

## EVALUATING AVIAN COMMUNITY DYNAMICS IN RESTORED RIPARIAN HABITATS WITH MARK-RECAPTURE MODELS

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**ABSTRACT.**—Estimates of community attributes such as species richness, local extinction, and turnover are critical when evaluating ecological restoration efforts. Estimates of species richness based on counts can be biased by variation in the probability of detection among different species. We quantified the effects of livestock exclusion on riparian bird communities using mark-recapture models to account for variation in species detection rates. Specifically, we estimated species richness and other community parameters for fenced and grazed sites with robust design models where closed-captures were treated as mixtures, and then used transition rates to calculate derived vital rates for avian communities. Estimates of species richness based on unadjusted counts were correlated with estimates from robust design models, but counts failed to detect important temporal changes in species richness. Estimates of species richness from robust design models increased at fenced and grazed sites over an 8-year period, but community vital rates were unaffected by cattle exclusion. We examined qualitative changes in abundance of birds in four nesting guilds, and concluded that temporal changes may have been driven by regional dynamics in avian communities. Our mark-recapture analysis allowed us to compare standardized estimates of community parameters between habitats, observers, and time periods after accounting for variation in detection rates. Robust design models are a useful tool that will facilitate accurate assessments of community dynamics following future restoration efforts. *Received 12 March 2007. Accepted 29 June 2008.*

Community attributes such as species richness, rates of local extinction and colonization, and community turnover are often used as metrics to evaluate the condition of natural systems (Nichols et al. 1998, McCoy and Mushinsky 2002). Community dynamics can be useful for examining spatio-temporal changes in species distributions, drivers of biodiversity loss, and the importance of regional versus local processes in maintaining species richness and evenness (Griffiths 1997, Adler and Lauenroth 2003, Hansen et al. 2005). Knowledge of community dynamics is also important in evaluating the effects of land use prac-

tices and habitat fragmentation on biodiversity, as well as the potential benefits of habitat remediation and ecological restoration (Balmford and Bond 2005). Conservation efforts for rare or declining species often rely on habitat restoration as a means of reversing or mitigating negative population trends, and improvements in habitat quality or increased connectivity among habitat patches are expected to increase the probability of persistence for animal populations (Schrott et al. 2005). Development of effective methods for evaluation of restoration efforts is increasingly important as restoration ecology becomes an integral tool for wildlife conservation (McCoy and Mushinsky 2002).

Methodological problems can result in misleading conclusions about community dynamics if inappropriate methods are used to estimate community-level parameters. Observed species counts are often used to describe species richness, but can result in biased estimates due to variation in probability of detection among species (Nichols et al. 1998). Sampling situations where detection probabilities of species are  $<1$  can result in biased estimates of the probabilities of extinction and colonization that underestimate rates of community turnover. Two methods that account for variation in effort and probability of de-

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tection when estimating species richness include species accumulation curves (Colwell and Coddington 1994) and mark-recapture models (Boulinier et al. 1998, Nichols et al. 1998, Kéry and Schmid 2004, Wintle et al. 2004).

Detection probabilities of different species are important to consider when evaluating a newly-restored community. A subset of species may be rare and occur at low abundance in many types of natural and restored communities (Howe 1999, Maina and Howe 2000). Colonization will increase species richness in recently restored habitats, but colonizing species may be represented by only a few individuals. Individuals of relatively rare species will have lower probabilities of detection than abundant species, but documenting the occurrence of colonizing species is important for characterizing changes in the community and evaluating the efficacy of restoration or remediation efforts. Consequently, robust estimation of parameters that account for differences in detection among species is crucial when evaluating community responses to changes in land use, management, or habitat improvements.

Assessment of animal community responses to riparian habitat restoration is a current situation in which sampling issues are particularly relevant. Riparian habitats typically support more animal species than surrounding communities, especially those adjacent to grassland or agricultural lands (Kauffman and Krueger 1984, Brand et al. 2008). Riparian zones are important as breeding and wintering sites for bird communities, and as stopover sites for migratory birds in arid or semi-arid regions (Knopf and Samson 1994, Skagen et al. 1998, McComb et al. 2005). However, exposure of riparian habitats to livestock grazing can result in species-poor communities if cattle negatively impact plant community structure, water quality, and other site characteristics. Exclusion of livestock from riparian habitats is one method of habitat restoration in the Great Plains region of the United States. Ungrazed riparian zones tend to have a much higher volume of vegetation than the surrounding landscape. Several characteristics of undisturbed riparian habitats, including the extent of visual obstruction and number of bird species relative to the surrounding land-

scape, may influence probabilities of detection for the avian community. Differences in habitat structure can potentially result in biased estimators of community attributes if restored and reference sites are compared to assess whether restoration goals have been achieved.

We evaluated bird community dynamics in response to livestock exclusion with a mark-recapture approach. Robust design models combine open and closed population estimators, and have usually been applied to animal populations (Kendall et al. 1997, Sandercock 2006). We used robust design models to estimate community-level parameters, an approach adopted by at least three other bird monitoring programs, including the North American Breeding Bird Survey, Swiss Avian Monitoring Program, and the French Breeding Bird Survey (Boulinier et al. 1998, Kéry and Schmid 2004, Jiguet et al. 2005). One issue that can arise in applications of closed population models is that abundance may not be identifiable if detection probabilities are heterogeneous (Link 2003), but a solution is to model closed captures as mixtures where detection rates differ among subsets of species in the community (Pledger 2000). Our objectives were to: (1) use robust design models where closed-captures were treated as mixtures to obtain quantitative estimates of species richness that accounted for variation and heterogeneity in detection probabilities among species and habitats; (2) evaluate bird community dynamics by estimating the probabilities of local extinction and turnover, the number of colonizing species, and rates of change in species richness; (3) compare changes in species richness within grazed and restored riparian sites over time; and (4) use qualitative methods to examine if changes in avian nesting guilds occurred in response to livestock exclusion.

## METHODS

*Study Area and Data Collection.*—We conducted this study in 1996–1997 and 2004–2005 at the Kansas Army Ammunition Plant (KSAAP), a 5,555-ha military installation in Labette County, southeast Kansas (37° 18' N, 95° 10' W). The field site was historically tall-grass prairie dominated by big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum*

*virgatum*), and Indian grass (*Sorghastrum nutans*) in upland sites, and riparian woodland along creeks and river valleys (Eifler et al. 1995). Most of KSAAP is leased for livestock grazing allotments. Allotments at KSAAP riparian sites were grazed by cattle year-round at stocking rates of 1.2 ha/animal unit prior to our study, and were reduced to 2.2 ha/animal unit in 1995 (C. D. Deurmyer, pers. comm.).

No attempt was made to manage upland habitats separately from riparian habitats at KSAAP before 1995, resulting in the continued presence and grazing by cattle in riparian sites. Fences were erected in March 1996 around three riparian sites to permanently exclude cattle (hereafter, fenced sites), and three grazed riparian sites were paired with the three fenced sites to serve as reference sites (hereafter, grazed sites). Fenced sites ranged from 5.7 to 11.2 ha in size ( $n = 3$ ), and grazed sites ranged from 6.5 to 11.8 ha in size ( $n = 3$ ). Each grazed site was adjacent to its paired fenced site to minimize differences in landscape-level characteristics such as adjacent land use and topography. Grazed sites were downstream from paired fenced sites to minimize possible effects of run-off from grazing areas. Fenced and grazed sites had similar habitat width, stream length, and percent slope when cattle were permanently excluded. Duration of grazing in the 10-year period of 1996–2005 varied slightly among replicate plots. Replicate plots one through three were grazed 10, 8, and 9 years, respectively.

A single observer (D. E. Hoover) conducted 10-min biweekly fixed-radius point counts at fenced and grazed sites in 1996–97 (Hoover 1997). Counts were conducted between dawn and 1000 hrs CST from mid-May to mid-July to survey the breeding bird communities, and each site was visited four times throughout the season. Surveys were not conducted in rain or if wind speed was  $>16$  kph. Survey points were within 15 m of the stream bank and were set at 150-m intervals along the stream. The last point in the fenced site and the first point in the grazed site were at least 300 m apart. Each study site included three to five point count stations depending on size of the site. The observer recorded all birds seen or heard within 50 m of each survey point. Species encountered while the observer moved between points were recorded only if they were mem-

bers of a species not previously encountered. A second observer (T. N. Johnson) followed the same protocols in 2004–2005 and conducted point counts two and three times, respectively, at the same study sites (Johnson 2006). We adjusted survey points to 200-m intervals in 2004–05 to ensure independence among survey points, but six of the survey points were used during both sampling periods.

A sampling design that included randomization of observers among time periods during the study would have minimized potential observer bias. This design was not possible because the original observer was not available to repeat surveys. Using the same observer may have been an advantage, but was not essential because we estimated period-specific probabilities of detection in our analysis. We expected that changes in detection probability would coincide with a change in observer between 1996–97 and 2004–05, if observer effects were relevant.

We were interested in quantifying community dynamics of forest birds using riparian study sites for breeding. We included avian species that met either of the following criteria: birds listed as breeding species within a 10-county region of southeast Kansas by the Kansas Breeding Bird Atlas (Busby and Zimmerman 2001), and species recorded on Breeding Bird Survey routes within the same region (2001–2005; Sauer et al. 2005). We discarded records of migratory species not known to breed in southeast Kansas, including Mourning Warblers (*Oporornis philadelphia*) and Song Sparrows (*Melospiza melodia*); species only observed above the riparian canopy, including Turkey Vultures (*Cathartes aura*) and Chimney Swifts (*Chaetura pelagica*); and transient waterfowl, including Canada Geese (*Branta canadensis*).

*Statistical Analyses.*—Robust design models are based on primary sampling occasions that are subdivided into secondary sampling occasions (Pollock 1982, Kendall et al. 1997). The avian community at fenced and grazed sites was assumed to be open to changes in composition among different years, but closed to changes within a single breeding season. Annual breeding seasons were the primary sampling occasions and repeated visits to each site within a breeding season were the sec-

ondary sampling occasions. Lack of closure among secondary sampling occasions was possible but our surveys were timed to coincide with the peak of the breeding season, and most species should have been available for detection during all of our point counts. Our study included four primary sampling occasions and two to four secondary sampling occasions per primary occasion (1996–1997: 4 each, 2004: 2, and 2005: 3). Parameter estimation could have been aided by additional secondary occasions per year. However, data from 1996–1997 were analyzed retrospectively, and the number of surveys conducted in 2004–2005 were constrained by climatic conditions and sampling effort for other projects (Johnson 2006). Inclusion of multiple secondary occasions in every year of our study allowed us to model variation and heterogeneity in probability of detection.

Robust design mark-recapture models are typically applied to encounter histories of individuals to examine population dynamics. We used robust design models to examine community dynamics based on detection records for different species of landbirds encountered during visits to the study plots (Brose et al. 2003, Kéry and Schmid 2004). We created encounter histories separately for each species and study site for the entire sampling period of 1996 to 2005. Detections were pooled from all point count stations within a site per sampling occasion. Thus, each encounter history contained detections of a species during 13 visits to a study site during the period 1996–2005, where detections and non-detections were coded as 1 and 0, respectively (Appendix).

We initially used full heterogeneity models to analyze our data because heterogeneity in the probability of detection is a common feature of data from community studies of terrestrial vertebrates, including breeding bird surveys (McShea and Rappole 1997, Boulinier et al. 1998, Herzog et al. 2002, Selmi and Boulinier 2003, Bailey et al. 2004, Brand et al. 2008). Full heterogeneity models estimate seven types of parameters in community studies. Our main interest was in estimation of species richness ( $N$ ) and local persistence of species ( $\phi$ ). The models also include five additional parameters: probability of emigration ( $\gamma''$ ), probability of immigration ( $\gamma'$ ), the pro-

portion (mixture) of the community with a particular detection probability ( $\pi$ ), initial detection probabilities for mixtures within the community with high and low detection rates ( $p_\pi$  and  $p_{1-\pi}$ ), and subsequent detection probabilities for each mixture ( $c_\pi$  and  $c_{1-\pi}$ ). The global model for full heterogeneity model types ( $M_{\text{th}}$ , after Otis et al. 1978) allows variation in each parameter estimate over time ( $t$ ) with behavioral responses to detection ( $b$ ) caused by changes in detection probability after the initial detection of a species, and heterogeneity of detection among species ( $h$ ). We found that all parameters for these models consistently collapsed into estimates that were constant for time and behavioral response to detection (results not shown). Large standard errors for several parameters also indicated that model  $M_{\text{th}}$  was over-parameterized. Thus, we opted to start with a global model that included only time and heterogeneity in detection ( $M_{\text{h}}$ ); the probability of subsequent detection ( $c$ ) was not estimated.

We used robust design models where closed captures were modeled as mixtures to compute parameter estimates separately for all six replicate study plots in Program MARK (White and Burnham 1999, Pledger 2000). Robust design models were applied to encounter histories per species and used to estimate six community-level parameters (Table 1). Next, we used parameter estimates of  $\hat{N}$  and  $\hat{\phi}$  to calculate four derived vital rates for avian communities (Nichols et al. 1998).

(1) The probability of local extinction ( $E$ ) was:

$$\hat{E} = 1 - \hat{\phi}_{ij}$$

where  $\hat{\phi}_{ij}$  is the probability of a species persisting from time  $i$  to time  $j$ , and time  $i < j$ . Estimates of local extinction were limited to the duration of our study period and subsequent recolonization would be possible.

(2) The probability of turnover among local species ( $T$ ) was the probability that a new species entered the community between time  $i$  and time  $j$ :

$$\hat{T} = 1 - \hat{\phi}_{ji}$$

where  $\hat{\phi}_{ji}$  is estimated by reverse-time modeling of the encounter histories. An estimate of one indicates that all species present in time

TABLE 1. Estimated and derived community parameters calculated by application of robust design closed-capture mixture models to encounter histories for individual species in avian communities.

Community parameter	Symbol	Definition
Estimated parameters		
Local persistence	$\phi$	Probability that a species is present from time $i$ to time $j^a$
Temporary emigration	$\gamma''$	Probability that a species is present at time $i$ but absent at time $j$
Immigration	$\gamma'$	Probability that a species is absent at time $i$ and remains absent at time $j$
Mixture	$\pi$	Proportion of community with a high detection rate
High detection	$p_\pi$	Probability of detection for the high detection group
Low detection	$p_{1-\pi}$	Probability of detection for the low detection group
Species richness	$N$	Number of species corrected for the probability of detection
Derived parameters		
Local extinction	$E$	Probability of local extinction of a species from time $i$ to time $j$
Local turnover	$T$	Probability of local turnover that a new species is present at time $j$ but not time $i$
Number of colonizers	$B$	Number of new colonizing species present at time $j$ but not time $i$
Rate of change	$\lambda$	Finite rate of change in species richness between time $i$ to time $j$

<sup>a</sup> Time  $i$  to time  $j$  represents intervals among primary sampling periods.

$j$  are new species in the community that were not present at time  $i$ .

(3) The number of local colonizers ( $B_{ij}$ ) was the number of species present at time  $j$  but not at time  $i$ :

$$\hat{B}_{ij} = \hat{N}_j - \hat{\phi}_{ij}\hat{N}_i$$

where  $\hat{N}_i$  and  $\hat{N}_j$  are the estimated number of species at times  $i$  and  $j$ , and  $\hat{\phi}_{ij}$  is the probability of local species persistence.

(4) The finite rate of change in species richness ( $\hat{\lambda}$ ) between time  $i$  and time  $j$  was:

$$\hat{\lambda} = \frac{\hat{N}_j}{\hat{N}_i}$$

where  $\hat{N}_i$  and  $\hat{N}_j$  are estimates of species richness at times  $i$  and  $j$ , respectively. Each of the four derived vital rates was calculated for the 8-year interval between the 1996–97 and the 2004–05 sampling occasions.

We considered 12 candidate models to estimate community parameters. Candidate models included  $M_h$  (heterogeneity in detection) as suggested by Otis et al. (1978) and Boulinier et al. (1998), and  $M_0$  (all parameters constant), as well as 10 different permutations of these models where one parameter was modeled as a function of time, while other parameter(s) in the same model were held constant. We allowed each parameter to vary over time, or remain constant within a subset of the community (proportion of the commu-

nity with a high or low detection probability), across subsets, within a sampling period, or across all sampling periods for the most simplified model  $M_0$  (Table 2). We also examined a reduced two-period model which allowed  $N$  to vary between 1996–97 (first period) and 2004–05 (second period) (Kendall et al. 1997). The two-period model yielded estimates of species richness for comparison to uncorrected counts to examine whether imperfect detection would affect our conclusions regarding the restoration of riparian bird communities.

Goodness-of-fit tests are not available for robust design models in Program MARK. We adjusted the variance inflation factor from  $\hat{c} = 1$  (no overdispersion) to 10 (high overdispersion) by increments of 0.5 to evaluate the potential effects of overdispersion. Changes in model rankings were used to evaluate the sensitivity of our model conclusions. Model fit was calculated with Akaike's Information Criterion values corrected for small sample sizes ( $AIC_c$ ). Model selection was based on differences in  $AIC_c$  values ( $\Delta AIC_c$ ) relative to the minimum  $AIC_c$  model, where  $\Delta AIC_c$  values  $\leq 2$  were considered parsimonious (Burnham and Anderson 2002). The relative strength of support for each model was calculated by the ratio of Akaike weights ( $w_i/w_j$ ).

We tested for statistical significance between parameter estimates for fenced and

TABLE 2. Differences in corrected Akaike Information Criterion values ( $\Delta AIC_c$ ) for robust design closed-capture mixture models fit to encounter histories for riparian bird communities in southeast Kansas, 1996–1997 to 2004–2005.

Model structure <sup>a</sup>						Replicate 1		Replicate 2		Replicate 3		
$\phi$	$\pi$	$\gamma''$	$\gamma'$	$p$	$N$	$K$	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed
c	c	random	mix	c	6	6	0.0	0.0	0.5	0.0	0.0	0.0
c	c	random	mix	period	7	7	0.2	0.1	0.0	1.4	0.5	0.5
c	t	t	t	mix	t	16	29.1	14.7	13.0	8.2	13.7	26.3
c	t	t	t	c	t	15	51.7	21.8	29.1	31.8	40.3	45.3
c	c	random	mix	mix	t	9	4.3	3.9	4.0	2.5	3.5	4.4
c	c	c	c	mix	c	7	1.6	2.2	2.3	2.2	2.2	1.9
c	c	c	c	mix	t	10	5.9	6.2	5.9	4.8	5.7	6.4
c	c	c	c	t	t	16	20.1	16.0	16.0	5.4	4.3	11.4
c	c	c	t	t	t	17	19.3	17.4	17.5	7.8	5.0	13.6
c	c	t	t	t	t	19	25.9	21.2	19.6	13.2	8.8	18.4
c	t	t	t	t	t	22	34.7	28.8	26.3	18.3	15.9	28.2
t	t	t	t	t	t	24	36.9	34.5	31.8	38.8	21.2	31.7

<sup>a</sup> Model structure for the six parameters included: c = constant, mix = a mixture of detection probabilities for two groups within the avian community, period = separate parameters for 1996–97 and 2004–05, random = random temporary emigration with  $\gamma''$  and  $\gamma'$  set to be equal, and t = time-dependent variation among primary sampling sessions. A  $\Delta AIC_c$  value = 0 indicates the minimum-AIC<sub>c</sub> model.

grazed sites using Program CONTRAST (Version 2, Hines and Sauer 1989). All other statistical tests were performed using SAS System (Version 8.01, SAS Institute Inc. 2000) and  $P$ -values were considered significant at  $\alpha \leq 0.05$ . We used parametric bootstrapping in Program MATLAB (Version 6.1, Mathworks 2000) to obtain estimates of variance and make statistical comparisons among the four derived parameters ( $E$ ,  $T$ ,  $B$ , and  $\lambda$ ) for avian communities at fenced and grazed sites. We modeled  $\hat{N}$  as random draws from a normal distribution and  $\hat{\phi}$  as draws from a *beta* distribution to bound draws between 0 and 1. Estimates of variance for derived parameters were taken directly from bootstrap distributions ( $n = 100,000$  replicates). We calculated bias-corrected 95% confidence intervals to compensate for slight discrepancies between the estimates of derived parameters calculated with the above formulae and the means of the bootstrap distributions. Thus,

$$\begin{aligned} & \text{bias-corrected percentiles} \\ & = \Phi(2\Phi^{-1}[F] \pm 1.96) \end{aligned}$$

where  $\Phi$  is the normal cumulative distribution,  $\Phi^{-1}$  is the inverse normal cumulative distribution,  $F$  is the fraction of bootstrap values smaller than the value from the community vital rates, and 1.96 is the critical value for the 95% confidence interval.

*Guild Analysis.*—We assigned bird species

to one of four guilds based on habitats primarily used for nesting: ground-nesters, shrub/low foliage nesters (hereafter, shrub-nesters), sub-canopy/canopy nesters (hereafter, canopy-nesters), and cavity-nesters. Birds were assigned to guilds using the species accounts of Ehrlich et al. (1988) and Martin (1995). All species were included in nesting guilds except Eastern Phoebe (*Sayornis phoebe*) and Brown-headed Cowbird (*Molothrus ater*). We excluded phoebes from the guild analysis but examined changes in abundance of Brown-headed Cowbirds between fenced and grazed sites because cowbirds are closely associated with cattle (Goguen and Mathews 2001).

We were unable to use mark-recapture methods to examine guild dynamics because the number of species per guild was low. We estimated relative abundance of riparian birds instead. The mean number of detections per species was pooled among sampling points within a site and we used the maximum number of individuals detected during a given visit. We averaged across sites within a treatment to ascertain the mean number of detections within a treatment for each year. We compared the summed responses of individuals within each guild to evaluate differences in mean abundance for all guilds between treatments and to test for year by treatment interactions. We used a mixed effects repeated measures

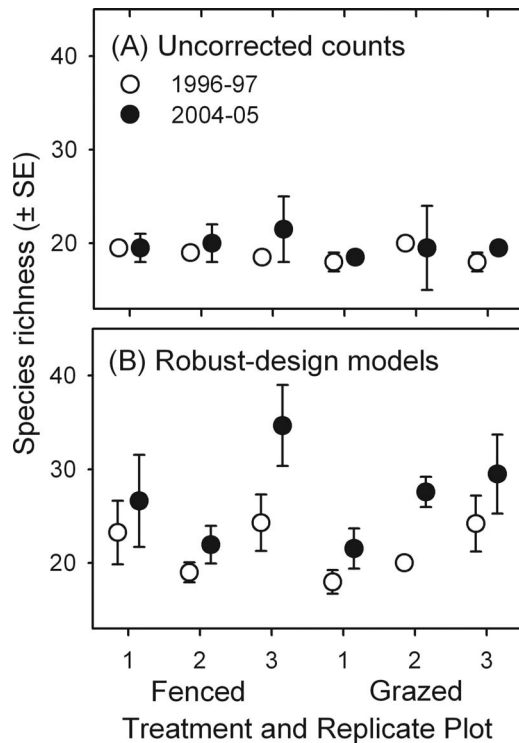


FIG. 1. Estimates of species richness from (A) uncorrected counts, and (B) robust design closed-capture mixture models applied to encounter data for riparian bird communities at fenced and grazed sites in south-east Kansas, 1996–1997 to 2004–2005.

analysis of variance with year as the repeated variable. Covariance structure for measurements among time periods was initially unknown, and our five candidate models included: compound symmetry, unstructured, autoregressive, heterogeneous autoregressive, and autoregressive moving average. We calculated the most appropriate model covariance structure and improved model fit by comparing models using Akaike’s Information Criterion adjusted for small sample sizes ( $AIC_c$ ).

RESULTS

*Counts of Species Richness.*—We observed 51 species of birds in riparian habitats during the 4 years of the study; 43 species at fenced sites and 44 species at grazed sites. Estimates of species richness based on uncorrected counts ranged from  $19.0 \pm 0.6$  (SE) to  $20.3 \pm 2.3$  species per year in fenced sites ( $n = 3$ ) and from  $17.6 \pm 1.3$  to  $20.6 \pm 1.8$  species per year in grazed sites ( $n = 3$ , Fig. 1A). Estimates of species richness based on uncorrected counts were not different between treatments in 1996–97 ( $\chi^2_1 = 0.4$ ,  $P = 0.53$ ) or 2004–05 ( $\chi^2_1 = 0.3$ ,  $P = 0.58$ ).

*Estimated Species Richness.*—The top two models for each study site had the same model structure for all six parameters (Table 2). Five of the six riparian study sites had the same best-fit model, parameters  $\phi$  and  $\pi$  were constant, emigration was random ( $\gamma'' = \gamma'$ ),  $p$  was constant within the high and low detection groups, and species richness ( $N$ ) was constant over the periods 1996–1997 and 2004–2005 (hereafter,  $N_c$  model). Replicate #2 in the fenced treatment had a different best-fit model than the other five sites, but differed in the model structure for only species richness, which differed between the periods 1996–1997 and 2004–2005 (hereafter,  $N_{period}$  model). For all riparian sites, 2–3 models had  $\Delta AIC_c$  values  $\leq 2$ , and were an equally parsimonious fit to the data. Rankings of the subordinate models varied by site and treatment.  $N_c$  remained the minimum- $AIC_c$  model in five of six plots even if  $\hat{c}$  was adjusted up to a value of 10.  $N_{period}$  was the top-ranked model for replicate #2 in the fenced treatment but  $N_c$  became the minimum- $AIC_c$  model if  $\hat{c}$  was adjusted from 1 to 10.

The  $N_{period}$  model garnered a similar amount of support as the  $N_c$  model in all six sites (Table 3) and ratios of Akaike weights for the

TABLE 3. Akaike weights ( $w_i$ ) for the top four models that had >10% of the support among all of the candidate models.

Model structure	Replicate 1		Replicate 2		Replicate 3	
	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed
$\phi$ c	0.39	0.40	0.34	0.43	0.39	0.43
$\pi$ c	0.37	0.39	0.44	0.21	0.31	0.33
$\gamma''$ random	0.05	0.06	0.06	0.12	0.07	0.05
$\gamma'$ c	0.17	0.13	0.14	0.15	0.13	0.17

two models were close to one ( $w_j/w_i = 0.5$  to 1.3). Thus, we report parameter estimates from the  $N_{\text{period}}$  model for comparison to estimates of species richness based on counts. Parameter estimates and associated standard error and confidence intervals from the  $N_{\text{period}}$  model varied among sites (Table 4). Apparent species persistence was consistently high ( $\hat{\phi} > 0.8$ ), but tended to be somewhat lower in grazed sites. Estimates of temporary emigration were low across all sites ( $\hat{\gamma} \leq 0.03$ ). The proportion of each community with a high detection rate varied among sites, ranging from  $\hat{\pi} = 0.53$  to 0.79. The detection probability for the high detection subset of the community ranged from  $\hat{P}_{\pi} = 0.89$  to 1.00, whereas detection probabilities for the low detection group were  $\hat{P}_{1-\pi} = 0.18$  to 0.48. We detected no significant differences in estimates among fenced and grazed site for any of the five transition parameters for avian communities (Table 4). Finally, estimates of species richness corrected for detection probabilities were not different between treatments in 1996–1997 (Fig. 1B;  $\chi^2_1 = 0.6$ ,  $P = 0.44$ ) or 2004–05 ( $\chi^2_1 = 0.3$ ,  $P = 0.58$ ).

**Derived Parameters.**—The probability of local extinction was low and tended to be higher in grazed ( $\hat{E} = 0.07$  to 0.14) than fenced sites ( $\hat{E} = 0.06$  to 0.09) from 1996 to 2005, but site differences were not significant (Table 5). Turnover rates ( $\hat{T} = 0.11$  to 0.19) were not different between fenced and grazed communities. The number of colonizers was highest in one of the three fenced riparian sites ( $\hat{B}_{ij} = 11.9$ ), but both fenced and grazed sites acquired between five and 12 colonizers in the period from 1996 to 2005. The rate of change in species richness ( $\hat{\lambda}$ ) was  $>1$  for all riparian study sites, but the 95% confidence intervals included one for five of six sites, indicating no significant difference from stationarity for all but one riparian bird community at our study site. We detected no differences in the rate of change in species richness between fenced and grazed communities.

**Comparison of Estimates of Species Richness.**—Estimates of species richness based on uncorrected counts were consistently lower than estimates from the robust design mark-recapture models (Fig. 1), both in 1996–1997 (0 to 34.5% lower) and 2004–2005 (9.7 to 61.2% lower). Uncorrected counts and esti-

mated values of species richness were positively correlated if we pooled values from the two sampling periods ( $r = 0.62$ ,  $P = 0.03$ ,  $n = 12$ ). Use of uncorrected counts as an index of species richness would have missed important temporal changes in avian communities in our study area. Estimates of species richness based on uncorrected counts were slightly higher in 2004–2005 than 1996–1997 in two of three fenced sites (Fig. 1A; 11% and 16% higher) and in one of three grazed sites (12% higher), but the difference between time periods was not significant overall ( $\chi^2_1 = 0.7$ ,  $P = 0.39$ ). In contrast, estimates of  $\hat{N}$  from the robust design models indicated that species richness increased markedly between the two time periods (Fig. 1B). Species richness increased at both fenced (14 to 42% increase) and grazed sites (16 to 22%) and was a highly significant temporal change ( $\chi^2_1 = 10.5$ ,  $P = 0.001$ ).

**Guild Responses.**—Riparian bird communities included species in four nesting guilds (Table 6). The shrub- and canopy-nesting guilds were the most diverse components of the riparian bird communities, each consisting of 15 species. Ground-nesters were the least diverse guild, and increased in species richness from two to four species between 1996–97 and 2004–2005. The two colonizing species were Black-and-white Warbler (*Mniotilta varia*) and Kentucky Warbler (*Oporornis formosus*). The shrub-nesting guild gained three new species: Acadian Flycatcher (*Empidonax virescens*), Chipping Sparrow (*Spizella passerina*), and Dickcissel (*Spiza americana*). The canopy guild gained four species in the interval between sampling periods: Fish Crow (*Corvus ossifragus*), Red-shouldered Hawk (*Buteo lineatus*), Ruby-throated Hummingbird (*Archilochus colubris*), and Summer Tanager (*Piranga rubra*), but lost two species: Baltimore Oriole (*Icterus galbula*) and Eastern Kingbird (*Tyrannus tyrannus*). Finally, the cavity-nesting guild gained three new species: Northern Flicker (*Colaptes auratus*), Pileated Woodpecker (*Dryocopus pileatus*), and Red-headed Woodpecker (*Melanerpes erythrocephalus*).

Six species were encountered only in fenced sites, and four of the six species were cavity-nesters. Four species were encountered only in grazed sites, and three of the four spe-

TABLE 4. Community parameters estimated from robust design closed-capture mixture models applied to riparian bird communities in southeast Kansas, 1996–1997 to 2004–2005.

Parameter	Replicate 1		Replicate 2		Replicate 3		$\chi^2_1$	$P \leq$
	$\hat{\theta} \pm SE$	95% CI	$\hat{\theta} \pm SE$	95% CI	$\hat{\theta} \pm SE$	95% CI		
Local persistence of species ( $\hat{\phi}$ )								
Fenced	0.93 $\pm$ 0.05	0.72 to 0.99	0.92 $\pm$ 0.04	0.79 to 0.97	0.94 $\pm$ 0.06	0.67 to 0.99	1.95	0.16
Grazed	0.86 $\pm$ 0.06	0.71 to 0.96	0.81 $\pm$ 0.06	0.65 to 0.91	0.93 $\pm$ 0.06	0.72 to 0.98		
Random emigration ( $\hat{\gamma}'' = \hat{\gamma}'$ )								
Fenced	0.03 $\pm$ 0.17	0 to 1	0 $\pm$ 0	0 to 0	0 $\pm$ 0	0 to 0	0.00	1.00
Grazed	0 $\pm$ 0	0 to 0	0.03 $\pm$ 0.08	0 to 0.78	0 $\pm$ 0	0 to 0		
Proportion of community with a high detection rate ( $\hat{\pi}$ )								
Fenced	0.72 $\pm$ 0.06	0.58 to 0.82	0.79 $\pm$ 0.06	0.66 to 0.88	0.53 $\pm$ 0.07	0.39 to 0.66	0.01	0.91
Grazed	0.73 $\pm$ 0.21	0.25 to 0.96	0.69 $\pm$ 0.07	0.54 to 0.80	0.59 $\pm$ 0.07	0.45 to 0.72		
Probability of detection for high detection group ( $\hat{p}_{\pi}$ )								
Fenced	0.97 $\pm$ 0.05	0.41 to 1	1.00 $\pm$ 0	0.99 to 1	0.91 $\pm$ 0.03	0.83 to 0.96	0.23	0.61
Grazed	0.89 $\pm$ 0.14	0.33 to 0.99	1.00 $\pm$ 0.02	0 to 1	0.91 $\pm$ 0.04	0.81 to 0.96		
Probability of detection for low detection group ( $\hat{p}_{1-\pi}$ )								
Fenced	0.28 $\pm$ 0.09	0.14 to 0.48	0.44 $\pm$ 0.05	0.35 to 0.54	0.18 $\pm$ 0.05	0.10 to 0.30	1.36	0.24
Grazed	0.43 $\pm$ 0.11	0.24 to 0.64	0.48 $\pm$ 0.06	0.37 to 0.58	0.20 $\pm$ 0.06	0.11 to 0.33		

TABLE 5. Derived parameter estimates calculated from community parameters for riparian bird communities in southeast Kansas, 1996–1997 to 2004–2005.

Parameter	Replicate 1		Replicate 2		Replicate 3		$\chi^2_1$	$P \leq$
	$\hat{\theta} \pm SE$	95% CI	$\hat{\theta} \pm SE$	95% CI	$\hat{\theta} \pm SE$	95% CI		
<b>Local extinction of species (<math>\hat{E}</math>)</b>								
Fenced	0.07 $\pm$ 0.05	0.01 to 0.27	0.09 $\pm$ 0.04	0.03 to 0.22	0.06 $\pm$ 0.06	0 to 0.30	1.75	0.19
Grazed	0.14 $\pm$ 0.06	0.06 to 0.29	0.19 $\pm$ 0.06	0.09 to 0.34	0.07 $\pm$ 0.06	0.01 to 0.26		
<b>Local turnover of species (<math>\hat{T}</math>)</b>								
Fenced	0.18 $\pm$ 0.06	0.09 to 0.31	0.15 $\pm$ 0.05	0.07 to 0.27	0.13 $\pm$ 0.05	0.05 to 0.27	0.02	0.90
Grazed	0.19 $\pm$ 0.06	0.10 to 0.32	0.18 $\pm$ 0.05	0.10 to 0.31	0.11 $\pm$ 0.06	0.03 to 0.27		
<b>Number of colonizing species (<math>\hat{B}_{ij}</math>)</b>								
Fenced	5.0 $\pm$ 6.0	-6.9 to 16.6	4.6 $\pm$ 2.4	-0.1 to 9.2	11.9 $\pm$ 5.4	1.4 to 22.4	0.09	0.77
Grazed	6.1 $\pm$ 2.6	1.0 to 11.2	11.4 $\pm$ 2.1	7.6 to 15.7	7.1 $\pm$ 5.2	-3.2 to 17.3		
<b>Rate of change in species richness (<math>\hat{\lambda}</math>)</b>								
Fenced	1.14 $\pm$ 0.29	0.68 to 1.80	1.16 $\pm$ 0.13	0.92 to 1.42	1.43 $\pm$ 0.26	1.00 to 2.03	0.02	0.89
Grazed	1.20 $\pm$ 0.15	0.93 to 1.51	1.38 $\pm$ 0.08	1.22 to 1.54	1.22 $\pm$ 0.24	0.82 to 1.77		

TABLE 6. Mean number of individuals per species ( $\pm$  SE) detected each year at replicate plots of fenced and grazed riparian sites in southeast Kansas, 1996–1997 to 2004–2005. (Scientific names in Appendix).

Species	1996		1997		2004		2005	
	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed
<b>Ground-nesting Guild</b>								
Black-and-white Warbler					0.33 $\pm$ 0.33	0.67 $\pm$ 0.33		1.00 $\pm$ 0.58
Kentucky Warbler					0.33 $\pm$ 0.33	0.67 $\pm$ 0.67		0.33 $\pm$ 0.33
Northern Bobwhite		0.33 $\pm$ 0.33	0.67 $\pm$ 0.33	0.67 $\pm$ 0.67	1.00 $\pm$ 0.58	0.33 $\pm$ 0.33	0.67 $\pm$ 0.33	0.33 $\pm$ 0.33
Wild Turkey								
<b>Shrub-nesting Guild</b>								
Acadian Flycatcher	0.67 $\pm$ 0.33	0.67 $\pm$ 0.33	1.00 $\pm$ 0.58	1.00 $\pm$ 0.58	0.67 $\pm$ 0.67	0.67 $\pm$ 0.67	0.33 $\pm$ 0.33	
American Goldfinch	0.33 $\pm$ 0.33	1.33 $\pm$ 1.33			0.33 $\pm$ 0.33	1.00 $\pm$ 1.00		
American Robin	0.67 $\pm$ 0.33	0.67 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	1.33 $\pm$ 0.33	0.33 $\pm$ 0.33
Blue-gray Gnatcatcher	1.67 $\pm$ 0.88	2.67 $\pm$ 1.33	1.00 $\pm$ 0.58	2.67 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33		0.67 $\pm$ 0.67
Brown Thrasher								
Chipping Sparrow	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	1.33 $\pm$ 0.88		0.33 $\pm$ 0.33	0.33 $\pm$ 0.33		
Common Grackle								
Dickcissel	0.67 $\pm$ 0.67		0.33 $\pm$ 0.33	1.00 $\pm$ 0.58	0.67 $\pm$ 0.67	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33
Field Sparrow					1.00 $\pm$ 0.58	0.33 $\pm$ 0.33	0.67 $\pm$ 0.33	0.67 $\pm$ 0.33
Gray Catbird					0.33 $\pm$ 0.33	0.33 $\pm$ 0.33		
Indigo Bunting	4.33 $\pm$ 0.88	2.33 $\pm$ 0.67	5.00 $\pm$ 1.00	4.33 $\pm$ 0.33	2.67 $\pm$ 0.33	2.00 $\pm$ 0.58	4.33 $\pm$ 0.33	2.00 $\pm$ 0.58
Northern Cardinal	7.33 $\pm$ 0.33	4.33 $\pm$ 0.33	5.67 $\pm$ 0.33	7.00 $\pm$ 1.00	6.67 $\pm$ 1.76	5.00 $\pm$ 2.00	7.00 $\pm$ 0.58	6.00 $\pm$ 1.73
Northern Mockingbird								
Wood Thrush	0.67 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33
Yellow-billed Cuckoo	3.67 $\pm$ 0.33	3.00 $\pm$ 0.58	3.00 $\pm$ 0.58	3.67 $\pm$ 0.33	4.33 $\pm$ 1.45	2.33 $\pm$ 0.33	3.00 $\pm$ 1.15	4.00 $\pm$ 1.15
<b>Canopy-nesting Guild</b>								
Baltimore Oriole	2.00 $\pm$ 1.15	1.67 $\pm$ 0.88	0.33 $\pm$ 0.33	0.67 $\pm$ 0.33				
Blue Jay			2.00 $\pm$ 1.00	3.67 $\pm$ 0.88	1.00 $\pm$ 0.58	2.33 $\pm$ 1.33	1.33 $\pm$ 0.88	3.33 $\pm$ 0.88
Eastern Kingbird			0.33 $\pm$ 0.33	0.33 $\pm$ 0.33				
Eastern Wood-Pewee	3.33 $\pm$ 0.88	1.67 $\pm$ 0.33	3.00 $\pm$ 0.58	2.33 $\pm$ 0.33	1.00 $\pm$ 0.58	1.33 $\pm$ 0.33	2.00 $\pm$ 0	1.00 $\pm$ 0.58
Fish Crow						0.33 $\pm$ 0.33		
Great Blue Heron		0.33 $\pm$ 0.33				0.67 $\pm$ 0.33		
Great Horned Owl						0.33 $\pm$ 0.33		
Green Heron	0.67 $\pm$ 0.33							
Mourning Dove	0.33 $\pm$ 0.33	0.33 $\pm$ 0.33			0.33 $\pm$ 0.33	0.33 $\pm$ 0.33		
Red-eyed Vireo	0.33 $\pm$ 0.33		1.00 $\pm$ 0.58	0.67 $\pm$ 0.67		0.67 $\pm$ 0.33		1.00 $\pm$ 0.58
Red-shouldered Hawk							0.67 $\pm$ 0.67	
Rose-breasted Grosbeak			0.33 $\pm$ 0.33	0.67 $\pm$ 0.67	0.33 $\pm$ 0.33			

TABLE 6. Continued.

Species	1996		1997		2004		2005	
	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed	Fenced	Grazed
Ruby-throated Hummingbird							0.33 ± 0.33	0.33 ± 0.33
Summer Tanager					0.67 ± 0.33		0.67 ± 0.33	0.67 ± 0.67
Yellow Warbler	0.33 ± 0.33	0.33 ± 0.33			0.67 ± 0.67		0.33 ± 0.33	
Cavity-nesting Guild								
Barred Owl	0.67 ± 0.33		0.33 ± 0.33		0.33 ± 0.33	0.67 ± 0.33	1.00 ± 0.58	
Carolina Chickadee	1.33 ± 0.33	2.67 ± 0.88	3.00 ± 0.58	4.00 ± 0.58	3.33 ± 0.67	1.67 ± 0.88	3.33 ± 1.20	5.67 ± 1.20
Carolina Wren	1.33 ± 0.33	1.33 ± 0.33	1.33 ± 0.33	0.67 ± 0.33	3.33 ± 1.20	2.33 ± 0.33	1.33 ± 0.67	1.00 ± 0.00
Downy Woodpecker	2.33 ± 0.67	3.00 ± 0.58	1.33 ± 0.33	1.33 ± 0.33	1.00 ± 0.58	1.67 ± 0.67	2.67 ± 0.88	2.00 ± 0.58
Eastern Bluebird	0.67 ± 0.67	1.00 ± 0		0.33 ± 0.33	0.33 ± 0.33	0.33 ± 0.33	1.33 ± 0.33	1.67 ± 0.67
European Starling	0.33 ± 0.33							
Great Crested Flycatcher	3.00 ± 0	4.00 ± 0.58	3.00 ± 0.58	2.67 ± 0.33	1.00 ± 0.00	1.67 ± 0.33	2.67 ± 0.33	2.33 ± 0.88
Hairy Woodpecker			0.33 ± 0.33		0.67 ± 0.33			
Northern Flicker					0.33 ± 0.33			
Pileated Woodpecker					0.33 ± 0.33	0.67 ± 0.33	0.33 ± 0.33	0.33 ± 0.33
Red-bellied Woodpecker	4.67 ± 0.33	3.00 ± 1.00	3.33 ± 0.33	4.00 ± 0	2.33 ± 0.33	2.67 ± 0.33	3.33 ± 0.67	4.33 ± 0.67
Red-headed Woodpecker							1.00 ± 1.00	
Tufted Titmouse	3.00 ± 1.00	4.00 ± 0.58	3.33 ± 0.33	3.67 ± 0.67	5.67 ± 2.19	1.67 ± 0.33	2.67 ± 0.67	3.67 ± 0.88
White-breasted Nuthatch	0.33 ± 0.33		1.00 ± 0	0.67 ± 0.33	1.67 ± 0.33	2.33 ± 0.33	1.00 ± 0.58	2.00 ± 1.00
Brood Parasite								
Brown-headed Cowbird	1.67 ± 0.67	2.67 ± 0.33	0.67 ± 0.33	1.33 ± 0.88	0.67 ± 0.33	1.67 ± 0.88	3.00 ± 1.15	0.67 ± 0.33

cies were in the canopy guild. Most species occupied both fenced and grazed sites but the number of individuals per guild varied. A subset of species within each guild showed positive responses to cattle exclusion and were consistently encountered more frequently in fenced sites. Positive responses to fencing were found in four species of cavity-nesters (27% of the guild), one species of ground-nester (25%), two shrub-nesters (13%), and one canopy-nester (0.7%). Some species were encountered more frequently in grazed sites, including one species of ground-nester (25%), one shrub-nester (0.7%), and five canopy-nesters (33%).

We detected no significant year by treatment interactions or between-treatment differences in abundance within the four guilds. Mean abundance in the ground nesting guild did not differ among years ( $\bar{x} = 0.0$  to 2.3 ground-nesters/site,  $F_{3,4} = 6.16$ ,  $P = 0.06$ ). Mean abundance of the shrub-nesting guild was lower in both fenced and grazed sites in 2005 than in 1996 ( $\bar{x} = 13.0$  to 21.3 shrub-nesters/site,  $F_{3,4} = 113.07$ ,  $P < 0.001$ ), and the difference was greater in the grazed sites, although not significantly. Mean abundance in the canopy guild differed among years ( $\bar{x} = 4.3$  to 9.0 canopy-nesters/site,  $F_{3,12} = 8.77$ ,  $P = 0.002$ ), which was driven by a decrease in abundance in both fenced and grazed study sites between 1997 and 2004. Mean abundance of the cavity-nesting guild in fenced and grazed sites was higher in 2005 than all other years of the study ( $\bar{x} = 16.0$  to 23.3 cavity-nesters/site,  $F_{3,12} = 3.39$ ,  $P = 0.05$ ). We detected a year by treatment interaction effect for Brown-headed Cowbird abundance ( $\bar{x} = 0.3$  to 3.3 individuals/site,  $F_{3,12} = 4.99$ ,  $P = 0.02$ ). Brown-headed Cowbirds were most abundant at grazed sites in 1996–2004 and at fenced sites in 2005 (Table 6).

#### DISCUSSION

We found no differences in avian species richness between fenced and grazed riparian habitats from observed counts of species encountered during bird surveys. However, when we used robust design closed-capture mixture models to account for variation among species in the probability of detection, species richness increased over an 8-year period at fenced and grazed sites in riparian hab-

itats. We detected new species in four different guilds of nesting birds in the 2004–05 sampling period. Cowbird abundance was highest at grazed and then fenced sites in the early and latter years of the study, respectively. Overall, our estimates of community parameters suggested avian community dynamics over the study period were similar at all of our study plots.

Livestock grazing can have negative effects on vegetation and associated vertebrate communities in riparian habitats, and exclusion of cattle can be an effective tool for habitat restoration. Evaluating effects of grazing and restoration efforts can be challenging because the avian community is not necessarily confined to riparian corridors, and birds may respond to disturbance at large geographic scales (Ammon and Stacey 1997). Studies which evaluate the effects of cattle exclusion on riparian birds often have small sample sizes and limited replication; these issues may partly explain the lack of treatment effects in our experiment. Similarly, our guild analysis was constrained because we were unable to estimate detection rates with a low number of species per guild. However, qualitative comparisons among guilds can be useful for exploring which subsets of the community may be most sensitive to effects of grazing or exclusion of cattle.

Estimated species richness in our study did not differ between fenced and grazed sites, despite 8 years of cattle exclusion. Previous studies of the effects of livestock exclusion have detected increases in species richness, diversity, and abundance among communities of riparian vertebrates in fenced habitats (Dobkin et al. 1998, Sarr 2002, Giuliano and Homyack 2004). We expected a higher number of breeding bird species to occur in fenced sites because riparian areas without livestock grazing usually have higher vegetation volume and structural diversity than those not grazed (Kauffman and Krueger 1984, Mills et al. 1991, Fleischman et al. 2003). Thus, riparian habitats in southeast Kansas may require longer periods of cattle exclusion or manual replanting of vegetation to increase avian species richness relative to sites impacted by grazing activity.

Regional processes could have contributed to the temporal changes in species richness in fenced and grazed habitats. Unexpectedly, we

observed an increase in estimated species richness and similar rates of local species turnover at fenced and grazed sites. Three nonexclusive factors may explain our observations. First, riparian vegetation and associated riparian bird communities can be affected by livestock stocking rates (Jansen and Robertson 2001a, b). Increases in avian species richness at grazed riparian sites could have been influenced by reductions in stocking densities that were implemented in 1995 at riparian sites and surrounding upland pastures. Second, the landscape matrix in which riparian zones are embedded can influence ecological processes within riparian areas through effects on habitat quality and species persistence (Dunford and Freemark 2004, Brand *et al.* 2008). If changes in livestock stocking rates in upland pastures impacted cowbird activity, reductions in rates of brood parasitism could have contributed to increases in species richness in riparian habitats, particularly among songbirds with open-cup nests. Last, species distributions are usually characterized by lower abundance near range boundaries. Higher rates of extinction and colonization may be expected if marginal populations are dependent upon immigration for persistence (Doherty *et al.* 2003, Karanth *et al.* 2006). Our study site was at an ecotone between tallgrass prairie and eastern deciduous forest, and several species of birds were at the margins of their breeding distributions. Southeast Kansas is the western boundary of the breeding range of Summer Tanagers and Kentucky Warblers (Busby and Zimmerman 2001), and these two species were only detected during the latter portion of our study. Overall, spatio-temporal changes in species distributions could have obscured potential differences in fenced and grazed riparian bird community dynamics if regional influences were an important factor in our study.

Previous analyses have usually assumed that probabilities of detection are identical among species, habitats, or time periods when comparing animal communities in grazed and ungrazed riparian habitats. Our analyses revealed significant heterogeneity in probability of detection among different species with a two- to five-fold difference in probability of detection in the low and high-detection subsets of the avian communities. Use of robust-

design models for mixtures allowed for standardized comparisons across habitats that controlled for interspecific variation in the probability of detection and potential differences among observers. Thus, temporal increases in species richness were likely due to changes in habitat between our two sampling periods, albeit at a larger geographic scale than the sampling protocols of our study.

The probability of detection of a species is a function of abundance, which ultimately influences probability of extinction. Species that occur at low abundance tend to have a lower probability of detection and a higher probability of extinction (Alpizar-Jara *et al.* 2004). Empirical relationships among these variables have implications for ecological restoration because the success of restoration efforts is usually measured against a reference community. Comparisons among communities could result in faulty inferences if differences or similarities are obscured by variation in probability of detection. Moreover, investigations of community dynamics must account for the imperfect detection of species that occur at low abundance to accurately quantify probabilities of extinction and persistence, as well as the rate of change in species richness after habitat restoration. Accurate estimates of community-level parameters will be critical in evaluating the suitability of restored habitats.

Our estimates of species richness demonstrate that unadjusted species counts can underestimate the number of avian species breeding in riparian habitats in the Great Plains. Our study joins a growing literature in demonstrating that mark-recapture methods are a useful tool for investigations of community dynamics because they yield robust estimates of species richness and other community attributes that improve inferences from faunal surveys in riparian habitats (Brand *et al.* 2008) and other environments (Boulinier *et al.* 1998, Bailey *et al.* 2004, Kéry and Schmid 2004, Wintle *et al.* 2004, Jiguet *et al.* 2005). Unbiased estimates of species richness are important because they allow ecologists to: (1) evaluate the efficacy of existing restoration efforts, (2) develop hypotheses about the pace and future trajectory of community recovery, and (3) ascertain whether additional effort will be required to achieve restoration project goals. Future use of mark-recapture

models to study community dynamics will aid evaluations of ecological responses to restoration efforts.

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APPENDIX. Encounter histories for bird species detected (1) or not detected (0) at replicate plots at fenced and grazed riparian sites during primary sampling periods in 4 different years and 13 secondary sampling periods within years (1996:4, 1997:4, 2004:2, 2005:3).

Species	Fenced			Grazed		
	Replicate 1	Replicate 2	Replicate 3	Replicate 1	Replicate 2	Replicate 3
Ground-nesting Guild			000000001000	0000000010001		0000000001001
Black-and-white Warbler						
<i>Mniotilta varia</i>						
Kentucky Warbler	0000000000010	00000000000100		0000000000010		0000000010000
<i>Oporornis formosus</i>						
Northern Bobwhite			0000000010100	0100000000000		0000000010000
<i>Colinus virginianus</i>						
Wild Turkey	0000001111011	0000100011010	0000100011010	0000000000110	00000000100000	0000000001000
<i>Meleagris gallopavo</i>						
Shrub-nesting Guild						
Acadian Flycatcher	0000000010000					
<i>Empidonax vireescens</i>						
American Goldfinch	0100010100100		0011111001000	0100101100000	00000000001000	0010001000000
<i>Carduelis tristis</i>						
American Robin			1000000001000		0000000001000	1100000000000
<i>Turdus migratorius</i>						
Blue-gray Gnatcatcher	1100010000100	00000000000010	00100000001010	1000110000000	1000000000000	0000000001001
<i>Poliopitila caerulea</i>						
Brown Thrasher	1000000000000	1110111100000	0000010000000	0000001000000	1110111101010	1101110100000
<i>Toxostoma rufum</i>						
Chipping Sparrow				0000000001000		
<i>Spizella passerina</i>						
Common Grackle		0000100000000				
<i>Quiscalus quiscula</i>						
Dickcissel		0000000001100				
<i>Spiza Americana</i>						
Field Sparrow		1000011011100	0000000011001	1010011100011	1111111110001	
<i>Spizella pusilla</i>						
Gray Catbird	0100000000000		0000000010000			1000000000000
<i>Dumetella carolinensis</i>						
Indigo Bunting	1111111111111	0111111110111	1111111111111	1111111111110	1111111111111	0111111111111
<i>Passerina cyanea</i>						
Northern Cardinal	1111111111111	1101111111111	1111111111111	1111111111111	1111111111111	1111111111111
<i>Cardinalis cardinalis</i>						

## APPENDIX. Continued.

Species	Fenced			Grazed		
	Replicate 1	Replicate 2	Replicate 3	Replicate 1	Replicate 2	Replicate 3
Northern Mockingbird		0000001110001			0001001010000	
<i>Mimus polyglottos</i>						
Wood Thrush	100000000100	1000000000000		0000100000000	1000100000000	
<i>Hylotichia mustelina</i>						
Yellow-billed Cuckoo	111111111011	1111111111110	1111111111111	1111111011011	1111111111111	0111111111111
<i>Coccyzus americanus</i>						
Canopy-nesting Guild						
Baltimore Oriole	0000100000000			0000010000000		0000100000000
<i>Icterus galbula</i>						
Blue Jay	0000100011000	1110001100001	1111111110111	0000110001110	1111111111111	1111111110110
<i>Cyanocitta cristata</i>						
Eastern Kingbird			0000100000000		0000001000000	
<i>Tyrannus tyrannus</i>						
Eastern Wood-Pewee				1110111010010	1111110001000	1111111110110
<i>Contopus virens</i>	1111101100111		1111111111111			
Fish Crow				0000000001000		
<i>Corvus ossifragus</i>						
Great Blue Heron				0001000001000	0000000010000	
<i>Ardea herodias</i>						0000100010000
Great Horned Owl						0000000010000
<i>Bubo virginianus</i>						
Green Heron	0001000010000	1010000000000				
<i>Butorides virescens</i>						
Mourning Dove			0100000011000		0000000001000	00100000110000
<i>Zenaidura macroura</i>						
Red-eyed Vireo	1000110000000		0000100000000		0000101000100	0000000000100
<i>Vireo olivaceus</i>						
Red-shouldered Hawk		0000000000010				
<i>Buteo lineatus</i>						
Rose-breasted Grosbeak			0000100010000			0000100000000
<i>Phaeucticus ludovicianus</i>						
Ruby-throated Hummingbird			0000000000110	0000000000110		
<i>Archilochus colubris</i>						
Summer Tanager	0000000001100	0000000001000	0000000000011	00000000000100		
<i>Piranga rubra</i>						
Yellow Warbler	0000000000100		1000000010000		1000000000000	
<i>Dendroica petechia</i>						

## APPENDIX. Continued.

Species	Fenced			Grazed		
	Replicate 1	Replicate 2	Replicate 3	Replicate 1	Replicate 2	Replicate 3
Cavity-nesting Guild						
Barred Owl	1000000000001	0000000001010	1000100000000	0000000010000	0000000010000	0000000010000
<i>Strix varia</i>						
Carolina Chickadee	0001111101111	1001111011010	1011011111111	1100111110111	1011011010111	1110011100111
<i>Poecile carolinensis</i>						
Carolina Wren	0111010101111	0110001011000	1101110111111	0100011101100	1101001111011	0010000001111
<i>Thryothorus ludovicianus</i>						
Downy Woodpecker	1011000100101	1111100010101	1101111101111	1100101010101	0111001011011	1111010011111
<i>Picooides pubescens</i>						
Eastern Bluebird	0000000010111	1010000000100		0100001000001	0110000010010	0110000000100
<i>Sialia sialis</i>						
European Starling			0100000000000			
<i>Sturnus vulgaris</i>						
Great Crested Flycatcher	1111111101111	1111111111110	1111111110111	1110111110101	1011110110111	1111011110111
<i>Myiarchus crinitus</i>						
Hairy Woodpecker	0000000010000	0000000100000	0000000010000			
<i>Picooides villosus</i>						
Northern Flicker	0000000010000					
<i>Colaptes auratus</i>						
Pileated Woodpecker		0000000010010			0000000010000	0000000010100
<i>Dryocopus pileatus</i>						
Red-bellied Woodpecker	1111111111111	1111111111111	1111111111111	1100111101111	1111111111111	1111111111111
<i>Melanerpes carolinus</i>						
Red-headed Woodpecker	0000000000100					
<i>M. erythrocephalus</i>						
Tufted Titmouse	1111111111110	1111111111110	1111111011111	1111111111111	1111111111111	1111111111111
<i>Baeolophus bicolor</i>						
White-breasted Nuthatch	0000001011000	0100011001010	0000010011010	0000000001100	0000001010010	0000001011100
<i>Sitta carolinensis</i>						
Other Species						
Brown-headed Cowbird	1001010010100	0100011100100	0010000001100	1101100011000	0011110001000	0100000000111
<i>Molothrus ater</i>						
Eastern Phoebe					0001000000000	0100000001000
<i>Sayornis phoebe</i>						