers for two breeding seasons (2003–2004, $n = 37$ birds)

and monitored sandpiper nests for eight seasons (2001–2008, $n = 246$ nests). We used resource utilization functions to examine resource selection with respect to five landscape features.

Results Home ranges of sandpipers were large in contiguous prairie ($\bar{x} = 8.4 \text{ km}^2$) and explain area-sensitive occurrence in fragmented prairie. Upland sandpipers selected grazed and burned sites with short vegetation within their home range. In contrast, nest site selection was influenced by fire frequency and birds selected infrequently burned sites with greater vegetative structure. Settlement decisions affected fitness because nest survival was low in burned and grazed sites (0.068), but higher in unburned and ungrazed sites (0.201–0.247).

Conclusions Our results raise concerns for conservation because private rangelands managed for livestock production are often homogeneous landscapes with

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heavy grazing and frequent fires. Rotational grazing and fire could be used to restore heterogeneity to grasslands but the duration of rotation, patch size, and optimal configuration require further investigation.

Keywords *Bartramia longicauda* · Fire · Grassland · Habitat selection · Home range · Landscape heterogeneity · Nest survival · Radio-telemetry · Resource utilization functions · Tallgrass prairie

Introduction

Intensification of agricultural production has led to population declines and range contractions among wildlife associated with agroecosystems worldwide (Donald et al. 2001; Johnson et al. 2011). Steep population declines of vertebrates associated with temperate grasslands are an emerging conservation crisis, but the ecological mechanisms of ongoing losses remain poorly understood (Brennan and Kuvlesky 2005; Reinking 2005; Cagle 2008). Protection of temperate grasslands is challenging because fertile soils are suitable for rowcrop agriculture. A majority of this biome has now been converted to agricultural production, and biofuels and high prices for commodities provide economic incentives for continuing habitat loss (Hoekstra et al. 2005; Rashford et al. 2010). Wildlife conservation in agroecosystems cannot be based solely on setting aside protected areas, but must identify wildlife-friendly methods that balance agricultural yields with biodiversity (Green et al. 2005).

In many regions of the world, grassland birds persist in rangelands that are in private ownership and managed by grazing for livestock production (Batáry et al. 2007; With et al. 2008; Azpiroz et al. 2012; Valentine et al. 2012). In mesic grasslands, prescribed fire is often used to improve forage quality, promote a uniform grazing distribution, and control undesirable plants (Reinking 2005; Valentine et al. 2012). Heavy grazing and frequent fires improve yields among cattle and other livestock, but create a homogeneous landscape with reduced vegetative structure (Fuhlendorf et al. 2006; McNew et al. 2014). Changes in habitat structure can affect bird distributions and community assemblages by negatively impacting species that require tall herbaceous vegetation, while favoring species that use shortgrass habitats (Reside et al. 2012,

Little et al. 2013). Heterogeneous landscapes may promote biodiversity if habitat requirements of individual species vary among life-stages, or if community assemblages are a mixture of specialist and generalist species (Fuhlendorf et al. 2006; Powell 2006; Azpiroz et al. 2012). However, management for landscape heterogeneity cannot meet conservation goals without a mechanistic understanding of the interactive effects of grazing and fire on habitat structure and habitat-specific demographic performance.

The goal of our study was to investigate the interactive effects of prescribed fire and grazing on home range size, resource selection, and nest survival of a grassland bird in managed rangelands. Four aspects of our project were novel. First, we conducted one of the first long-term population studies of upland sandpipers (*Bartramia longicauda*). Second, we used radio transmitters to track movements and space use of birds for two breeding seasons, and located nests for eight breeding seasons. Upland sandpipers are secretive breeders but radio-telemetry provided an unbiased set of locations for bird movements and allowed us to locate and monitor a large sample of nests. Third, our field site was Konza Prairie Biological Station, a Long-Term Ecological Research site with ~60 experimental units managed with different combinations of prescribed fire and grazing for >40 years (Knapp et al. 1998). Konza Prairie provided a unique experimental landscape for our investigation of resource selection because it is a heterogeneous mosaic of prairie habitats. Last, we used new resource utilization functions (RUF) to investigate space use, resource selection, and nest placement of upland sandpipers in relation to different features of the experimental landscape. RUFs use multiple regression models to relate non-uniform space use to landscape features within a home range, while accounting for spatial autocorrelation among multiple locations (Millspaugh et al. 2006). Understanding the ecological linkages among grazing, fire, habitat heterogeneity, and resource selection will aid wildlife conservation in grasslands managed for livestock production.

Methods

Study site and study species

Our 8-year field study was conducted during April–July of 2001–2008 at Konza Prairie Biological Station, a

3,487 ha field site in the Flint Hills ecoregion of eastern Kansas (Fig. 1). The Flint Hills ecoregion contains the largest remaining tracts of tallgrass prairie in North America (~2.7 million ha), and is dominated by native species of perennial, warm-season grasses with a diverse community of broad-leaf forbs (Reinking 2005). Most lands are privately owned and managed for production of cattle (*Bos taurus*) because shallow, rocky soils are unsuitable for cultivation. Grazing systems in the ecoregion include intensive early-stocking or season-long stocking of steers, and cow-calf operations (Towne et al. 2005; With et al. 2008). Prescribed burning is widely used to improve quality of forage plants and mass gain by livestock, and to reduce encroachment by woody plants (Knapp et al. 1998; Mohler and Goodin 2012). The Flint Hills remain a stronghold for declining species of grassland vertebrates because current land use is similar to past ecological conditions of periodic fires every 2–5 years and episodic grazing by migratory plains bison (*Bison bison*, Fuhlendorf and Engle 2004; Reinking 2005; Powell 2006).

Konza Prairie has been managed as an experimental field station since 1971 and is subdivided into ~60

experimental units (mean area = 55 ha, range = 3–226 ha). Each experimental unit is subjected to 1 of 5 fire treatments with prescribed fire at return intervals of 1, 2, 4, 10, or 20 years. Prescribed fires were usually conducted in March or April, but a few experimental units were burned in summer, fall, or winter. Experimental units received 1 of 3 grazing treatments: grazed by bison, grazed by cattle, or ungrazed. The nine units of the bison area (961 ha) were grazed year-round at a stocking density of 4.7 ha per animal unit (bull or cow-calf pair). The four units of the cattle area (312 ha) were grazed for a 6-month growing season at a stocking density of 3.2 ha per animal unit (cow-calf pair). Target utilization rates for consumption of forage grasses were 25–30 % in the bison area and 50 % in the cattle area. Stocking densities and utilization levels at Konza Prairie were moderate compared to local ranches where stocking densities can be 1.7–2.1 ha per animal unit with utilization rates of 60–70 % (Towne et al. 2005, Smart et al. 2010). Each combination of fire and grazing treatments was replicated 2–3 times across the site.

Upland sandpipers are migratory shorebirds that use temperate grasslands in North and South America (Blanco and López-Lanús 2008; Houston et al. 2011). Range contractions and population declines have led to listings as a species of conservation concern in 24 states and provinces (Vickery et al. 2010; Houston et al. 2011). Upland sandpipers are unusual among grassland birds because relative abundance is often highest in disturbed habitats with intensive grazing or recent fire (Fuhlendorf et al. 2006; Powell 2006). Upland sandpipers are an area-sensitive species and are absent from small patches in fragmented prairie (Vickery et al. 1994; Johnson and Igl 2001). Nest site selection and nest survival are poorly understood and available data have been collected opportunistically during waterfowl surveys (Kirsch and Higgins 1976; Kantrud and Higgins 1992; Garvey et al. 2013). Conservation planning for upland sandpipers has been limited by problems of imperfect detectability, an unknown link between abundance and productivity, and incomplete demographic data (Vickery et al. 2010).

Field methods

Upland sandpipers were captured in late April and early May before birds started nesting. We caught roosting birds at night with a long-handled dip net and

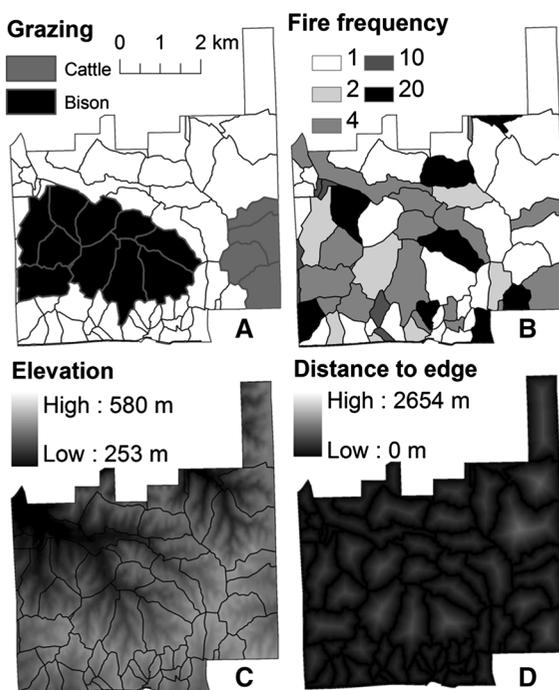


Fig. 1 Experimental landscape at Konza Prairie Biological Station, Kansas with spatial variation in **a** grazing treatments, **b** long-term fire treatments, **c** elevation, and **d** distance to edge of experimental units

high-powered spotlights. Sandpipers were marked with a numbered metal band and a unique combination of colored leg bands, and sexed with genetic markers (Casey et al. 2011). We marked a subset of birds with 3.8 g VHF radio transmitters attached to the back with an elastic leg-loop harness (model PD-2, Holohil Systems, Carp, ON, Mong and Sandercock 2007). We relocated radio-marked upland sandpipers with two methods. In 2002–2008, we used portable radio receivers (R2000, ATS, Isanti, MN) to approach radio-marked birds on foot, and recorded locations of bird sightings and nests with handheld GPS units (± 5 m; Garmin, Olathe, KS). In 2003–2004, we collected intensive movement data by locating radio-marked birds twice per day for the duration of the breeding season (~ 70 days from late April to mid-July). We triangulated bird positions from a vehicle equipped with an integrated null-peak triangulation system that included a GPS unit, a radio receiver with dual antennas, and a digital compass (Sailcomp 103AC, KVH Industries, Middletown, RI; Cox et al. 2002). We estimated coordinates for each set of triangulated locations with Program Locate (ver. 2, Tatamagouche, NS; UTM's projected in NAD 1983, Zone 14 N).

In 2001, we located nests by rope-dragging and systematic searching of prairie habitats. In 2002–2008, we found nests by monitoring radio-marked birds daily until the sandpiper was found attending a clutch of eggs. Each year, we also located a few nests by flushing incubating birds during our field work. At first discovery, we recorded the nest location with a handheld GPS unit, counted nest contents, and floated the eggs in a cup of lukewarm water. Egg buoyancy was used to estimate stage of incubation and predict expected hatch date (Sandercock unpublished data). We marked nests with a single piece of blue flagging at a distance of 10–30 m. Nests were relocated by taking a compass bearing from the flag and by using natural landmarks near the nest site. We captured unmarked parents at the nest for a genetic study of parentage (Casey et al. 2011), and monitored nests at a distance by telemetry until the end of incubation. We visited the nest 1–2 days before the predicted hatch date to check eggs for signs of hatching. We returned to the nest in 8–24 h if eggshells were pipped and within 1–2 days if the chicks were tapping. Nests were *successful* if one or more eggs successfully hatched and we captured chicks at hatching. In a few cases, the precocial young

departed the nest before a scheduled hatch check. We considered nests to be successful if pipped eggshells were left in the nestbowl, or if a parent gave distraction displays near the nest site. Nests *failed* if eggs disappeared before the expected hatch date, or if remains at the nest site indicated eggs were destroyed by predators, weather events, or trampling.

Statistical analyses

We tested five factors that we hypothesized a priori to be important for space use and nest site selection by upland sandpipers. Three explanatory variables were related to management of experimental units: (i) ungrazed versus grazed by bison or cattle, (ii) years since burn or the short-term effects of fire management (0 vs. ≥ 1 years), and (iii) frequency of experimental burn or the long-term fire management (annual burns vs. fire return intervals of ≥ 2 years, Fig. 1). Two additional variables described the landscape in terms of: (iv) absolute elevation, and (v) distance to edge of the experimental unit as an index of habitat heterogeneity. We predicted sandpipers should use disturbed areas of high prey abundance but avoid edges if predation risk was high. Edge effects could be important because vegetative composition and habitat structure differed between adjacent experimental units. Elevation might affect space use because upland sandpipers often perch on fence posts during courtship displays and brood defense. Upland sandpipers are ground-nesting birds, and we predicted that nesting birds might use ungrazed or unburned sites if vegetative cover conceals the clutch or incubating parents from predators.

Long-term data on grazing and prescribed fires were compiled from the data archives of the Konza Prairie LTER program (www.konza.ksu.edu). We combined bison and cattle into one grazing treatment because both species have similar effects on plant community and habitat structure (Towne et al. 2005). Year of burn had short-term effects on vegetative structure by removing aboveground plants when sandpipers were settling on home ranges for breeding. In contrast, fire frequency had long-term effects on vegetative structure by mediating competition among plant functional groups. Fire return intervals of 1–2 years maintain tallgrass prairie as a mesic grassland dominated by warm-season grasses, whereas fire return intervals ≥ 4 years lead to encroachment by woody shrubs and changes in fire dynamics (Briggs

et al. 2005; Reinking 2005). Prescribed burn plans for Konza Prairie differed among years and we created separate rasters for each year of the study with the distribution of burned and unburned units. If a unit was affected by an unplanned wildfire, we used the actual fire history instead of the scheduled experimental treatment. GIS layers were available for elevation (GIS111) and boundaries of experimental units (GIS025). We derived a raster grid for distance to edge of the experimental units with the Spatial Analyst Euclidian distance tool.

Space use and habitat selection

We analyzed space use of upland sandpipers from intensive monitoring conducted during the breeding seasons of 2003–2004. We included radio-marked birds in our analyses if an individual had ≥ 30 locations within the 4-month breeding season, and ≥ 20 locations that were not associated with a nest or brood (Seaman et al. 1999). We censored birds that were transient or dropped radios. We used resource utilization functions (RUF) to quantify space use as a surface, and to relate differential space use to features of the prairie landscape. Resource utilization functions treat individual animals or populations as the experimental unit instead of point locations and define available habitat by an individual's home range instead of by arbitrary boundaries (Marzluff et al. 2004).

We built utilization distributions, extracted landscape metric values, and developed resource utilization functions with the RUF package in Program R (ver. 2.13.11, R Foundation for Statistical Computing, Vienna, Austria). The first step was to calculate a home range for each bird from the 99 % volume contour with Hawth's Tools for ArcMap (ver. 9.3, ESRI, Redlands, CA), using the Fixed Kernel Density Estimator and Percent Volume Contour tools. A unique smoothing parameter (h) was calculated for each bird with least-squares cross-validation (Gitzen and Millsaugh 2003). The second step was to create a raster of the utilization distribution within each home range polygon. We classified each 30×30 m cell within the home range with observed values of relative use that were scaled from 1 to 99 based on the relative height of the utilization distribution surface (Marzluff et al. 2004; Kertson and Marzluff

2010). Home ranges defined the available space, whereas utilization distributions measured differential space use within the home range. The last step was to use the Spatial Analyst Extraction tool to create spatially explicit data files as input for the RUF package in Program R. We matched relative use values with environmental data for each 30×30 m cell from raster grids for five landscape factors: grazing treatment, years since fire, frequency of fire, elevation, and distance to edge.

Space use data were \log_e -transformed to meet assumptions of linearity in the multiple regression models. Utilization distributions were then compared to landscape factors on a cell-by-cell basis to obtain standardized and unstandardized slope coefficients of relative resource use (Marzluff et al. 2004; Kertson et al. 2011). Slope coefficients tested the influence of landscape factors on space use by individual birds and the population, and to predict distributions on the experimental landscape at Konza Prairie.

In preliminary analyses, we found little evidence of sexual or annual differences in resource use, and pooled sexes and years in all analyses. For the population response, we calculated mean standardized slope coefficients for each landscape metric per bird ($\bar{\beta}$), and computed variance estimates that incorporated inter-animal variability (Marzluff et al. 2004). Standardized coefficients were considered significant predictors of space use if the 95 % confidence intervals did not overlap zero. We ranked the relative importance of significant landscape factors by the absolute value of the mean standardized slope coefficients. To assess individual heterogeneity, we tallied numbers of birds with standardized slope coefficients that were significantly different from zero. To predict space use of sandpipers at Konza Prairie, we used unstandardized slope coefficients combined with the configuration of the experimental landscape in 2003 and 2004. Predicted relative use was estimated with the raster calculator in ArcMap and projected in four quartiles: 0–25 %, 26–50 %, 51–75 %, and 76–100 % (Kertson et al. 2011).

Nest site selection

To investigate nest site selection, we created separate utilization distributions for each year of the study which we compared to the distribution of burned units

and other landscape factors. Most pairs were monitored for a single nesting attempt in one breeding season but our sample included a few birds monitored in multiple years and occasional renests. We hypothesized that resource selection might covary with the total area of Konza Prairie that was burned in a given year. We defined the available nesting area as the minimum convex polygon for all nest locations of upland sandpipers in our 8-year field study (2001–2008). We calculated the percentage of the nesting area burned each spring with a 30 m point grid and the Spatial Analyst Extraction tool. We used linear regression to compare the annual variation in selection coefficients for years since burn versus the percentage of the nesting area that was burned.

Nest survival

We modeled daily survival rates of sandpiper nests using the nest survival procedure in Program Mark (ver. 7.1, Colorado State University, Ft. Collins, CO). We created encounter histories for all nests monitored in our 8-year field study (2001–2008) where we had complete information for dates of monitoring and nest fate. Encounter histories included the date of initial nest discovery (i), the last date a nest was known to be active (j), the date that the nesting attempt was completed (k), the fate of the nest (0 = successful and 1 = failed), and the number of nests with the encounter history. The last two dates were set to be identical if a nest was successful ($j = k$), but bracketed the period of loss if a nest failed ($j < k$).

We modeled daily nest survival with a set of 25 a priori models that included an intercept-only model, single factor models, and additive models with different combinations of explanatory variables. Treatments for experimental units were group effects: grazed versus ungrazed, years since spring burn (0 vs. ≥ 1 years), and annual versus longer fire return intervals (1 vs. ≥ 2 years). We modeled elevation, distance to edge of the experimental unit, and age of nests as individual covariates. We did not include models with full time-dependence but modeled seasonal changes in daily nest survival as a linear or quadratic function of time. No single model received a majority of support from the dataset. We calculated support for each explanatory factor by summing Akaike weights (w_i) across all models that included

a landscape factor. To calculate predicted nest survival (S_n), we extrapolated daily nest survival (S_d) to a 29-d exposure period based on a 5-day laying period and a 24-day incubation period ($S_{29} = S_d^{29}$, Higgins and Kirsch 1975; Sandercock, unpublished data). We used the delta method to calculate standard errors for predicted nest survival (Powell 2007).

Results

Home range and habitat selection

Resource utilization functions for home ranges were based on 37 radio-marked upland sandpipers monitored intensively by radio-telemetry in 2003 and 2004 (16 females and 21 males). The average number of locations per individual was 54 ± 3 SE (range 32–90). Estimates of home range size should be unbiased because 99 % volume contours were not related to the number of locations per individual, year, or the interaction (Fig. SA.1). Home ranges of sandpipers during the breeding season were large and averaged 8.4 ± 1.4 km² (range 0.8–33.7), with a mean smoothing parameter (h) of 0.41 ± 0.03 km (range 0.15–1.00, Fig. SA.2). The average home range size was ~ 15 times larger than the experimental units managed with different grazing and fire treatments (55 ha).

The strongest predictor of space use was elevation, with greater use of high elevation sites at Konza Prairie ($\bar{\beta} = 0.24$, Fig. 2a; significant positive slope for 78 % of birds, Table SA.1). Upland sandpipers also selected habitats that were close to edges of experimental units ($\bar{\beta} = -0.20$; 60 % of birds), and in grazed ($\bar{\beta} = 0.13$; 56 % of birds) or recently burned areas ($\bar{\beta} = -0.12$; 65 % of birds). We used unstandardized coefficients to calculate a surface of predicted space use for upland sandpipers at Konza Prairie (Table SA.2). Predicted space use changed between 2003 and 2004 because rotational burning of experimental units created a dynamic landscape (Fig. SA.3).

Nest site selection

Analyses of nest site selection were based on an average of 31 nests per year (range 16–37; total $n = 246$). Most nests were found by radio-tracking

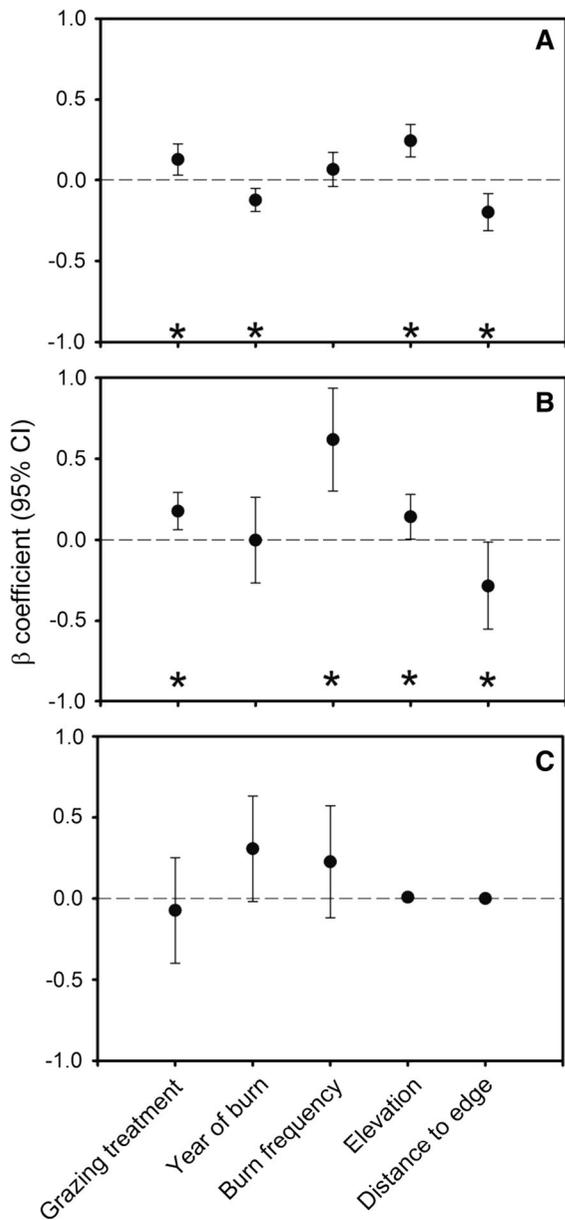


Fig. 2 Slope coefficients ($\beta \pm 95\%$ CI) for habitat selection and nest survival of upland sandpipers at Konza Prairie, Kansas during 2001–2008. Coefficients were taken from resource utilization functions for the **a** home ranges of individual upland sandpipers ($n = 37$ birds) in 2003–2004, and **b** annual distributions of nests in 2001–2008 ($n = 16$ –37 nests per year, 246 total). Coefficients for daily nest survival **c** were taken from single factor models of nest survival ($n = 238$ nests). Asterisks denote significance where 95 % CI do not include zero

(67 %), but some were located by flushing incubating birds (30 %) or by rope-dragging (3 %). Upland sandpipers were flexible in nest site selection, and

nests were found in a range of different habitats (Fig. 3). The strongest predictor for nest placement was the long-term fire return interval, with strong selection of experimental units with infrequent fires that were rested for one or more years between spring burns ($\beta = 0.62$, Fig. 2b; 75 % of years, Table SA.1). Nest site selection was also affected by distance to experimental unit edge ($\bar{\beta} = -0.29$; 100 % of years), grazing treatment ($\bar{\beta} = 0.18$; 75 % of years), and elevation ($\bar{\beta} = 0.14$; 100 % of years). Sandpipers selected nest sites in edge habitats near unit boundaries, areas with grazing by bison or cattle, and upland sites in the landscape (Fig. 2b). Years since burn was a significant predictor of nest placement in 6 of 8 years but the overall $\bar{\beta}$ coefficient was nonsignificant because selection coefficients were both positive and negative. Contrary to our prediction, the percentage of Konza Prairie that was burned did not explain annual variation in selection coefficients for years since burn ($r^2 = 0.14$, $p = 0.36$).

Nest survival

Analyses of nest survival were based on 238 sandpiper nests that were active from 29 April through 9 July in a 72-day nesting period. Nest fate included 82 nests that

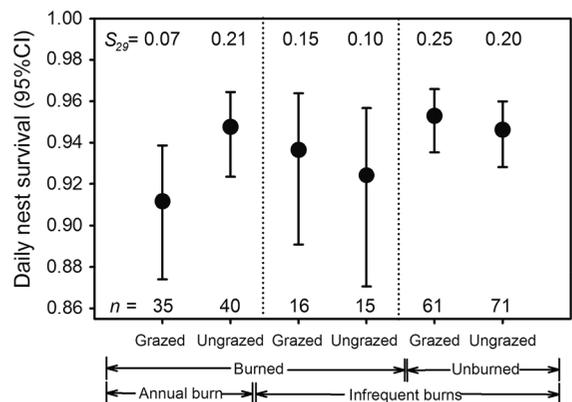


Fig. 3 Effects of rangeland management on daily survival rates of nests of upland sandpipers at Konza Prairie, Kansas during 2001–2008. Daily nest survival rates were extrapolated to a 29-day exposure period for the nesting cycle (S_{29}). Rangeland management treatments for experimental units included: grazed or ungrazed, burned with prescribed fire in spring or unburned, and burned with annual spring fires or on a longer fire return interval. Sample size of nests in each treatment is reported at the base of each estimate

successfully hatched and produced young (34 %), 121 nests destroyed by predators (51 %), 12 nests destroyed by heavy rain or hailstorms (5 %, 3 in 2005 and 9 in 2008), 17 nests that were abandoned (7 %), and six nests destroyed by trampling by bison or cattle (3 %). We observed predators eating eggs at ten nests, including gopher snakes (*Pituophis catenifer*), American crows (*Corvus brachyrhynchos*), and coyotes (*Canis latrans*). Upland sandpipers were vulnerable during incubation and a parent was killed at 2 of 9 nests lost to hailstorms (22.2 %), 1 of 6 trampling events (16.7 %), and 3 of 121 predation events (2.5 %).

We developed an a priori set of 25 candidate models to model daily nest survival of upland sandpipers (Table SA.3). No single model received the majority of support in our candidate set, and 95 % CIs for β coefficients in all single factor models included zero (Fig. 2c; Table SA.4). Years since burn was the strongest predictor of daily nest survival if we summed model weights for each explanatory factor ($\Sigma w_i = 0.42$). Daily nest survival was also related to elevation of the nest site ($\Sigma w_i = 0.36$) and age of the clutch ($\Sigma w_i = 0.32$). Frequency of burn, grazing treatment, and distance to unit edge received less support among our candidate models ($\Sigma w_i = 0.14$ – 0.21).

To calculate nest survival for a 29-day exposure period (S_{29}), we took daily survival (S_d) from an unconstrained model that included years since burn, frequency of burn, and grazing treatment. Daily survival rates ranged from $S_d = 0.9115$ – 0.9529 across the six treatments (Fig. 3). Nest survival was highest in unburned sites with vegetative cover from previous growing seasons, whether a site was grazed ($S_{29} = 0.247 \pm 0.057$ SE) or ungrazed (0.201 ± 0.049). Nest survival was also high in ungrazed areas, even with annual fires (0.210 ± 0.065). The lowest rate of nest survival occurred in experimental units managed with grazing and annual fires (0.068 ± 0.035). We used estimates from single factor models to examine the effects of burning and grazing alone. In a single factor model with years since burn, daily nest survival was higher for unburned units ($S_d = 0.9495 \pm 0.0056$) than units previously burned the same spring (0.9326 ± 0.0075), which resulted in a ~ 2 -fold difference in predicted nest survival between unburned ($S_{29} = 0.223 \pm 0.038$) and burned sites (0.132 ± 0.031). In contrast,

estimates from a model with grazing treatment showed daily nest survival was similar in grazed ($S_d = 0.9403 \pm 0.0067$) and ungrazed units ($S_d = 0.9443 \pm 0.0061$), and the difference in predicted nest survival was small ($S_{29} = 0.168$ vs. 0.190). A constant model gave low daily survival (0.9424 ± 0.005 SE) that resulted in predicted nest survival of 0.179 ± 0.025 . Daily survival of nests was higher at upland sites, and increased over the 29-day nesting cycle (Fig. 4a, b).

Discussion

The ecological factors and demographic causes of population declines in grassland vertebrates are poorly understood. Our 8-year field study provides new insights into the resource selection and habitat-specific

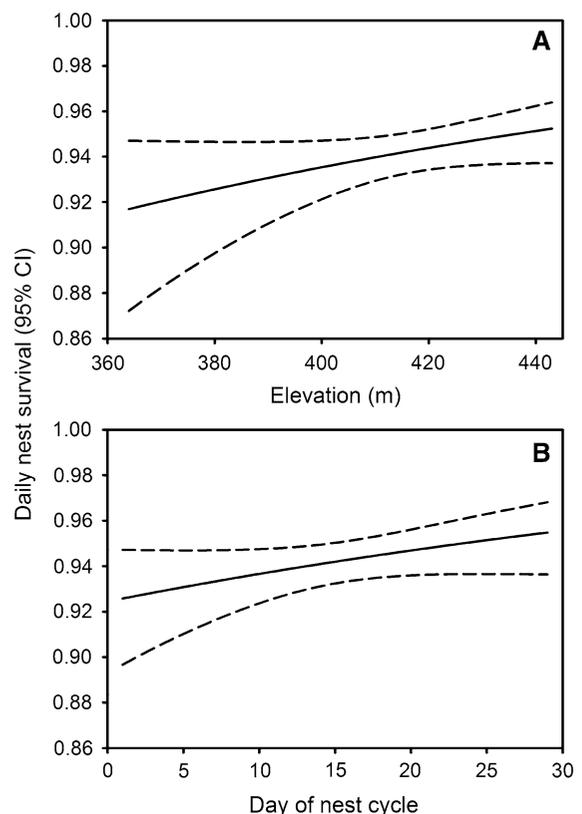


Fig. 4 Daily survival rates (95 % CI) of upland sandpiper nests as a function of: **a** elevation of the nest site, and **b** day of the nest cycle (day 1 = first laid egg and day 29 = hatching). Estimates were taken from the single factor model for each explanatory factor

demography for a species of conservation concern in managed rangelands. Our field study resulted in several unexpected findings. Upland sandpipers had large home ranges in contiguous tallgrass prairie, and habitat selection changed among different stages of the breeding cycle. Upland sandpipers used disturbed sites with short vegetation within their home range, but selected unburned and ungrazed sites with greater vegetative cover for nesting. Thus, landscape heterogeneity in managed rangelands will benefit individual species as well as community assemblages. Settlement decisions of sandpipers during nest site selection affected productivity because nest survival was lowest in grazed sites managed with annual fire, but higher in unburned and ungrazed sites. Our findings raise concerns because most private lands in the Flint Hills ecoregion are managed for cattle production with widespread use of prescribed fires. Conservation of grassland birds will require new approaches for restoration of heterogeneity to native grasslands and partnerships with private landowners.

Home range

Upland sandpipers had large home ranges in contiguous tallgrass prairie (8.4 km²), that were greater than their patch size requirements in fragmented prairie (200 ha, Vickery et al. 1994). Our estimates were based on utilization distributions during the summer breeding season, and were larger than past estimates based on unmarked birds and a pair of radio-marked birds (8–86 ha; Ailes and Toepfer 1977, Houston et al. 2011). Home ranges could be large because upland sandpipers are not a territorial species, and males rely on mate-guarding during the pre-laying period for paternity assurance (Casey et al. 2011). Konza Prairie was a heterogeneous landscape, and home ranges may also be large because patch size averaged 55 ha among the experimental units. Sandpiper home ranges might be smaller in managed rangelands with greater landscape homogeneity, or perhaps even larger in fragmented prairies. Overall, the home ranges of upland sandpipers (8.4 km²) were intermediate in size to the small territories of grassland songbirds (1–2 ha; Zimmerman 1966; Delany et al. 1995), and the much larger home ranges of greater prairie-chickens *Tympanuchus cupido* (>50 km²; Winder et al. 2014). Area requirements may explain why upland sandpipers are an area-sensitive species while prairie chickens are absent from

fragmented prairie systems (Vickery et al. 1994; Johnson and Igl 2001; Ribic et al. 2009). Protection of large habitat blocks for grassland species with large area requirements should also benefit associated wildlife species with smaller territories or home ranges.

Resource selection

Periodic fire, grazing by large herbivores, and climatic variability are key sources of disturbance that structure trophic interactions in temperate grasslands (Knapp et al. 1998). Fire and grazing impact nutritional quality of herbaceous plants through litter removal, reductions in light limitation, nutrient inputs, and elevated nutrient cycling. Fire also affects vegetative structure because fire suppression favors establishment by woody shrubs (Briggs et al. 2005). Our analysis of sandpiper home ranges showed that birds selected disturbed sites that were grazed or recently burned, which was consistent with habitat associations reported from transect surveys and other observational methods (Fuhlendorf et al. 2006; Powell 2006). However, we also found that habitat selection changed during nesting when sandpipers selected nest sites in habitats with infrequent fire and greater vegetative structure (Ailes 1980; Klemek 2008).

The ecological mechanisms underlying habitat selection may include food availability, microclimate, predation risk, or social factors. Upland sandpipers feed on terrestrial arthropods captured with a run-stop-search mode of foraging (Houston et al. 2011). The effects of fire on forage quality lead to higher rates of mass gain among ungulate grazers, but also benefit herbivorous insects. At Konza Prairie, densities of grasshoppers are 2–3 times higher in experimental units treated with grazing and annual fire (Evans 1988; Joern 2004), and carabid ground beetles reach peak abundance within 2–4 weeks of a spring fire (Cook and Holt 2006). Sandpipers probably forage in burned and grazed sites because of easier movement, greater food availability, and more efficient prey detection in open habitats. Selection of habitats with infrequent fire may be due to vegetative cover providing a cooler microclimate for incubation or concealment of the clutch from nest predators (Hovick et al. 2014; McNew et al. 2014).

Upland sandpipers selected grazed sites for both home ranges and nests at Konza Prairie. Past studies in the northern Great Plains reported that upland

sandpipers have higher nesting densities in ungrazed pastures (Ailes 1980; Bowen and Kruse 1993), and pastures rested in rotational grazing systems (Klemek 2008). However, stocking densities were $\sim 3\text{--}15\times$ higher in North Dakota (0.3–1.0 ha per head; Bowen and Kruse 1993) and may have resulted in less vegetative cover than grazing units at Konza Prairie (3.2–4.6 ha per animal unit; this study). Losses of nests to trampling by livestock were rare at both sites ($<3\%$). Upland sandpipers may prefer grazed sites at Konza because grazing removes dominant warm-season grasses and favors a more diverse plant community with greater vegetative structure (Towne et al. 2005). Grazing could facilitate higher nest survival in unburned plots if vegetative structure reduces search efficiency of nest predators.

The Flint Hills ecoregion is characterized by prairie habitats with topographic relief, and elevation varied by >300 m across Konza Prairie. Upland sandpipers proved to be aptly named because radio-marked birds selected higher elevations for home ranges and nests. Hilltops are also important as activity centers where birds roost, display, and pair with mates. Upland sandpipers have a mate-defense mating system and unmated males perch on fence posts to give distinctive ‘wolf-whistle’ calls during courtship displays (Casey et al. 2011; Houston et al. 2011). Upland areas of the Flint Hills also have short vegetation because soils are shallow, hold less moisture, and are less productive (Briggs et al. 2005; Frey et al. 2008). Grazing intensity was high at upland sites of Konza Prairie because cattle tanks and fences were on ridge tops, and because bison used hilltops for grazing lawns, wallowing, and windy conditions to avoid hot summer temperatures and biting insects. Thus, selection of upland sites by sandpipers was also consistent with the habitat characteristics of burned and grazed sites.

The last factor affecting space use was proximity to edge of experimental units. Selection coefficients indicated sandpipers selected areas near the boundaries of experimental units at Konza Prairie. Thus, upland sandpipers require heterogeneity at a landscape level but also selected local sites where habitat heterogeneity was maximized. Selection of edge habitats was unexpected because most grassland birds avoid settling or nesting in edge habitats (Renfrew et al. 2005; Ribic et al. 2009). Upland sandpipers are typically solitary nesters, but social interactions or kin selection may affect nest site selection because birds

sometimes nest in semi-colonial clusters of related females (Bowen and Kruse 1993; Casey et al. 2011). Predation risk could be higher if predators use edge habitats to locate nests (Phillips et al. 2004; Klug et al. 2010). Distance to edge did not affect the nest survival rates of upland sandpipers, and evidence for edge effects in other grassland birds is also equivocal (Benson et al. 2013). We did not have enough telemetry locations to calculate resource utilization functions separately for the brood-rearing period. Male sandpipers provide sole parental care during brood-rearing (Sandercock unpublished data), and nesting near edges could help males lead the young to nearby brood-rearing sites. Males attending broods often used burned or grazed areas during the latter part of the growing season once the herbaceous layer was established.

Habitat-specific demography

Nest site selection had a strong effect on nest survival of upland sandpipers at Konza Prairie. Years since burn had the greatest effect on daily nest survival and predicted rates of nest survival were 2–3 times higher in unburned sites than burned sites. Grazing treatments had little effect on nest survival, which was consistent with a lack of grazing effects in previous studies (Bowen and Kruse 1993; Klemek 2008). Relatively high daily nest survival in unburned sites and increases in daily survival with nest age suggest that vegetative structure plays a role in concealment of the clutch from nest predators. Grassland songbirds also have higher nest survival at unburned sites in tallgrass prairie (Shochat et al. 2005; Churchwell et al. 2008). Moreover, height of vegetation at the nest measured as a visual obstruction reading has a strong positive effect on daily nest survival of prairie chickens and grassland songbirds (Frey et al. 2008; McNew et al. 2014).

Experimental units managed with grazing and annual fires had the lowest rates of nest survival of any habitat strata. Our findings raise concerns for conservation because most native grasslands in the Flint Hills ecoregion are managed with intensive grazing and annual burning. With et al. (2008) calculated that 90 % of the total grassland area of the Flint Hills is rangelands managed for cattle production, with limited area in hayfields (7 %) or CRP cover ($<3\%$). Mohler and Goodin (2012) used satellite imagery to map burned areas in the Flint Hills

and found that up to 48 % of the total grassland area can be burned in a given year, and up to 75 % of grassland area in counties that are mainly prairie (>80 % grassland; Chase and Wabaunsee Co., Kansas). Moreover, about 27 % of the grassland area in the Flint Hills was burned every 1–2 years during the 11-year period from 2000 to 2010. Low nest survival among upland sandpipers in Kansas (0.18, this study) was comparable to birds in Saskatchewan (0.20, Garvey et al. 2013), but much lower than the apparent nest success of sandpipers breeding in the Dakotas (0.67; Kirsch and Higgins 1976; Kantrud and Higgins 1992; Bowen and Kruse 1993). Upland sandpiper populations could be buffered against poor nest survival because they lay replacement clutches, and annual survival is relatively high (~ 0.7 , Sandercock, unpublished data). Nevertheless, current rangeland management could be reducing population viability of upland sandpipers and other grassland birds in the Flint Hills ecoregion (With et al. 2008; McNew et al. 2012; this study).

Conclusions

Management for habitat heterogeneity can benefit avian communities if individual bird species have different habitat requirements for breeding (Fuhlendorf et al. 2006). Upland sandpipers have been viewed as a grassland specialist that are abundant in sites disturbed by heavy grazing or fire (Powell 2006). Tracking birds with telemetry revealed that habitat requirements also include undisturbed sites with vegetative cover for nesting, where nest survival is higher. Our results could be a general feature of precocial birds if habitats with different vegetative structure are selected during foraging for egg-laying, concealment of ground nests, and brood-rearing of mobile young (Anteau et al. 2012; Beatty et al. 2014; Lande et al. 2014; McNew et al. 2014). Thus, landscape heterogeneity helps to maintain species richness, but may also be beneficial for individual species where habitat requirements vary seasonally among different life-stages.

Restoration of habitat heterogeneity to agroecosystems remains a major challenge for wildlife conservation (Johnson et al. 2011). In the Great Plains, extant grasslands are confined to states with little public land and changes to rangeland management must remain

profitable for private landowners. One approach for restoring heterogeneity is patch-burn grazing, where rotational fire and grazing are used to create habitat patches that vary in grazing utilization and vegetative structure (Fuhlendorf and Engle 2004). Patch-burn grazing can improve nest survival (Churchwell et al. 2008; Hovick et al. 2012), and increase vertebrate diversity in temperate grasslands (Fuhlendorf et al. 2006, 2010; Coppedge et al. 2008). To improve conservation strategies for grassland ecosystems, landscape ecologists still need to investigate the scale of patch sizes needed for habitat manipulations, the timing of grazing and prescribed fires that maximize habitat heterogeneity, and the optimal landscape configuration for patches that differ in habitat structure. Multi-scale experimental studies are rare in ecological studies of landscape heterogeneity, but could be used to develop conservation plans for communities of species that vary in space use, resource requirements, and dispersal ability (Debinski and Holt 2000; Sandel and Smith 2009).

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