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PROFILE

Long-Term Community Dynamics of Small Landbirds with and Without Exposure to Extensive Disturbance from Military Training Activities

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Abstract Military training activities are known to impact individual species, yet our understanding of how such activities influence animal communities is limited. In this study, we used long-term data in a case study approach to examine the extent to which the local small landbird community differed between a site in northeast Kansas that experienced intensive disturbance from military training activities (Ft. Riley Military Installation) and a similar, nearby site that experienced minimal human disturbance (Konza Prairie Biological Station). In addition, we characterized how the regional pool of potential colonizers influenced local community dynamics using Breeding Bird Survey data. From 1991 to 2001, most species of small terrestrial landbirds (73%) recorded during breeding surveys were found at both sites and the mean annual richness at Ft. Riley (39.0 ± 2.86 [SD]) was very similar to that of Konza Prairie (39.4 ± 2.01). Richness was maintained at relatively constant levels despite compositional changes because colonizations compensated local extinctions at both sites. These dynamics were driven primarily by woodland species that exhibited stochastic losses and gains and were present at a low local and regional abundance. Our results suggest that military training activities may mimic natural disturbances for some species in this area because the small landbird community did not differ markedly between sites with and sites without extensive human disturbance. Although our results suggest that military training is not associated with large changes in the avian community, additional studies are needed to determine if this pattern is found in other ecological communities.

Keywords Anthropogenic disturbance · Community dynamics · Grassland birds · Military training · Songbird conservation

Military installations play an important role in providing critical habitat for many native species (Cohn 1996). The Department of Defense serves as one of the largest land stewards in the United States, overseeing installations that cover >10^6 ha (Cohn 1996) and span a range of biomes and their component species. In recent years, there has been greater recognition of the potential of military installations to provide conservation opportunities for native species, including those that are classified as threatened or endangered (Smith and others 2002; Althoff and others 2005; Warren and others 2007). As the breadth of work to understand the influence of military training on organisms that inhabit military lands has increased, so too has recognition of military installations as areas that provide critical habitat for animal populations. Studies of ecological effects of military training initially focused on understanding how soil processes and vegetation were influenced by military training (Ayers 1994; Wilson 1988; Grantham and others

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2001) but has since expanded to assessing the influence of troop training on wildlife (Delaney and others 1999; Smith and others 2002; Leis and others 2008; Warren and Büttner 2008a, b). This body of work has provided a better understanding of how training can influence native organisms while simultaneously allowing military planners to maintain the training mission objectives of the U.S. military.

The majority of research on military training impacts on native animals has focused on threatened and endangered species that reside on military installations. Less frequent are studies that focus on how entire biological communities are influenced by training, particularly for vertebrates (Severinghaus and Severinghaus 1982; Schaeffer and others 1990; Schueck and others 2001; Graham and others 2008; Leis and others 2008). Importantly, the few studies of vertebrate communities that have been conducted are limited in several ways: most have been of short duration (i.e., <5 years), lacked one or more reference sites that experienced minimal anthropogenic disturbance, or failed to take into account regional processes that could influence local community dynamics (Severinghaus and Severinghaus 1982; Schaeffer and others 1990; Schueck and others 2001; Leis and others 2008). Because of this, additional studies are needed that (1) collect data over longer time scales to quantify temporal variability within communities, (2) use reference sites located outside of military installations to provide better resolution of the influence of training activities, and (3) assess how regional species pools contribute to local population structure via colonization and extinction events (Cornell 1999; Loreau and Mouquet 1999; Collins and others 2002; Turner and others 2003). Studies that simultaneously address all of these factors offer the best opportunity for quantifying how ecological communities may be influenced by military training activities.

In this study, we adopt a case study approach to explore long-term dynamics of the small landbird community at two study areas that lie at opposite ends of the disturbance spectrum. One study area is an active military training installation that experiences extensive disturbance via military training activities; in marked contrast, the other site serves as a prairie preserve that experiences minimal human disturbance. Our research was conducted at the landscape scale and, although it lacks spatial replication, the approach we take provides several important benefits. First, both study sites are dominated by tallgrass prairie and are located in close proximity to each other (i.e., 10 km at their closest point), providing a rare opportunity to standardize factors that pertain to ecosystem type and spatial location. Moreover, having study sites located in close proximity is particularly important for minimizing variation in regional processes that are known to influence local community dynamics (Brown and others 2001). In addition to these factors, our work provides valuable information regarding the extent to which military training influences a highly threatened ecosystem, as the tallgrass prairie that dominates both study sites and is considered one of the most endangered biomes in the United States (Knapp and others 1999). This is particularly true for the grassland birds that dominate both study areas, as these species have experienced consistent, long-term population declines for the past several decades (Peterjohn and Sauer 1999; Vickery and others 1999). Taken it its entirety, our study offers insights into how small landbird communities change over time relative to disparate levels in anthropogenic disturbance and provides an important step toward understanding how such factors can influence small landbird communities over the long term. Furthermore, our data allow for examining how species richness may be maintained in light of military training activities and for exploring the extent to which military training activities are compatible with the conservation of native biodiversity in the tallgrass prairie ecosystem.

Methods

Study Areas

Fieldwork was conducted at two study sites: Konza Prairie Biological Station (Konza Prairie; 39°05′N, 96°35′W) and Ft. Riley Military Installation (Ft. Riley; 39°10’N, 96°48’W). Both study sites are located in the Flint Hills region of northeastern Kansas (Fig. 1), an area within the tallgrass prairie biome whose climate is characterized by hot summers and cold, dry winters. Mean monthly temperatures in this area range from –2.7°C in January to 26.6°C in July, and mean annual precipitation is 83.5 cm, with the majority occurring during the growing season (Hayden 1998). Konza Prairie is a 3487-ha tallgrass prairie preserve dedicated to long-term ecological research (Knapp and Seastedt 1998). The site is divided into 60 watershed units, with different fire (frequency and timing) and grazing (ungrazed, bison, cattle) treatments applied to each watershed since 1972 (fire) and 1992 (bison) in a manner to reflect the natural disturbance events of tallgrass prairie (Knapp and others 1999; Briggs and others 2005). Ft. Riley Military, a 40,273-ha U.S. Army training area, is located northwest of Konza Prairie and ca. 10 km at its nearest point. Although Ft. Riley was established in 1853, it did not reach its full size until 1966 (McKale and Young 2000). At Ft. Riley, prescribed fire for reducing woody encroachment and wildfires resulting from year-round training activities take place but are not applied in a systematic manner. Comprehensive burn records are not available for the area surveyed on Ft. Riley; however, the combination of prescribed burning and wildfires is thought to cover approximately one-third of the site annually (P. B. Woodford, personal communication). This along with haying, but not grazing, results in a mosaic of habitats similar to that on Konza Prairie. Grasslands are the predominant habitat at both sites (i.e., 80–90% of the available habitat), with shrubland and woodlands comprising the remainder. Importantly, plant community data from Ft. Riley and Konza Prairie indicate that the relative proportion of habitats was similar at both sites over the years of this study (Briggs and others 2005; Althoff and others 2006).

At both Ft. Riley and Konza Prairie, grasslands that are burned every 1–6 years are dominated by big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*), with other grasses, forbs and woody species occurring at lower abundances (Knapp and others 1999; Althoff and others 2006). Grasslands burned every 7–20 years are also dominated by C_4 grasses but are interspersed with large stands of buckbrush (*Symphoricarpos orbiculatas*), wild plum (*Prunus americana*), and rough-leaved dogwood (*Cornus drummondii)*, with more woody plants as the mean fire interval increases (Heisler and others 2003). Woodlands typically occur along mesic lowlands and are characterized by chinquapin oak (*Quercus muhlenbergii*), bur oak (*Q. macrocarpa*), American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), and black walnut (*Juglans nigra*).

On Konza Prairie, disturbances are currently limited to the natural disturbances thought to structure this ecosystem historically (i.e., fire and grazing [Knapp and others 1999]), with minimal anthropogenic disturbance caused by scientific research and public activities, with the latter limited to a hiking trail located away from watersheds on which long-term data are collected. In contrast, anthropogenic disturbances at Ft. Riley are frequent and are not restricted to any particular habitat, although most occur in grasslands. Military training activities are conducted year-round and comprise maneuvers that use both infantry and heavy tracked and wheeled vehicles (e.g., tanks, armored personnel carriers) in areas largely outside of woodland habitats. The number of soldier training days, measured as 1 soldier training in the field on the installation for 1 day, varies annually and averaged approximately 1.6 million soldier training days during the current study (range: 644,000–3,415,000 per year). In addition to military activities, small-scale commercial timber harvest and other silvicultural operations also take place in woodland habitats, and most of Ft. Riley is open to public use year-round for fishing, hunting, and other forms of recreation.

As noted above, this study focuses on two study sites where the small landbird communities experience two distinct levels of anthropogenic disturbance and, therefore, lacks spatial replication. However, restricting our examination to these two sites has several advantages: both study sites are located close to one another, are dominated by tallgrass prairie, share a common regional species pool, exist at opposite ends of the spectrum of anthropogenic disturbance, encompass a long-term period over which data were collected, and are conducted in a threatened biome so that results have important management implications. Moreover, there is no a priori reason that the lack of interspersion between the two sites would be a stronger factor than the marked differences to which the two sites are impacted by military training activities. Nevertheless, because of the lack of spatial replication we limit our analysis to descriptive statistics that compare community structure between the two sites to investigate site, not treatment, differences as a first step toward understanding the extent to which military training influences small landbird communities.

Field Methods

Annual bird surveys were conducted during the summer breeding season (May–June) in each year from 1991 to 2001. At Konza Prairie, the variable distance transect method was used (Zimmerman 1993), an approach where an observer records all birds detected along a sampling transect and estimates their perpendicular distance from the transect (Burnham and others 1980). Fifteen transects ranging from 343 to 1490 m were established in grazed and ungrazed watersheds that are subject to burning at 1, 4, and 20 y intervals (for details see Zimmerman 1993). A single observer conducted surveys at Konza Prairie during the 11-year period, recording each bird seen or heard on either side of the focal transect and estimating its perpendicular distance from the transect. As the overwhelming majority (i.e., >99.5%) of birds were observed within 100 m of each transect, observations of individuals located > 100 m away were not included in our analysis (see below). All surveys were conducted during morning hours with low-wind conditions and no steady rain. At Ft. Riley, a similar technique was used to conduct bird surveys on 60 permanent sampling plots (100 × 200 m) where observers used the limited-distance (i.e., 100-m) strip transect method (Verner 1985). Ft. Riley plots were selected using a stratified random sampling design where plots were stratified by land cover and soil types (based on 1989 satellite images), and the numbers of plots selected were proportional to the areas they represented (Diersing and others 1992). Transects were established in habitats similar to those on Konza Prairie. Four surveyors conducted surveys at Ft. Riley during the 11-year period during morning hours and under similar conditions as the Konza Prairie surveys. During 1991–1998, a single observer walked a 100-m transect at a constant pace for 6 min and recorded all birds detected within a 100-m radius of his current position. During 1999–2001 surveys, a single observer walked along the same 100-m transect at a constant pace for 6 min and recorded all birds detected within an area bounded at 100 m perpendicular to the transect (for details see Althoff and others 2005). Although the areas surveyed by these two techniques differed slightly, they provide similar results because our analyses only considered whether species were present or absent (Bart and Klosiewski 1989; Althoff and others 2005).

To facilitate comparisons between data sets, all landbirds observed at a perpendicular distance >100 m from transects at Konza Prairie were excluded from analyses, making the transect widths fixed at 200 m at both sites. This excluded 35 observations of 14 species (<0.5% of all observations) at Konza Prairie, which led to no species being removed from analyses. Although all bird species detected were recorded during surveys, we restricted our analyses to small terrestrial landbirds (i.e., species <200 g in the orders Cuculiformes, Piciformes, and Passeriformes [excluding swallows]) because these species are best surveyed by these sampling techniques.

Because of differences in sampling programs, the amount of area surveyed differed between locations. The mean length of transects surveyed on Konza Prairie during 1991–2001 was 12,222 m (SE = 123.5 m), whereas the mean length of transects surveyed at Ft. Riley during the same period was 5982 m (SE = 12.2 m). Given these differences in sampling approaches, two options were available for attempting to mitigate differences in area sampled. First, it might have been possible to subsample the Konza Prairie data set in a way that equalizes the area sampled at the two study sites. However, this was not feasible because the perpendicular distance from the transect line was recorded for each bird observed, but not the location of each bird along the length of each transect. An alternative approach would be to use accumulation curves to estimate the asymptote between the area sampled and the number of additional species encountered to evaluate whether additional sampling at Konza Prairie led to a markedly higher estimate of bird richness at that site. Therefore, we constructed annual accumulation curves to estimate the asymptote between the areas sampled and the numbers of new species encountered. Visual examination of accumulation curves indicated that few additional species were encountered on Konza Prairie after ~6500 m of transects was surveyed (Rivers and others, unpublished data). Moreover, an examination of the number of new species encountered at Konza Prairie after the first ~6500 m of transects indicated that the additional survey effort at Konza Prairie typically added an average of only two new species per year (range, zero to seven). Taken together, these results suggest that the large differences in the amount of survey effort between sites had, at most, a limited influence on estimates of species richness, allowing us to use all available data from Konza Prairie in the comparison with Ft. Riley.

Regional Species Pool

We used North American Breeding Bird Survey (BBS) data (www.mbr-pwrc.usgs.gov/bbs/) to quantify the regional species pool of potential colonists at Konza Prairie and Ft. Riley during the 1991–2001 breeding seasons. To do so, we first constructed a 325-km-radius circle centered on a point equidistant between Konza Prairie and Ft. Riley that encompassed 92 BBS survey routes in Kansas, Nebraska, Iowa, Missouri, and Oklahoma (Fig. 1). We chose this distance because it represents, on a landscape scale, the diversity of habitats found on the two study sites and therefore the potential pool of colonizing individuals. In addition, we also chose this distance because it allowed us to examine a large sample of BBS routes (i.e., 54–77) in each year of the study. BBS data were used to create an index for assessing the likelihood that core or noncore species in the regional pool were able to colonize each of the study sites.

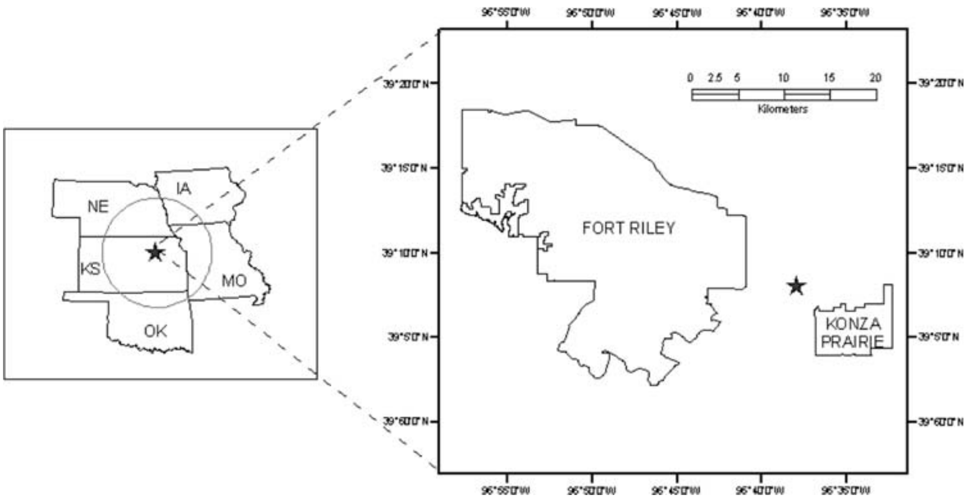

Fig. 1 Location of Fort Riley Military Installation and Konza Prairie Biological Station in northeastern Kansas, and location of the central point (*star*) and circle (325-km radius) used to determine the regional species pool for the study sites (see text for details)

To construct this index, we first determined the proportion of BBS survey routes on which each species was recorded in each year. Next, we calculated, for each study site, the mean proportion of routes on which core species were found, and the mean proportion of routes on which noncore species were found. Finally, we calculated the average proportion of routes on which core and noncore species were found over the 11-year study period to provide an index of their long-term relative abundance in the regional specie pool.

Data Analyses

The composition and dynamics of landbird communities were assessed at the site level and therefore across all habitat types found at Ft. Riley or Konza Prairie to examine if there was a change in landbird communities associated with military training activities. Because perpendicular-distance data were not recorded during surveys at Ft. Riley, we were unable to estimate detection probabilities and instead used raw values to estimate abundance at both sites for consistency. The relative abundance of each species for a given year was calculated as the number of observations of a particular species across all transects divided by the total number of observations of all species for a survey year. For estimates of richness, we summed the total number of species observed across all surveyed transects for each year separately for Ft. Riley and Konza Prairie. Jaccard's similarity index was used to assess (qualitative) similarity in compositions between the two sites (Magurran 1988).

Temporal changes in the bird communities at Ft. Riley and Konza Prairie were characterized by (1) measuring constancy in richness and the turnover of species in time and (2) evaluating whether compositional changes occurred over time following the general approach of Brown and others (2001). To evaluate constancy in richness, we measured colonization events by counting the number of times a species was not recorded at a site in year i but was recorded in year $i + 1$. We measured local extinction events by counting the number of times a species was recorded on a site in year i but was not observed in year $i + 1$. Turnover was calculated as the sum of colonizations and extinctions per year. We also computed the changes in richness that would have occurred in the absence of colonizations or extinctions. Following Brown and others (2001) cumulative colonizations were calculated by summing the total number of initial colonization events for each species over all years, whereas cumulative extinctions were calculated as the sum of all initial extinction events for each species over all years. Thus, only a single colonization or extinction was allowed for each species. The end of the cumulative colonization curve should provide an estimate of the time-averaged richness of the regional species pool (Brown and others 2001). In contrast, where the cumulative extinction curve ends provides an estimate of the number of species that might have been lost in an isolated or closed system (Brown and others 2001).

To evaluate whether change in community composition had occurred over the 11-year study period, we used time lag analysis (Collins 2000; Collins and others 2000). A Euclidean distance (ED) resemblance matrix for each site was calculated based on relative abundances of each bird species (for details see Collins and others 2000). ED values at each time lag (10 1-year to 1 10-year) were plotted against the square root of the time lag (independent variable). Linear regression analyses were used to evaluate if directional change occurred over time at the site level, as well as within different functional groups, based on habitat affiliation (i.e., grassland, shrubland, and woodland). The regression coefficient is a measure of signal versus noise in community change (Collins and others 2000). If the regression coefficient is small but significant, then stochastic variation is high and directional change slow, whereas a large, significant value indicates a stronger signal of directional change. The slope of the regression line indicates the rate and direction of change (Collins and others 2000): (1) if the slope of the regression line is significantly different from 0, positive, and linear, this suggests that the composition is unstable over time and undergoing directional change; (2) if the slope of the regression line is significantly different from zero but negative and linear, then the community is unstable but converging on a community characteristic similar to one of the earlier sample periods; or (3) if the slope of the regression line is not significantly different from zero, this implies that directional change is not occurring over time but the community may still be experiencing fluctuation or stochastic variation. In addition, we examined species-abundance distributions for the sites over time to evaluate whether there were qualitative changes in the distributions of abundances. Finally, we used Kendall's coefficient of concordance to detect whether ranks of individual species shifted markedly over time (Legendre and Legendre 1998).

Results

The total richness of small landbirds recorded was similar at Ft. Riley (52 species) and Konza Prairie (55 species) over the 11-year study period (Table 1). Mean annual richness also was very similar at Ft. Riley (39.0 ± 2.86 [SD]) and Konza Prairie (39.4 ± 2.01). Overall similarity was high between the two communities (Jaccard's similarity index = 73%), as 45 species were observed on both sites over the study period (Table 1). Moreover, the relative abundance of these shared species, averaged over 11 years, was highly correlated (Spearman's $r = 0.75$, $P < 0.001$; $n = 45$). Fifteen core species (i.e., a species present in each

Table 1 Small landbirds recorded at Konza Prairie Biological Station (KP) and Ft. Riley Military Installation (FR) during annual breeding surveys from 1991 to 2001

Habitat/species	KP rank[a]	FR rank[a]	KP mean RA[b] (SE)	FR mean RA[b] (SE)	KP years[c]	FR years[c]	KP gain[d]	FR gain[d]	KP loss[e]	FR loss[e]
Grassland										
Dickcissel	1	2	0.182 (0.012)	0.185 (0.015)	11	11	0	0	0	0
Brown-headed cowbird	2	1	0.175 (0.011)	0.190 (0.009)	11	11	0	0	0	0
Eastern meadowlark	3	4	0.101 (0.008)	0.087 (0.009)	11	11	0	0	0	0
Grasshopper sparrow	5	3	0.047 (0.006)	0.117 (0.011)	11	11	0	0	0	0
Common yellowthroat	9	13	0.025 (0.002)	0.018 (0.002)	11	10	0	1	0	0
Red-winged blackbird	10	7	0.024 (0.002)	0.027 (0.003)	11	11	0	0	0	0
Eastern kingbird	12	6	0.021 (0.005)	0.028 (0.003)	10	11	1	0	1	0
Henslow's sparrow	21	5	0.012 (0.003)	0.030 (0.009)	11	10	0	1	0	1
Lark sparrow	38	40	0.002 (0.001)	0.002 (0.001)	7	5	2	2	2	3
Loggerhead shrike	47	47	0.000 (0.000)	0.001 (0.001)	1	3	0	1	1	2
Western kingbird	51	37	0.000 (0.000)	0.003 (0.001)	1	8	1	3	1	3
Marsh wren	52	–	0.000 (0.000)	–	1	–	1	–	1	–
Scissor-tailed flycatcher	–	51	–	0.000 (0.000)	–	1	–	1	–	0
Shrubland										
Field sparrow	4	16	0.049 (0.004)	0.017 (0.002)	11	11	0	0	0	0
Brown thrasher	6	9	0.041 (0.004)	0.022 (0.004)	11	11	0	0	0	0
Bell's vireo	7	20	0.034 (0.004)	0.011 (0.002)	11	11	0	0	0	0
Northern cardinal	11	8	0.022 (0.002)	0.023 (0.003)	11	11	0	0	0	0
American goldfinch	16	17	0.015 (0.001)	0.016 (0.002)	11	11	0	0	0	0
Gray catbird	19	12	0.013 (0.003)	0.018 (0.002)	11	11	0	0	0	0
Blue grosbeak	35	–	0.004 (0.001)	–	6	–	1	–	2	–
Yellow-breasted chat	50	–	0.000 (0.000)	–	1	–	1	–	1	–
Northern mockingbird	55	–	0.000 (0.000)	–	1	–	1	–	1	–
Woodland										
Great-crested flycatcher	8	28	0.026 (0.003)	0.005 (0.002)	11	7	0	2	0	2
Eastern wood-pewee	13	43	0.020 (0.003)	0.002 (0.001)	11	2	0	1	0	0
Blue jay	14	15	0.018 (0.002)	0.017 (0.005)	11	11	0	0	0	0
Tufted titmouse	15	21	0.017 (0.002)	0.010 (0.001)	11	11	0	0	0	0
Yellow-billed cuckoo	17	18	0.015 (0.002)	0.013 (0.003)	11	11	0	0	0	0
Eastern towhee	18	23	0.014 (0.003)	0.008 (0.001)	11	10	0	1	0	1
White-breasted nuthatch	20	29	0.013 (0.001)	0.005 (0.001)	11	10	0	1	0	1
Black-capped chickadee	22	14	0.011 (0.002)	0.017 (0.002)	11	11	0	0	0	0
Red-bellied woodpecker	23	24	0.011 (0.001)	0.008 (0.003)	11	8	0	3	0	3
Indigo bunting	24	19	0.010 (0.003)	0.012 (0.002)	10	10	1	1	1	1
House wren	25	11	0.007 (0.001)	0.020 (0.002)	11	11	0	0	0	0
Blue-gray gnatcatcher	26	38	0.007 (0.001)	0.002 (0.001)	10	7	1	4	1	4
Baltimore oriole	27	22	0.007 (0.002)	0.008 (0.002)	9	11	2	0	2	0
Eastern bluebird	28	31	0.006 (0.001)	0.004 (0.001)	10	6	0	2	1	2
Bewick's wren	29	–	0.006 (0.001)	–	10	–	1	–	1	–
Carolina wren	30	32	0.006 (0.002)	0.004 (0.001)	10	8	1	2	0	1
Red-eyed vireo	31	27	0.005 (0.001)	0.006 (0.001)	9	10	1	1	1	1
Summer tanager	32	–	0.005 (0.001)	–	10	–	1	–	1	–
Northern flicker	33	33	0.004 (0.001)	0.004 (0.002)	7	7	2	3	2	3
Louisiana waterthrush	34	–	0.004 (0.001)	–	10	–	1	–	0	–
Downy woodpecker	36	41	0.004 (0.001)	0.002 (0.001)	8	6	1	1	1	2
Kentucky warbler	37	36	0.003 (0.001)	0.003 (0.001)	9	9	2	2	1	1

Table 1 continued

Habitat/species	KP rank[a]	FR rank[a]	KP mean RA[b] (SE)	FR mean RA[b] (SE)	KP years[c]	FR years[c]	KP gain[d]	FR gain[d]	KP loss[e]	FR loss[e]
Red-headed woodpecker	39	39	0.002 (0.001)	0.002 (0.001)	5	6	3	2	2	2
Orchard oriole	40	30	0.002 (0.001)	0.004 (0.001)	5	9	1	2	2	2
American robin	41	34	0.002 (0.001)	0.003 (0.001)	6	8	0	1	1	2
Yellow warbler	42	25	0.002 (0.001)	0.006 (0.001)	4	10	3	1	2	1
Hairy woodpecker	43	35	0.001 (0.000)	0.003 (0.001)	6	9	2	2	2	2
Black-and-white warbler	44	46	0.001 (0.000)	0.001 (0.000)	5	7	4	2	3	2
Common grackle	45	10	0.001 (0.001)	0.022 (0.005)	2	11	1	0	1	0
Northern parula	46	45	0.001 (0.000)	0.001 (0.001)	3	5	1	2	0	2
Acadian flycatcher	48	–	0.000 (0.000)	–	1	–	1	–	0	–
Wood thrush	49	–	0.000 (0.000)	–	1	–	1	–	1	–
Black-billed cuckoo	53	–	0.000 (0.000)	–	1	–	0	–	1	–
Rose-breasted grosbeak	54	44	0.000 (0.000)	0.002 (0.001)	1	5	1	3	1	4
European starling	–	26	–	0.006 (0.002)	–	9	–	1	–	2
Warbling vireo	–	42	–	0.002 (0.001)	–	6	–	4	–	3
Willow flycatcher	–	49	–	0.001 (0.000)	–	3	–	1	–	2
Eastern phoebe	–	48	–	0.001 (0.000)	–	3	–	3	–	2
American redstart	–	50	–	0.000 (0.000)	–	2	–	2	–	2
Worm-eating warbler	–	52	–	0.000 (0.000)	–	1	–	1	–	0

Note: Species were assigned to one of three functional groupings (grassland, shrubland, or woodland) based on Zimmerman (1993). See Appendix for AOU (1998) classification of species

[a] Relative abundance rank

[b] Mean relative abundance from 1991 to 2001

[c] Number of years recorded

[d] Number of years of gain (i.e., number of years a species was recorded in year $i + 1$ but was not recorded in year i)

[e] Number of years of loss (i.e., number of years a species was recorded in year i but was not recorded in time $i + 1$)

year of the study) were shared between the study sites (Table 1). Of these, the dickcissel and brown-headed cowbird (see Appendix for scientific names of species recorded on surveys) had the highest mean annual abundance at both sites. Species that were recorded at only one site were typically of low abundance and the mean ranks of these groups were similar at both sites (relative abundance rank: Ft. Riley mean = 45.4, SD = 9.16, $n = 7$ species; Konza Prairie = 43.7, SD = 9.96, $n = 10$ species). Of the species that were observed at both sites, the majority (33/45) were ranked similarly (i.e., ranks at both sites were within 10 positions of one another; see Table 1).

Richness remained relatively constant over the study period at Ft. Riley and Konza Prairie, despite changes in species composition and differences in the extent of disturbance from military training activities (Fig. 2a, b). Deviations from initial and final richness were 0% and 2% for Ft. Riley and Konza Prairie, respectively. Richness appeared to be maintained over time due to frequent, but offsetting, colonization and extinction events (Fig. 2c, d). However, the patterns of these events differed considerably between the two sites. At Ft. Riley, there were two large colonization and two large extinction events that were disjunct in time, whereas at Konza Prairie, colonization and extinction events appeared to act in a compensatory way (i.e., occurred in adjacent years). Moreover, average turnover (sum of colonizations and extinctions, Fig. 2c, d) over time was higher at Ft. Riley (12.0 ± 3.4 [SD]) than at Konza Prairie (7.9 ± 2.0), and the cumulative extinction curves indicate that loss of species from the study sites would have been greater at Ft. Riley (~50%) than at Konza Prairie (~40%) in the absence of colonization events (Fig. 2a, b). At both sites, all of the colonization and extinction events were restricted to those species with a low relative abundance, with abundances of species declining precipitously with two or more colonizations or extinctions (Fig. 3).

Despite the relative constancy in richness over time, directional change in community composition was detected with time-lag regression analysis. At the site level, the regression between ED and the square root time lag was significant and positive for Konza Prairie (slope = 14.9, $r^2 = 0.22$, $P < 0.001$), indicating directional change in the community. The regression coefficient was fairly small, however, indicating that change is occurring slowly with

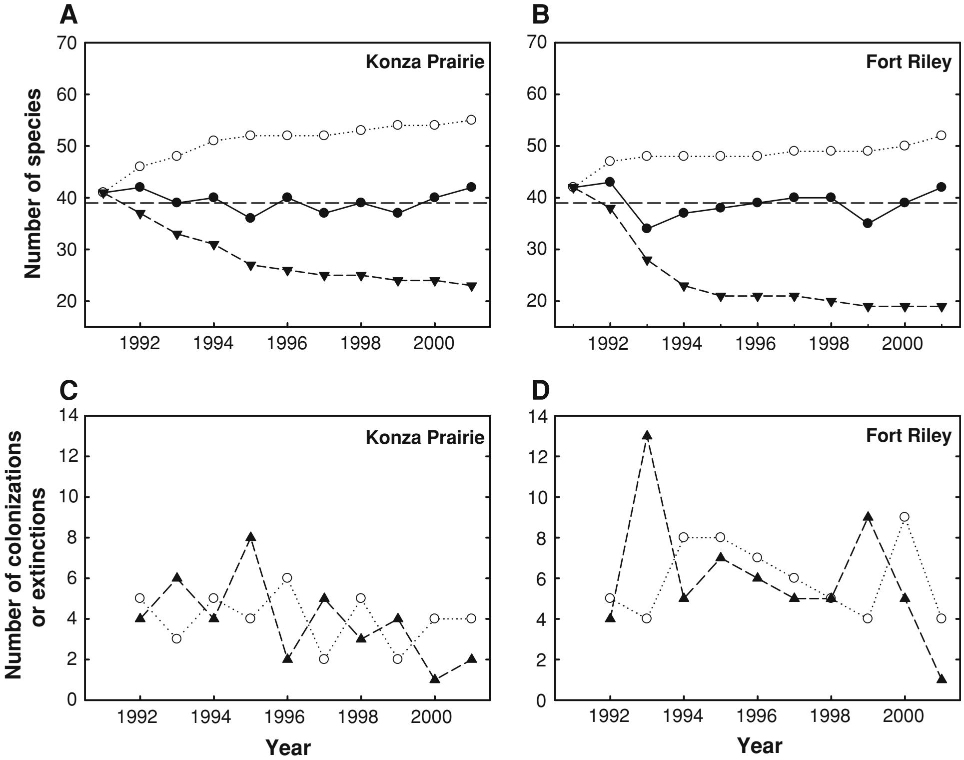

Fig. 2 Long-term dynamics of small landbird richness at Konza Prairie and Ft. Riley. **a**, **b** Temporal variation in species richness (*filled circles*) in comparison to mean richness (*dashed line*), and cumulative initial colonizations (*open circles*) and extinctions (*filled triangles*) of new species over time. When constructing accumulation curves, only the first colonization or extinction event for each species was included, although some species colonized or went extinct multiple times (following Brown and others 2001). **c**, **d** Total number of extinction (*filled triangles*) and colonization events (*open circles*) over time

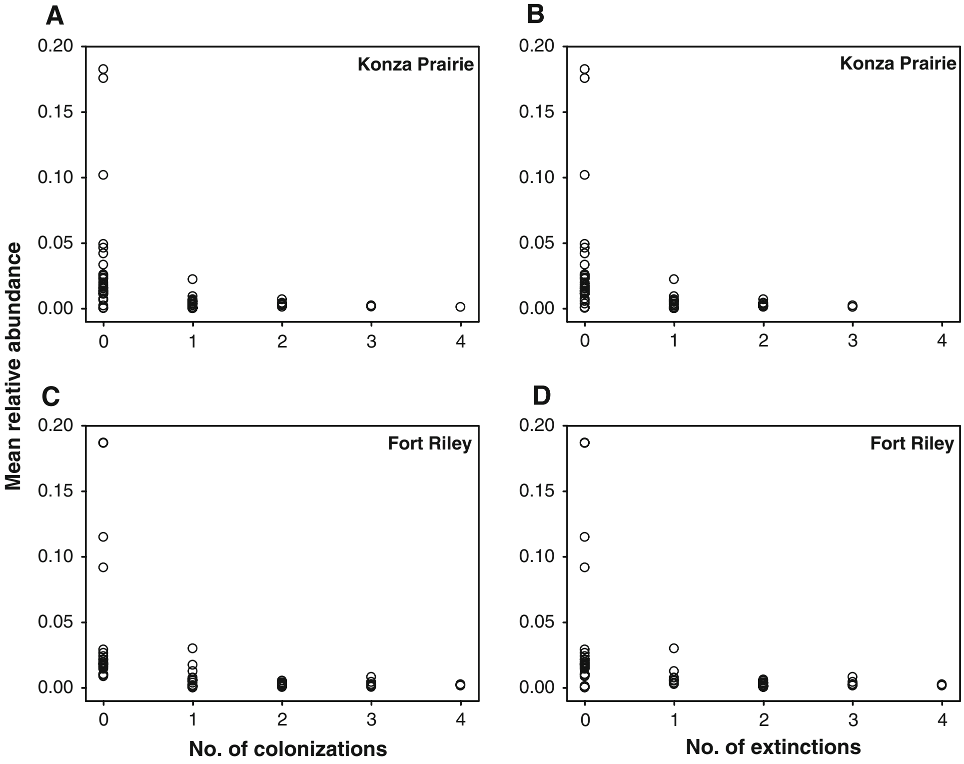

Fig. 3 Relative abundance (number of individuals of a given species divided by all individuals recorded, averaged over 11 years) of landbird species vs. their number of colonizations (*left*) or extinctions (*right*) at Konza Prairie (**a**, **b**) and Ft. Riley (**c**, **d**). Note that species experiencing more than two colonization events or more than two extinction events were consistently rare at both sites

considerable noise related to stochastic processes. Although the regression for Ft. Riley was not significant (slope = 9.9, $P > 0.05$), the relationship was also positive, suggesting directional change over time as well. When small landbird communities were examined according to habitat affiliation (grassland, shrubland, woodland), directional change was

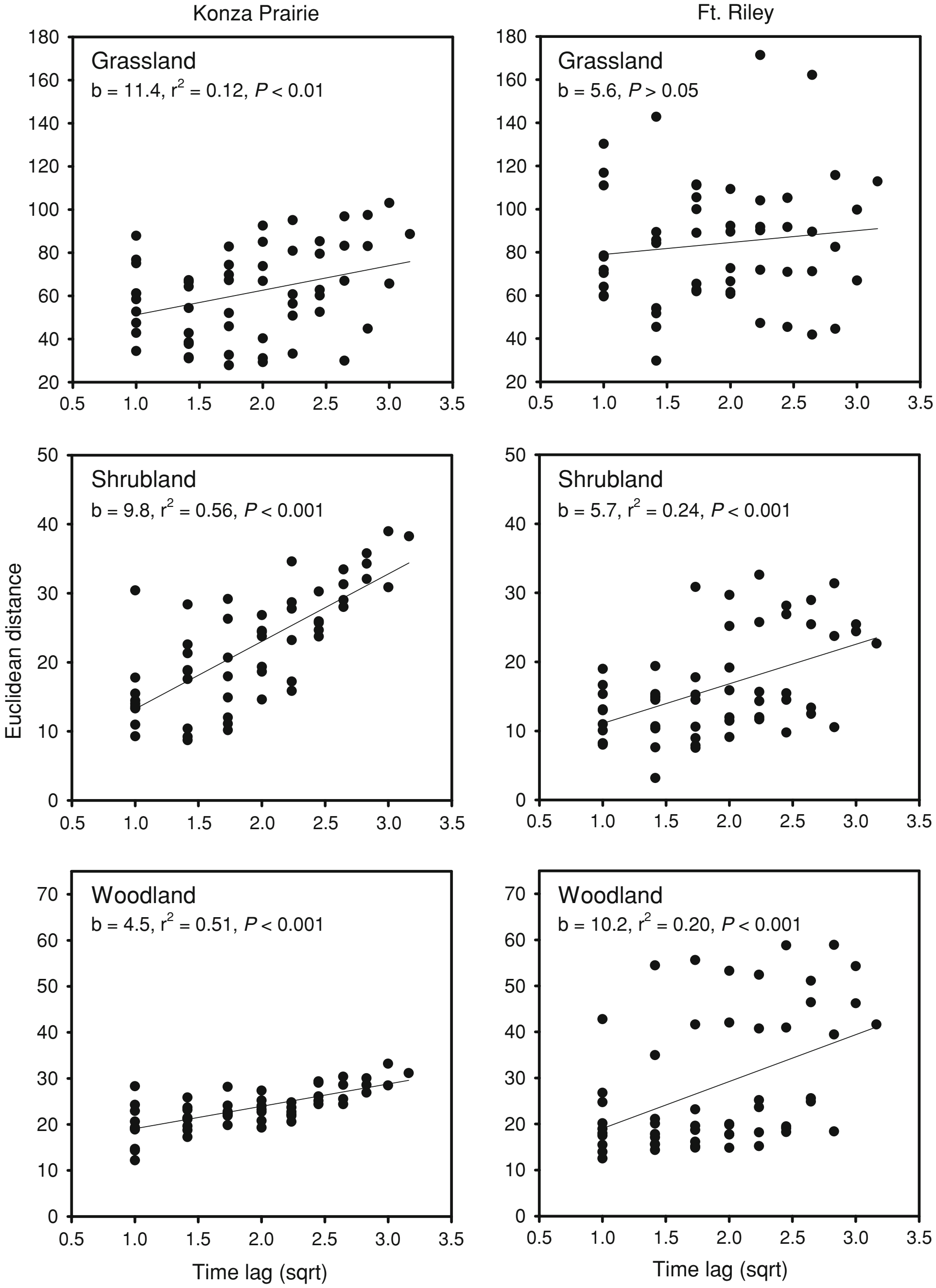

Fig. 4 Time lag regression analysis of compositional change in bird communities for three functional groupings (grassland, shrubland, and woodland) at Konza Prairie (*left*) and Ft. Riley (*right*)

detected for both sites for all habitat groups, except the grassland group at Ft. Riley (Fig. 4). The strongest and most rapid changes occurred for those species affiliated with shrublands and woodlands, whereas changes in composition for the grassland sites appeared to be driven by stochastic processes. Qualitative examination of the rank abundance curves for Ft. Riley and Konza Prairie at the site level indicated that the shape of these curves did not change over time (Fig. 5), but major changes in the rankings due to shifts in abundance, as well as loss or gain of species, did occur (Kendall's $W = 0.76$ for Ft. Riley and 0.85 for Konza Prairie) (Fig. 5, inset). The most dominant species rarely changed appreciably in rank; rather, most of these changes occurred among subdominant and rare species in the community.

For the regional species pool, mean richness of small landbirds ranged from 80 to 88 species per year (Table 2). The proportion of the regional species pool present at Ft. Riley (40–51%) and Konza Prairie (42–51%) was similar in each year. When considered from a regional perspective, species fell into two groups: core species, which were observed on most BBS routes and occurred at short minimum dispersal distances; and rare species, which were regionally uncommon and were typically found on BBS

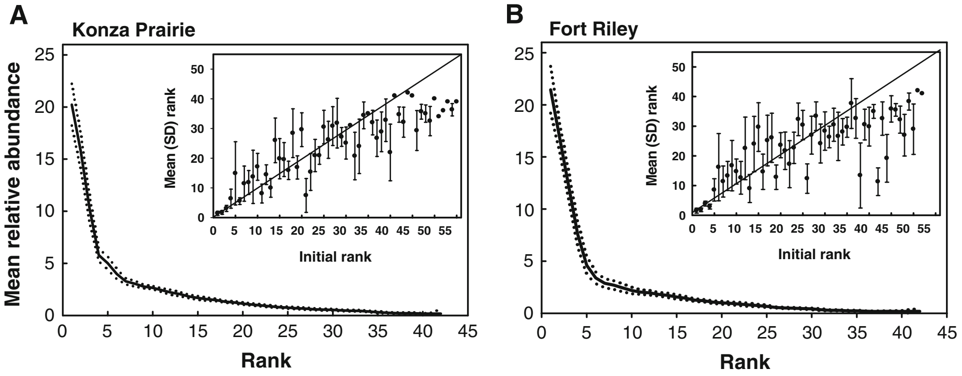

Fig. 5 Mean ranked species abundance distributions (*solid line*) and 95% confidence intervals (*dashed lines*) of landbirds at **a** Konza Prairie and **b** Ft. Riley, illustrating qualitatively similar distributions over the survey period (1991–2001). *Inset*: 11-year mean (SD) of each species rank based on its initial rank

Table 2 Regional species pool dynamics of core (i.e., those recorded in each of 11 years) and noncore species at Konza Prairie Biological Station and Ft. Riley Military Installation

Year	n^{a}	Richness[b]	Konza Prairie $\mathrm{RA}^{\mathrm{c}}_{\mathrm{mean}}$		Ft. Riley $\mathrm{RA}^{\mathrm{c}}_{\mathrm{mean}}$	
			Core	Noncore	Core	Noncore
1991	58	84	0.66	0.47	0.78	0.43
1992	63	86	0.65	0.46	0.78	0.42
1993	64	84	0.64	0.45	0.76	0.41
1994	66	85	0.65	0.44	0.78	0.40
1995	60	83	0.65	0.44	0.76	0.41
1996	61	87	0.64	0.42	0.77	0.38
1997	59	88	0.67	0.44	0.79	0.41
1998	56	80	0.67	0.47	0.77	0.44
1999	54	81	0.69	0.47	0.79	0.44
2000	77	85	0.70	0.47	0.81	0.45
2001	69	82	0.69	0.45	0.80	0.42
Mean (SE)	62.5 (2.0)	84.1 (0.7)	0.66 (0.006)	0.45 (0.005)	0.78 (0.005)	0.42 (0.006)

[a] Number of BBS routes surveyed (of 92 possible routes) within a 325-km radius of a point central point to Konza Prairie and Ft. Riley

[b] Total richness of small terrestrial landbirds (<200 g) in the orders Cuculiformes, Piciformes, and Passeriformes (excluding swallows) that were recorded on all BBS survey routes

[c] The average proportion of BBS survey routes on which core or noncore species was recorded. This value was calculated by taking the proportion of BBS routes on which each species was recorded and then averaging the proportion of routes separately for all species in each of the core and noncore designations

routes >50 km from Ft. Riley and Konza Prairie when they were recorded. In general, those species present at both Ft. Riley and Konza Prairie in all years had higher regional relative abundances than noncore species (Table 2).

Discussion

Alternative Scenarios for the Maintenance of Species Richness at Ft. Riley in Light of Military Training Activities

We found that mean species richness was similar at both Ft. Riley and Konza Prairie over the 11-year period and contained a comparable community of small landbirds, despite clear differences in the extent of anthropogenic disturbances caused by military training activities. Although directional change in community composition was detected at both sites, richness remained constant over time, as did the relative proportion of habitats available to birds (Briggs and others 2005; Althoff and others 2006). The two sites did appear to differ in the patterns of extinction and colonization, with those at Ft. Riley larger and occurring in different, nonadjacent years. In contrast, colonization and extinction events were smaller and compensating at Konza Prairie, resulting in lower average turnovers of species. The cumulative numbers of extinction and colonization events were similar, as were the relative abundance ranks of most species, at the two sites. In addition, the regional species pool appeared to exert a similar influence at both sites.

Given that Ft. Riley and Konza Prairie lie at opposite ends of a continuum of anthropogenic disturbance, why are avian community dynamics similar despite widespread and frequent anthropogenic disturbance? One explanation for the similarity of small landbird communities between the two sites relates to the natural disturbances that historically structure tallgrass prairie communities and the spatial distribution of training. Many of the grassland and shrubland species present at the study sites require the natural disturbance of fire, which can originate during training activities, to maintain critical habitats and prevent succession to woody vegetation (Zimmerman 1993). Woodland birds responded differently at the study sites, as none of the species observed are known to require disturbance to maintain their habitat. As noted above, most military training occurs largely outside of woodland habitats because training at Ft. Riley is focused on the use of mechanized vehicles that takes place in grassland and shrubland areas. Thus, the combination of limited military disturbance in woodlands, coupled with stronger levels of military disturbance in grasslands and shrublands, appears to have led to similar long-term dynamics in the local landbird communities at both study sites.

An alternative explanation for the similarity in community dynamics between the sites is that military training activities negatively impact the small landbird communities but the landscape surrounding Ft. Riley provides source populations for recolonizing Ft. Riley. This appears possible because the core species at Ft. Riley are also regionally abundant species. To address this question, detailed data on reproductive success at both study sites and adjacent areas are needed. Available data, limited to a single species (the dickcissel), suggest that nest successes at Konza Prairie and Ft. Riley are generally similar (Rivers and others 2003; Jensen and Cully 2005). However, nest success data are lacking for other species which precludes a meaningful analysis of sink-source dynamics of the small landbird community at Ft. Riley. Given the lack of data on reproductive success and adult survival in areas of military activity and the possibility that Ft. Riley could be a sink population, this community-level analysis should be taken as the first step toward determining the extent to which military training activities may influence reproductive success, adult survival, and, ultimately, local population dynamics.

It should be noted that although richness was maintained at both study sites, compositional changes and shifts in abundance appeared to be more pronounced at Ft. Riley, the site that experienced disturbances caused by military training activities. This suggests that the primary impact of military training may not be on richness of species per se but, rather, on their abundances in the community. This has important implications for land managers concerned with assessing the impacts of human activities on natural communities. Often managers focus on richness as a gauge of the extent to which disturbance influence ecological communities. Yet, our work suggests not only that changes in the number of species should be assessed, but also whether substantial shifts in abundance or composition occur over time should be considered, because such shifts could have important implications for community structure and function over long timescales (see Althoff and others 2005).

Are Military Training Activities Compatible with Conserving Native Biodiversity in Tallgrass Prairie?

Disturbances caused by military training activities can lead to significant changes in soil and vegetation characteristics and may therefore have long-term consequences for organisms inhabiting military installations (e.g., Johnson 1982; Wilson 1988; Milchunas and others 2000; Prosser and others 2000; Foster and others 2006; Althoff and others 2007). Nevertheless, it is clear that military installations can provide critical habitat for numerous organisms, including many that are currently classified as threatened or endangered species (Warren and others 2007). How, then, are military training activities potentially compatible with conservation of biological diversity? Warren and others (2007) have argued that military training leads to spatially heterogeneous patterns of disturbance on the landscape because of the manner in which military training occurs. Specifically, training activities provide realistic training scenarios during which maneuvers are conducted in a manner consistent with military training doctrine (Herl and others 2005; Warren and Herl 2005). Because not all maneuver areas are optimal for military training activities, training is typically restricted to the most desirable locations (Herl and others 2005), which leads to spatially heterogeneous patterns of disturbance such that some areas experience heavy impacts of training while others are relatively free of disturbance. Spatially disproportionate training provides distinct patches of disturbance across an installation which, in turn, can provide habitat for species that differ markedly in the extent to which they require disturbance (Fuhlendorf and Engle 2001, 2004; Warren and others 2007).

As noted above, military disturbance at Ft. Riley occurs largely in grassland and shrubland habitats, with minimal influence in woodland areas, and ultimately leads to a small landbird community similar to that found at Konza Prairie. The similarity in bird communities suggests that military training activities may be compatible with the maintenance of the local landbird community at Ft. Riley, particularly for grassland birds that may benefit from some levels of disturbance from military training. As a group, grassland birds have experienced consistent long-term population declines in the United States and Canada, and these declines have been attributed largely to conversion of grassland habitats to row-crop agriculture (Askins 1993; Peterjohn and Sauer 1999; Vickery and others 1999). The tallgrass prairie in the

Flint Hills region of northeastern Kansas is exceptional in this regard because upland soils in this area are unsuitable for cultivation and only allow for ungulate grazing, which may simulate historical grazing by American bison (*Bos bison*, Knapp and others 1999). Research on grassland birds in this region has demonstrated that disturbances occurring at different spatial and temporal scales are necessary to provide a habitat mosaic for the diversity of grassland-dependent birds (Zimmerman 1993; Cully and Michaels 2000; Powell 2006) and the disturbance from military training may be able to generate such a habitat mosaic. For example, fires occurring in the spring at Ft. Riley that are caused by training activities and allowed to burn may simulate fire from lighting strikes, which historically limited woody encroachment into tallgrass prairie (Hoch and others 2002; Heisler and others 2003; Briggs and others 2005). Likewise, impacts from heavy tracked and wheeled vehicles might also simulate soil compaction and vegetation trampling from the large herds of bison that once roamed this region of North America (Warren and others 2007). Although spatially explicit data regarding the intensity of military training activities are not available for the period of this study, our observations in the field indicate that training impacts are not homogeneous and, instead, lead to a mosaic of habitats at Ft. Riley. It is important to note, however, that grassland birds may not be representative of other small-bodied organisms in their ability to rapidly respond to habitat disturbances, as birds are volant and able to colonize patches more easily than similar-sized organisms with a more limited dispersal capability. Therefore, additional research to understand how other vertebrate communities respond to military training is clearly warranted.

The long-term constancy of the small landbird community at the two sites was rather unexpected given the marked differences in the extent of anthropogenic disturbance caused by military training. However, once the role of natural disturbance is considered, it would appear that military training may provide disturbance that is needed by many component species in the grassland shrubland habitat while avoiding woodland habitats whose species do not require disturbance. Although training activities are unlikely to replace natural disturbances, it appears as though they promote disturbances that are beneficial to some native species. As concern has been raised about the conservation of early successional habitats and the species that inhabit these areas (Askins 1993; Robbins and others 1989; Brawn and others 2001; Hunter and others 2001; Litvaitis 2001), military installations provide a unique opportunity to conserve early successional habitats because their large, contiguous areas are subjected to varying levels of disturbance. This is particularly true for Ft. Riley, as it is located in an historic range of tallgrass prairie, a critically endangered biome for which $< 4\%$ of the original habitat remains (Samson and Knopf 1994). Nevertheless, it should be emphasized that this study lacks spatial replication and thus is unable to determine causation with respect to how military training influences native communities. Thus, additional research is needed in tallgrass prairie and other ecosystems to determine how closely military training activities approximate natural disturbances and how these activities impact native species at the level of the community.

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Appendix

Classification (following AOU [1998] and subsequent supplements) of species observed at Konza Prairie Biological Station and Ft. Riley Military Installation during annual surveys conducted in 1991–2001

Family/species	Scientific name
Cuculidae	
Black-billed cuckoo	*Coccyzus erythrophthalmus*
Yellow-billed cuckoo	*Coccyzus americanus*
Picidae	
Red-headed woodpecker	*Melanerpes erythrocephalus*
Red-bellied woodpecker	*Melanerpes carolinus*
Downy woodpecker	*Picoides pubescens*
Hairy woodpecker	*Picoides villosus*
Northern flicker	*Colaptes auratus*
Tyrannidae	
Eastern wood-pewee	*Contopus virens*
Acadian flycatcher	*Empidonax virescens*
Willow flycatcher	*Empidonax traillii*
Eastern phoebe	*Sayornis phoebe*
Great crested flycatcher	*Myiarchus crinitus*
Western kingbird	*Tyrannus verticalis*
Eastern kingbird	*Tyrannus tyrannus*
Scissor-tailed flycatcher	*Tyrannus forficatus*
Laniidae	
Loggerhead shrike	*Lanius ludovicianus*
Vireonidae	
Bell's vireo	*Vireo bellii*
Warbling vireo	*Vireo gilvus*
Red-eyed vireo	*Vireo olivaceus*

Appendix continued

Family/species	Scientific name
Corvidae	
Blue jay	*Cyanocitta cristata*
Paridae	
Black-capped chickadee	*Poecile atricapillus*
Tufted titmouse	*Baeolophus bicolor*
Sittidae	
White-breasted nuthatch	*Sitta carolinensis*
Troglodytidae	
Carolina wren	*Thryothorus ludovicianus*
Bewick's wren	*Thryothorus bewickii*
House wren	*Troglodytes aedon*
Marsh wren	*Cistothorus palustris*
Sylviidae	
Blue-gray gnatcatcher	*Polioptila caerulea*
Turdidae	
Eastern bluebird	*Sialia sialis*
Wood thrush	*Hylocichla mustelina*
American robin	*Turdus migratorius*
Mimidae	
Gray catbird	*Dumetella carolinensis*
Northern mockingbird	*Mimus polyglottos*
Brown thrasher	*Toxostoma rufum*
Sturnidae	
European starling	*Sturnus vulgaris*
Parulidae	
Northern parula	*Parula americana*
Yellow warbler	*Dendroica petechia*
Black-and-white warbler	*Mniotilta varia*
American redstart	*Setophaga ruticilla*
Worm-eating warbler	*Helmitheros vermivorus*
Louisiana waterthrush	*Seiurus motacilla*
Kentucky warbler	*Oporornis formosus*
Common yellowthroat	*Geothlypis trichas*
Yellow-breasted chat	*Icteria virens*
Thraupidae	
Summer tanager	*Piranga rubra*
Emberizidae	
Eastern towhee	*Pipilo erythrophthalmus*
Field sparrow	*Spizella pusilla*
Lark sparrow	*Chondestes grammacus*
Grasshopper sparrow	*Ammodramus savannarum*
Henslow's sparrow	*Ammodramus henslowii*
Cardinalidae	
Northern cardinal	*Cardinalis cardinalis*
Rose-breasted grosbeak	*Pheuticus ludovicianus*
Blue grosbeak	*Passerina caerulea*
Indigo bunting	*Passerina cyanea*
Dickcissel	*Spiza americana*
Icteridae	
Red-winged blackbird	*Agelaius phoeniceus*
Eastern meadowlark	*Sturnella magna*
Common grackle	*Quiscalus quiscula*
Brown-headed cowbird	*Molothrus ater*
Orchard oriole	*Icterus spurius*
Baltimore oriole	*Icterus galbula*
Fringillidae	
American goldfinch	*Carduelis tristis*

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