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POSTFLEDGING SURVIVAL AND MOVEMENT IN DICKCISSELS (*SPIZA AMERICANA*): IMPLICATIONS FOR HABITAT MANAGEMENT AND CONSERVATION

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Abstract.—When land managers incorporate the habitat needs of grassland birds into their planning, they typically rely on management recommendations based on habitat use by adults during nesting. Habitat requirements for other critical life stages are seldom known and may differ from those of nesting adults. Using radiotelemetry, we examined survival and habitat use by juvenile Dickcissels (*Spiza americana*) during the postfledging period. In 2003 and 2004, we monitored 60 fledgling Dickcissels for ≤30 days after they left the nest. Mortality rates were highest during the first week after leaving the nest, and only 33% of the fledglings survived the first four weeks after leaving the nest. Estimated mean survival times were 16.9 ± 1.6 days after birds left the nest. In both years, fledgling survival was positively associated with dense vertical and horizontal structure of forbs at nests. Survival tended to be positively associated with vertical grass density on adult territories and negatively associated with patchily distributed forbs on adult territories. Fledgling habitat use was restricted to areas where Dickcissels nested and adjacent fields. Habitats used included corn and soybean fields, grasslands, and wetlands. Our results suggest that the fledgling period is a critical stage for Dickcissels and that fledglings require habitat similar to habitat used for nesting. *Received 24 June 2005, accepted 14 March 2006.*

Key words: agriculture, Dickcissel, fledgling stage, grassland birds, habitat use, radiotelemetry, *Spiza americana*, survival analysis, tallgrass prairie.

Supervivencia Durante el Período Posterior al Emplumamiento en *Spiza americana:* Implicancias para el Manejo de Hábitat y Conservación

Resumen.—La información sobre las necesidades de hábitat para las aves de pastizal incorporada en los planes de manejo normalmente se basa en recomendaciones hechas con base en el uso de hábitat de aves adultas durante la nidificación. Los requerimientos durante otras etapas importantes de la vida son rara vez conocidos y éstos pueden ser diferentes de los de los adultos que se encuentran nidificando. Utilizando radiotelemetría, examinamos la supervivencia y uso de hábitat de juveniles de *Spiza americana* durante el período posterior al emplumamiento. Durante los años 2003 y 2004, monitoreamos 60 volantones durante los 30 días posteriores al abandono del nido. Las tasas de mortalidad más altas fueron durante la primera semana después del abandono del nido, y sólo el 33% de los volantones sobrevivieron las cuatro primeras semanas posteriores al abandono del nido. El tiempo promedio de supervivencia estimado fue de 16.9 ± 1.6 días después de abandonar el nido. En ambos años, la supervivencia de los volantones se relacionó positivamente con la estructura vertical y horizontal de hierbas distintas a pastos en los territorios de adultos. La supervivencia tendió a estar relacionada positivamente

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con la densidad de pasto vertical en los territorios de adultos y a negativamente con las hierbas distintas a los pastos distribuidas en parches en los territorios de aves adultas. El uso de hábitat por parte de los volantones se restringió a los lugares en que *S. americana* se reproduce y a campos adyacentes. Los hábitats utilizados fueron campos de maíz y de soya, pastizales y humedales. Nuestros resultados sugieren que el periodo de emplumamiento es un período crítico para *S. americana,* y que los volantones requieren de un hábitat similar al utilizado para la nidifcación.

Agriculture has greatly affected North American grassland ecosystems, and the bird populations associated with grassland habitats have shown more consistent declines than any other bird group in North America (Knopf 1994, Rich et al. 2004, Sauer et al. 2004). Conservation of species and communities in the former tallgrass prairie ecoregion is complicated not just by habitat loss and fragmentation, but also by the fact that all of the remaining fragments must be actively managed to compensate for the disruption of fire and grazing regimes that are critical to maintaining tallgrass prairie.

Land managers depend on information about habitat needs of species of conservation concern in their efforts to manage remaining grassland fragments. In the case of grassland birds, management guidelines tend to be based on habitat use by nesting adults (e.g., Johnson et al. 2004). Little information on other critical life stages is available to be incorporated into these plans.

One potentially critical life stage is the fledgling stage (Lang et al. 2002, Kershner et al. 2004). This is generally defined as the period after young birds leave the nest, before they become independent of their parents. During the fledgling stage or postfledging period, birds learn crucial life skills and face the highest mortality risks of their lives (Parsons et al. 1976, Greenwood and Harvey 1982, Magrath 1991, Vega Rivera et al. 1998, Monrós et al. 2002, Wheelwright et al. 2003). Fledglings of many species are not capable of much movement or flight for at least the first few days after leaving the nest (e.g., Anders et al. 1997, Kershner et al. 2004), which makes them more vulnerable to predators and environmental conditions (e.g., heat, rain). Only recently have techniques such as radiotelemetry advanced to the point where relatively small and secretive passerines can be studied during the fledgling stage. Recent studies of grassland species have confirmed that fledglings have high rates of mortality, emphasizing the need to understand this life-history stage in birds of conservation concern (Kershner et al. 2004, Suedkamp Wells 2005).

Survival studies of birds during the fledgling stage can improve estimates of population productivity and vulnerability and provide information on factors beyond nesting success that affect productivity (Anders et al. 1997, Powell et al. 1999, Suedkamp Wells 2005). Because adult habitat needs are often the focus of management activities intended to help grassland birds, it is important to know whether the habitat needs of fledglings are the same as those of adults. Once the flying ability of fledglings improves, they become capable of moving to habitats beyond their natal area (Dhondt 1979, Anders et al. 1997, Vega Rivera et al. 1998, Yackel Adams et al. 2001, Kershner et al. 2004), possibly using different habitats than adults used.

We studied the postfledging ecology of Dickcissels (*Spiza americana*), a grassland bird species of conservation concern (U.S. Fish and Wildlife Service [USFWS] 2002, Rich et al. 2004), to provide information about their survival and habitat use. Our specific objectives were (1) to measure survival during the fledgling stage to determine whether it is a critical life-history stage in Dickcissels and (2) to evaluate the habitat use of Dickcissel fledglings and the effects of environmental variables on survival.

Methods

Study Areas

Our study area was divided between two wildlife refuges in the Missouri River Valley of eastern Nebraska and western Iowa. Boyer Chute National Wildlife Refuge (NWR) encompasses 1,356 ha, including 820 ha of grassland (USFWS unpubl. data). DeSoto NWR covers 2,947 ha, including 664 ha of grassland (USFWS 2001). Both refuges are in what was historically the tallgrass prairie region. Today, the refuge land consists of restored grassland fragments of variable age and composition interspersed with agricultural fields, wetlands, and forests. All grasslands are actively managed using prescribed burning at approximately three- to five-year intervals.

We defined grassland fragments or fields using the boundaries set by the refuge managers. We used radiotransmitters to mark nestlings from nests in 11 distinct fields in 2003 and 19 fields in 2004. Field boundaries were defined by fence lines or transitions between management regimes, or both. The fields we used ranged in size from 4.3 to 132.5 ha (mean ± SE = 25.2 ± 6.7 ha) and were embedded in a landscape of row-crop fields, small wetlands, forested areas, and a variety of grasslands. Our fields were dominated by tallgrass species such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), with varying densities of forbs and woody shrubs.

Nest Location and Radiotransmitter Attachment

We located Dickcissel nests from May through August 2003 and 2004 by incidental flushes and observation of adults. We monitored nest contents by visiting each nest once every three days. Nestlings in our study area typically fledged when they were seven or eight days old (Berkeley 2004); we marked fledglings when they were five days old to minimize the chance that we would cause them to fledge early. We randomly selected one nestling per brood and fitted it with a Micropip radiotransmitter (weight: 0.45–0.55 g) with a 13-cm whip antenna and a battery life of three (Ag 317 battery) or four (Ag 379 battery) weeks (Biotrack, Wareham, Dorset, United Kingdom). Transmitters were attached using a figure-eight leg harness constructed with elastic beaded cord, a method previously used for Dickcissels (Walk 2001, Suedkamp Wells et al. 2003, Suedkamp Wells 2005) and other small passerines (Rappole and Tipton 1991, Powell et al. 1998, Norris and Stutchbury 2002). The transmitter packages were 3–4% of the nestlings' masses when marked, and ≤3% of their body weight at fledging. In addition, we marked all nestlings in a brood with a federal leg band and a unique combination of colored leg bands.

Radiotracking

We located fledglings once daily while their movements were within 5 m of their nests, and twice daily as they began to move >5 m away, until they were found dead or left the area. We located individuals by following their signal with a handheld three-element Yagi antenna and R2000 receiver (Advanced Telemetry Systems, Isanti, Minnesota) until the bird was seen (usually flushed). For younger, less mobile birds, we used the receiver to approach within 10 m of the signal and searched the vegetation until they were found. We limited searching to ≤30 min, after which point we left to avoid further stressing the bird. For all marked birds, we recorded distance and direction moved from nests and habitats used.

If a bird's signal was lost, we searched for the signal by walking around the field where the fledgling was last located and listening for the signal in adjacent fields. Signals could be detected ≤1.5 km away under ideal conditions, but detection distance varied widely, depending on vegetation and bird behavior.

We assigned four different fates to fledglings: (1) died—on the basis of recovery of dead bird or disappearance of individuals when they were too young to have left the area on their own (e.g., out of the nest only one to three days); (2) survived and left the area—individuals were old enough and observed to be flying well enough to be able to leave the area before their signal was lost; (3) survived, and radiotransmitter expired—the date the signal was lost matched the estimated expiration date of the radiotransmitter battery; or (4) unknown fate—the bird was of an ambiguous age when its signal was lost and we could not assign a fate, or an undamaged radiotransmitter was recovered without the bird. These fates were assigned for descriptive purposes and were not used in survival analyses, where all individuals whose signals were lost as well as those whose fates were not confirmed were right-censored (see below).

Variables Measured

Morphometric variables.—We recorded age (days), flattened wing length (mm), tarsus length (mm), and mass (g) for all marked birds and their siblings. Wing chord, tarsus, and mass were correlated ($r > 0.70$ for each pair), and a correlation-based principal component analysis (PCA) found that these variables loaded equally on principal components (PCs; Berkeley 2004). Thus, we chose to use mass alone in further analyses, because the ecological significance is comparatively easy to interpret and so that this study will be comparable with other postfledging studies that use mass. Mass increases with age, and the age of nestlings varied at the time we weighed them. We used the residuals of the regression of nestling age on mass—mass (g) = 9.8 + 0.8 age when marked (days) ($F = 8.20$, df = 1 and 89, $P = 0.005$)—as a standardized value for mass in survival and movement analyses (Berkeley 2004).

Environmental variables.—We recorded habitat measurements at three spatial scales: nest-site level (four points 5 cm from the nest); adult territory level (five random points between 2 and 10 m from the nest); field level (nine random points across the grassland fragment containing the nest). We measured nest site- and territory-level vegetation structure at least one week after young left their nests to minimize disturbance to fledglings. We measured vegetation at the field level in July each year. We measured the density of woody shrubs and forbs around nests, within territories, and across fields using the point-centered quarter method (Cottam and Curtis 1956, Rotenberry and Wiens 1980). The mean and coefficient of variation (CV) of these density estimates describe the horizontal vegetation structure at each scale. Grasslands also vary in the height and composition of vegetation in the vertical scale. We used the "Wiens pole" method of placing a narrow pole vertically at each measurement site and recording the number of times that vegetation touched the pole at each height (Rotenberry and Wiens 1980, Martin et al. 1997). These "hits" were recorded as either grasses, forbs, or woody shrubs. The number of times that vegetation in each category touched the Wiens pole also provided a measure of grass, forb, and shrub densities at the point. The percentage of total hits from grass, forbs, and shrubs provides an estimate of vegetation composition. Litter depth and maximum vegetation height were also recorded at each site measured with the Wiens pole. Maximum vegetation height was defined as the height of the tallest plant touching the pole. The means of all vegetation measures were calculated and used in further analyses unless otherwise noted.

We used field boundaries defined by the NWR managers that represented boundaries between different habitats or management regimes. Field size and the ratio of area to perimeter were calculated from geographic-information-system (GIS) layers provided by the NWRs.

We recorded habitat use of fledglings that left their natal fields, defining habitat types on the basis of classifications from GIS layers provided by the NWRs. Available habitat was measured in a 100-m buffer surrounding the natal field, using ARCGIS, version 8 (ESRI, Redlands, California). This radius represents the potential habitat available for the initial movement from the natal field; we compared the first recorded use of areas outside the natal field with this measure of habitat availability.

DATA ANALYSIS

Means are presented as $\bar{x}$ ± SE. All analyses were conducted with JMP, version 5 (SAS Institute, Cary, North Carolina). We analyzed relationships between explanatory variables and survival using univariate models. Because many of the vertical vegetation variables measured were correlated with each other, PCAs were used to condense these variables. The PCs were interpreted using the PC loadings, which reflect the direction and correlation of the original variables on the PC (Bailey et al. 2002). The PCAs were done separately by year, because variables did not load identically onto the PCs in both years (Table 1). These analyses were done using six measures of vertical vegetation structure at each of three spatial scales (nest-site, territory, and field levels; Table 1). Instead of using mean numbers of vegetation contacts with the Wiens pole as measures of vertical vegetation densities in PCAs, absolute measures (calculated using total numbers of vegetation contacts) were used (Table 1). We used the minimum number of PCs that accounted for ≥90% (cumulative percentage) of the variation among the variables in survival and movement analyses, and the effects of PCs from the same spatial scale were tested together against survival in multivariate models. Each PC was interpreted on the basis of the component loadings (Table 2). In 2003, birds were monitored in only 11 fields, with a skewed number of birds per field,

Table 1. Loadings of six vertical vegetation-structure variables onto principal components (PCs) and the percentage of variation among the variables explained by each PC in principal component analyses (PCAs), separated by year and spatial scale. Loadings greater than 0.40 and less than –0.40 were considered to explain a large portion of the variation among the data that loaded onto the PCs. Loadings between –0.40 and 0.40 are not shown.

		2003			2004		
		Nest	Territory	Field	Nest	Territory	Field
		Cumulative variation explained					
	PC1	55.4	41.9		50.8	53.4	54.8
	PC2	92.8	76.4		87.9	84.9	85.1
	PC3		92.8			97.7	
		Variables entered in PCA					
Absolute grass density	PC1	–0.47			–0.43		
	PC2						
	PC3		0.88			0.87	
Absolute forb density	PC1		0.54		0.41	–0.51	–0.48
	PC2	0.58			–0.42		
	PC3						
Absolute shrub density	PC1	0.42					
	PC2		0.67		0.57	0.69	0.65
	PC3						
Percent grass	PC1	–0.54	–0.54		–0.56	0.53	0.50
	PC2						
	PC3						
Percent forbs	PC1		0.59		0.43	–0.55	–0.54
	PC2	0.59			–0.41		
	PC3						
Percent shrubs	PC1	0.44					
	PC2		0.67		0.57	0.68	0.66
	PC3						

so we did not analyze the effects of habitat at the field level.

We estimated survival of Dickcissel fledglings with the nonparametric Kaplan-Meier procedure (Kaplan and Meier 1958, Lee and Go 1997). The survival time in this procedure is a measure of the interval between an origin and the occurrence of a given event (Lee and Go 1997). In the present study, the interval is defined as beginning the day a nestling left the nest and ending when it was found dead, its signal was lost, or its radiotransmitter was recovered. The initiation of the monitoring interval was the same for all birds, because they were all marked before they left the nest; thus, no left-censoring was needed. Marked nestlings that did not survive to leave the nest are not included in the analyses. Observations were right-censored if the exact survival time was unknown because the fate of the bird could not be determined owing to signal loss or the recovery of an intact radiotransmitter. Right-censoring of the data calculates survival probabilities while taking into account that some individuals have incomplete observations and, thus, unknown survival times (Collett 2003).

We used Cox proportional hazard regression models to relate survival times of fledglings to explanatory variables (SAS Institute 2002). Overall significance of the model is tested using a likelihood-ratio test. Output of this analysis includes a parameter estimate (β) and a relative risk ratio for each explanatory variable. Risk ratios <1 indicate that higher values of the explanatory variable are associated with lower risks of mortality (or higher survival), and risk ratios >1 indicate that higher values of the explanatory variable are associated with higher risks of mortality (or lower survival). Explanatory variables used in univariate

Table 2. Results of univariate Cox proportional hazard models relating habitat variables at three spatial scales to survival of marked Dickcissel fledglings over a 30-day monitoring interval in eastern Nebraska and western Iowa in 2003 and 2004.

	β[a]	SE[b]	L-R χ^2[c]	P[d]	Risk ratio[e]
Nest-site level					
Mean horizontal forb density (m^2)	–0.04	0.03	4.35	0.037	0.96
Mean horizontal shrub density (m^2)	–0.01	0.04	0.12	0.732	0.99
Maximum vegetation height (cm)	–0.01	0.01	1.61	0.204	0.99
Mean litter depth (cm)	0.08	0.09	0.80	0.371	1.09
Mean horizontal CV forb density (m^2)[f]	NA	NA	NA	NA	NA
Mean horizontal CV shrub density (m^2)[f]	NA	NA	NA	NA	NA
Territory level					
Mean horizontal forb density (m^2)[f]	0	0	1.99	0.159	1.00
Mean horizontal shrub density (m^2)[f]	0.07	0.07	0.67	0.415	1.07
Maximum vegetation height (cm)[f]	NA	NA	NA	NA	NA
Mean litter depth (cm)	–0.03	0.15	0.05	0.826	0.97
Mean horizontal CV forb density (m^2)[f]	1.27	0.64	3.50	0.062	3.56
Mean horizontal CV shrub density (m^2)[f]	0.68	0.50	1.74	0.187	1.98
Field level					
Mean horizontal forb density (m^2)	0	0	1.80	0.179	1.00
Mean horizontal shrub density (m^2)	0	0.04	–0.01	0.961	1.00
Maximum vegetation height (cm)	0	0.02	0	0.946	1.00
Mean litter depth (cm)	0.31	0.40	0.65	0.419	1.37
Mean horizontal CV forb density (m^2)[f]	1.33	1.24	1.73	0.189	3.80
Mean horizontal CV shrub density (m^2)[f]	0	0	0	1.000	1.00

[a] A parameter estimate for each variable tested where a positive value corresponds to a risk ratio that is >1, and a negative value corresponds to a risk ratio that is <1.

[b] Standard error of β.

[c] Likelihood-ratio test statistic representing the test on the null hypothesis that the parameter estimate for the variable is zero.

[d] P-value indicates significance of the effect of the variable in the model.

[e] A relative value that relates a unit increase in the explanatory variable to an increase or decrease in the relative risk of fledgling mortality; ratio < 1: risk of mortality decreased; ratio > 1: risk of mortality increased.

[f] Mean horizontal CV forbs and mean horizontal CV shrubs not available at the nest-site level; mean horizontal forb and shrub density data at the adult territory level were not available for 2003; maximum vegetation height was not measured at the territory level in either year.

Abbreviations: CV = coefficient of variation, NA = not available.

analyses from both years were pooled and tested for year effects. We added year as a factor in further analyses if differences were detected between years.

Because of variation in survival times, sample sizes of tracking locations among fledglings were unequal. Thus, movement analyses were done by testing dependent variables against distance moved away from nests on three separate days (days 1, 7, and 15 of each bird's postfledging period) that represented times when movement and flight abilities among individuals were markedly different.

The possible relationships between field size and shape and fledgling survival and movement were evaluated using multiple regression. The size and shape of the fields were evaluated against the average values for survival probability and movement of fledglings from nests in each field.

We compared habitats used by fledglings after they left their natal fields to the availability of habitats (Manly et al. 1993). Expected use of habitats was calculated using the proportion of the habitat type in the environment, and observed use was calculated as the proportion of individuals moving to fields of that habitat type. We tested the hypothesis that fledglings move to habitat types in proportion to their availability in the surrounding environment by calculating the log-likelihood chi-square test (Manly et al. 1993).

Results

Fledgling Survival

We followed the fates of 27 fledglings in 2003 and 33 fledglings in 2004. We assigned fates to 52 of the 60 birds; 8 birds (13%) fledged but were assigned an unknown fate. During the monitoring period, 32 fledglings (53%) died as a result of predation or other causes, such as heat stress or disease. Of the birds known to have survived, 9 fledglings survived and left the area (15%), and 11 survived until their radiotransmitters expired (18%) while remaining in the natal area (e.g., they were resighted after their radiotransmitters had failed). The rate of mortality did not differ significantly between years (Cox proportional-hazard model, likelihood-ratio [hereafter, L-R] χ^2 = 0.02, df = 1 and 60, P = 0.878), so the data from both years were pooled to construct a survival curve (Fig. 1). The mean survival time of the 60 individuals that fledged was 16.9 ± 1.6 days over a 30-day monitoring period starting when the birds left the nest. After eight days out of the nest, only 22 of the 60 fledglings (36.7%) were alive, after which mortality rates leveled off (Fig. 1).

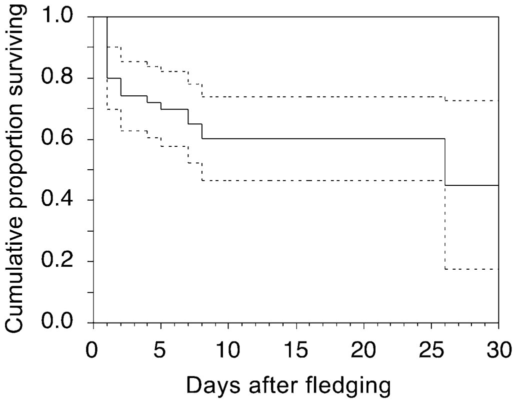

Fig. 1. Kaplan-Meier survival curve (solid line) and 95% confidence intervals (dashed lines) for 60 radiomarked Dickcissel fledglings in 2003 and 2004. The *y*-axis shows the cumulative proportion of fledglings surviving over a 30-day monitoring period. The *x*-axis shows time to event or the amount of time an individual was monitored before it died, its signal was lost, or its radiotransmitter was recovered. The curve is adjusted (by right-censoring of observation times) for individuals whose fates were unknown (signals were lost, or undamaged radiotransmitters were recovered without the bird). Mean survival time for fledglings = 16.9 ± 1.6 days for a period of up to four weeks.

Relationships with mass.—The relative risk of mortality was not affected by nestling mass (when controlling for nestling age by using residual mass; L-R χ^2 = 2.34, df = 1 and 59, P = 0.125, $\beta = -0.16 \pm 0.10$, risk ratio = 0.85).

Habitat relationships at the nest-site level.—Univariate analyses of the effects of nest-site-level habitat on survival found a significant effect of forb density (Table 2). Higher densities of forbs were associated with a significant reduction in the risk of fledgling mortality (Table 2).

In the 2003 PCA of vertical vegetation structure, PC1 was heavily loaded by low mean vertical grass densities and high mean vertical shrub densities and explained 55% of the variation, whereas PC2 was heavily loaded by high mean vertical forb densities and explained an additional 37% of variation (Table 1). The overall model of PC1 and PC2 on survival of fledglings was not significant (L-R χ^2 = 5.53, df = 2 and 23, P = 0.063). However, higher values of the individual variable PC2 in the model were associated with a significant reduction in the relative risk of mortality. Principal component 1 did not have a significant effect on survival times (Table 3).

In 2004, PC1 was heavily loaded by high mean vertical forb densities and low mean vertical grass densities, and PC2 was heavily loaded by low mean vertical forb densities and high mean vertical shrub densities (Table 1). A multivariate model of PC1 and PC2 on survival times of fledglings was marginally significant (L-R χ^2 = 6.02, df = 2 and 30, P = 0.050), where higher values of PC1 were associated with a significant reduction in the relative risk of mortality (Table 3).

Habitat relationships at the adult territory level.—In univariate survival analyses, higher variation of forb densities on territories, as indicated by the CV, showed a trend to increase the risk of fledging mortality (Table 2). Other univariate analyses at this spatial scale were not significant (Table 2).

In 2003, PC1 was heavily loaded by high mean vertical forb densities and low mean vertical grass densities, PC2 was heavily loaded by high mean vertical shrub densities, and PC3 was heavily loaded by high mean vertical grass densities (Table 1). A multivariate model of PC1, PC2, and PC3 on survival times was

Table 3. Results of multivariate Cox proportional hazard models relating principal components (PCs) representing habitat composition to survival of marked Dickcissel fledglings over a 30-day monitoring interval in eastern Nebraska and western Iowa in 2003 and 2004.

Year	Principal component	β [a]	SE [b]	L-R χ^2 [c]	P [d]	Risk ratio [e]
		Nest-site level				
2003	PC1 (high shrub, low grass)	–0.06	0.33	0.04	0.845	0.94
2003	PC2 (high forbs)	–0.92	0.72	5.14	0.023	0.26
2004	PC1 (high forbs, low grass)	–0.61	0.32	6.01	0.014	0.54
2004	PC2 (high shrubs, low forbs)	0.15	0.30	0.26	0.608	1.16
		Territory level				
2003	PC1 (high forbs, low grass)	–0.18	0.30	0.41	0.523	0.84
2003	PC2 (high shrubs)	0.23	0.26	0.78	0.377	1.26
2003	PC3 (high grass)	–0.68	0.54	2.05	0.152	0.50
2004	PC1 (low forbs)	0.03	0.24	0.01	0.915	1.03
2004	PC2 (high shrubs)	–0.04	0.17	0.08	0.782	0.96
2004	PC3 (high grass)	–0.56	0.52	2.04	0.153	0.57
		Field level				
2004	PC1 (high grass, low forbs)	0	0	0	1.000	1.00
2004	PC2 (high shrubs)	0	0	0	1.000	1.00

[a] A parameter estimate for each variable tested where a positive value corresponds to a risk ratio that is >1, and a negative value corresponds to a risk ratio that is <1.

[b] Standard error of β.

[c] Likelihood-ratio test statistic representing the test on the null hypothesis that the parameter estimate for the variable is zero.

[d] P-value indicates significance of the effect of the variable in the model.

[e] A relative value that relates a unit increase in the explanatory variable to an increase or decrease in the relative risk of fledgling mortality; ratio < 1: risk of mortality decreased; ratio > 1: risk of mortality increased.

not significant (L-R χ^2 = 2.43, df = 3 and 23, P = 0.487), and none of the individual PCs in the model was significantly associated with survival times in 2003 (Table 3).

In 2004, PC1 was heavily loaded by high mean vertical grass densities and low mean vertical forb densities, PC2 was heavily loaded by high mean vertical shrub densities, and PC3 was heavily loaded by high mean vertical grass densities (Table 1). A multivariate model of PC1, PC2, and PC3 on survival times was not significant (L-R χ^2 = 2.20, df = 3 and 30, P = 0.53). Once again, none of the PCs in the model was significantly associated with survival in this year, but there were tendencies for fledgling survival to be positively associated with PC3 (Table 3).

Habitat relationships at the field level.—No univariate field-level vegetation variables were significantly associated with the relative risk of mortality (Table 2). Survival of fledglings tended to differ among fields (all P < 0.050), so all analyses were blocked by field to account for these differences. In 2004, PC1 was heavily loaded by high mean vertical grass densities and low mean vertical forb densities, and PC2 was heavily loaded by high mean vertical shrub densities (Table 1). A multivariate model of PC1 and PC2 on survival times was not significant (L-R χ^2 = 18.68, df = 13 and 32, P = 0.133). None of the individual PCs in the model significantly affected survival time (Table 3).

Fledgling Movement and Habitat Use

By 15 days, the rate at which fledglings moved was significantly greater in 2004 than in 2003 (Fig. 2). After one day out of the nest, fledglings had moved 3.7 ± 1.1 m in 2003 and 6.5 ± 1.0 m in 2004 (ANOVA, F = 3.35, df = 1 and 64, P = 0.072). By seven days after leaving the nest, fledglings had moved 93.1 ± 25.9 m in 2003 and 123.2 ± 19.7 m in 2004 (ANOVA, F = 0.85, df = 1 and 29, P = 0.363). After 15 days, fledglings had moved 141.8 ± 63.9 m in 2003 and 355.3 ± 46.9 m in 2004 (ANOVA, F = 7.26, df = 1 and 19, P = 0.015). The maximum distances recorded in 2003 and 2004 were 401 and 1,060 m, respectively.

Habitat relationships with distance moved.—Spatial habitat variables (independent variables same as those in Tables 2 and 3) and morphometric variables had no significant effects on movement from nests on postfledging days 1, 7, and 15 (all $P > 0.10$) .

Postfledging movement was not related to either field size or field shape (as measured by the area-to-perimeter ratio) after one ($R^2 = 0.10$, $F = 0.61$, df = 2 and 6, $P = 0.57$) or seven days out of the nest ($R^2 = 0.24$, $F = 0.23$, df = 2 and 6, $P = 0.80$). After 15 days out of the nest, there was a relationship between movement and field shape and size ($R^2 = 0.51$, $F = 5.17$, df = 2 and 6, $P = 0.049$). There was a significant positive partial correlation with field size ($\beta = 5.79$, $P = 0.036$) and a negative, though not significant, partial correlation with field shape ($\beta = -2.75$, $P = 0.111$).

Habitat use.—Fledgling movement was limited to natal fields and adjacent areas during both years of the study. All fledglings started out in grasslands in both years. The fledglings that left their natal fields moved to crop fields (primarily soybean and corn), other grasslands, and wetlands (Fig. 3). The null hypothesis that fledglings used habitat types in proportion to their availability was not supported. Available habitat surrounding the natal fields comprised crop fields (38%), wetlands (7%), other grasslands (30%), and other habitats, primarily woodlands (25%). During their initial movement from their natal fields, fledglings used croplands slightly more than expected from availability (44%), wetlands less than expected (6%), grasslands more than expected (50%), and fledglings were never observed in the other habitat types (L-R $\chi^2 = 9.87$, df = 3, $P = 0.020$). If all subsequent fields used are compared with available habitat, crop fields are used less than expected (34%), as are wetlands (2%) and other habitats (0%), whereas grasslands are used at a rate higher than expected based on habitat availability (64%; $\chi^2_3 = 39.14$, $P < 0.001$).

DISCUSSION

FLEDGLING SURVIVAL

The low survival rate of fledgling Dickcissels in their first four weeks after leaving the nest (Fig. 1) reinforces concerns that the fledgling

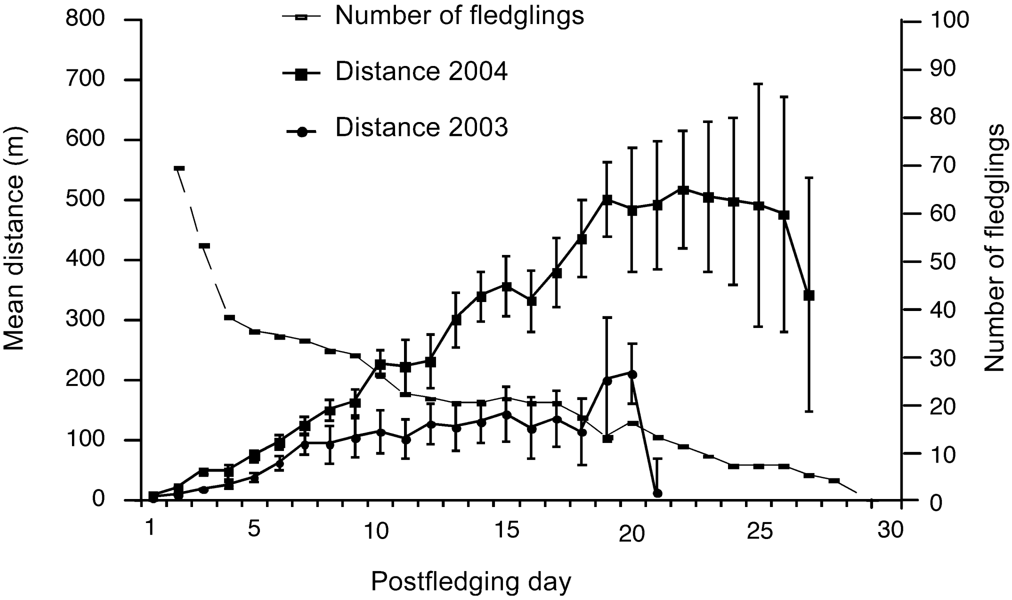

Fig. 2. Mean distance Dickcissel fledglings moved from their nests per postfledging day in 2003 and 2004. The x-axis shows postfledging day, the left y-axis shows the mean distance fledglings moved from their nests (m), and the right y-axis shows the number of fledglings monitored per day. The circles summarize movement in 2003, the large squares summarize movement in 2004, and the small squares show the sample size each day. Standard error bars for movement in each year are shown. For 2003, mean distance = 63 m, maximum distance = 401 m. For 2004, mean distance = 162 m, maximum distance = 1,060 m.

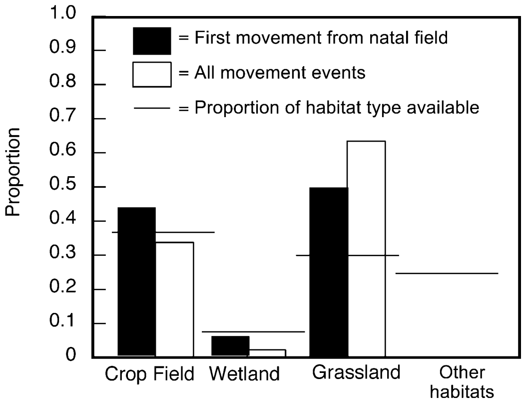

Fig. 3. Habitat use by Dickcissel fledglings that moved from their natal fields in 2003 and 2004. Proportions of the fledglings using each habitat type after their first movement from their natal site (black bars; *n* = 16) and using each habitat type for all movement events (open bars; *n* = 47) are shown in relation to the proportion of each habitat type available surrounding the natal fields (line).

stage is a critical period in the life history of Dickcissels. This low survival is consistent with the earlier work on passerine fledglings that was based on observations of color-marked birds. For example, juvenile survival in Great Tits (*Parus major*) was estimated at only 25% during the first 10 weeks after fledging (Dhondt 1979).

More recently, radiotelemetry has made it possible to follow a wider range of small passerines after they leave the nest. The survival of Dickcissel fledglings in our study was lower than the 54% survival over 29 days reported for Dickcissels in Missouri (Suedkamp Wells 2005) but similar to that for Lark Buntings (*Calamospiza melanocorys*; 37% over 21 days; Yackel Adams et al. 2001). Survival of juvenile Eastern Meadowlarks (*Sturnella magna*) was higher in both Illinois (56–69% over 13 weeks; Kershner et al. 2004) and Missouri (61% over 10 weeks; Suedkamp Wells 2005).

Several lines of evidence suggest that repeated radiotracking of fledglings did not adversely affect birds or cause the high mortality we documented. First, studies of small passerines have failed to find adverse effects from being radiomarked using the leg-harness method (Rappole and Tipton 1991, Powell et al. 1998, Naef-Daenzer et al. 2001, Walk 2001, Norris and Stutchbury 2002, Suedkamp Wells 2005). Also, a study of wild-caught male Dickcissels measured stress levels to determine whether birds fitted with radiotransmitters using the leg-harness method experienced adverse effects from being radiomarked. This study did not show long-term elevated levels of fecal glucocorticoid levels, a hormone indicating an individual's stress level, though the birds did show an initial stress response associated with handling (Suedkamp Wells et al. 2003). In addition, fledglings exhibit little of the fear response shown by adults, which suggests that any stress response would likely be lower than that of adults. Finally, observations of unmarked fledglings are consistent with the high mortality levels we measured during the days just before and after fledging (L. I. Berkeley unpubl. data).

In the present study, the highest fledgling-mortality rates occurred during the first eight days of the monitoring interval. High mortality during this initial period after leaving the nest was also observed in Dickcissels in Missouri (Suedkamp Wells 2005) and has been reported in other species (Naef-Daenzer et al. 2001, Yackel Adams et al. 2001, Keedwell 2003, Cohen and Lindell 2004, Kershner et al. 2004). For example, 71% of fledgling deaths of Eastern Meadowlarks occurred within one week after leaving the nest, with 64% of these deaths occurring in the first three days postfledging (Kershner et al. 2004). Such dramatic mortality rates immediately after fledging are likely a result of the poor movement, flight, and foraging skills of these young birds (McFadzen and Marzluff 1996, Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Kershner et al. 2004).

The decrease in mortality observed during the latter part of the fledgling stage runs counter to some studies where mortality is high immediately after fledging and spikes again when birds become independent from their parents or move away from their natal areas (e.g., Sullivan 1989, Anders et al. 1997). This transition to independence may be a critical life-history event, distinct from fledging, where mortality increases as juveniles with limited foraging skills have to start finding their own food and where predation risk may increase as vigilance and defense by parents decreases (Weathers and Sullivan 1991, Wheelwright and Templeton 2003). Our observations of Dickcissels with radiotransmitters, as well as other color-marked fledglings, suggest that fledglings depend on their parents for food for at least four weeks after leaving the nest (Berkeley 2004). Color-marked adults and fledglings were seen in proximity to each other, with adults feeding the fledglings, even after radiotransmitters had expired. It is possible that we did not see a second spike in mortality in the present study because birds had not yet become independent and that mortality increases in fledglings more than 30 days out of the nest. However, a rise in mortality was not observed for Eastern Meadowlarks, even though the fledglings were followed past the time when they became independent of their parents (Kershner et al. 2004), which suggests that at least some grassland passerines do not experience a mortality peak as they become independent of postfledging parental care.

Predation was a major cause of mortality for Dickcissel fledglings (Berkeley 2004), as it has been for other species (Sullivan 1989, Anders et al. 1997, Yackel Adams et al. 2001, Powell et al. 2003, Cohen and Lindell 2004, Kershner et al. 2004). Dickcissel fledglings were easy to approach and often remained still when found, instead of flying away as observed in other species (Soler et al. 1994, Anders et al. 1997, Keedwell 2003, Kershner et al. 2004). Snakes were a key predator of young Dickcissels both in the nest (Klug 2005) and after fledging. Western plains garter snakes (*Thamnophis radix*), red-sided garter snakes (*T. sirtalis parietalis*), and fox snakes (*Elaphe vulpina*) were observed eating both marked and unmarked nestlings and fledglings. Judging from studies of nest predation (Klug 2005), small and medium-sized mammals are also likely predators of fledglings.

Variables Affecting Survival

Nestling growth is often used as an indicator of body condition, and low postfledging survival is generally associated with smaller birds (reviewed by McCarty 2001). However, Dickcissels that were heavier as nestlings did not have higher survival as fledglings.

Variation in survival times among individuals was explained by nest-level and territory-level habitat, but not by field-level variables. The chances of fledgling survival in the present study were higher in association with dense vertical and horizontal vegetation structure at the nest-site level, which suggests that both types of structure may be important for Dickcissel young in this region. At the territory level, fledgling survival tended to be lower on territories with a patchy distribution of forbs. These results suggest that a more consistent cover of forbs within 10 m of the nest may have been beneficial to these birds. Because dense forbs at the nest (in addition to dense forbs at the territory level, mentioned above) were also positively associated with survival, we suggest that a consistently higher cover of forbs across territories may be important for Dickcissels during their postfledging period.

Given that predation was a key cause of death in the present study, the positive associations of dense horizontal and vertical vegetation structure (particularly forbs) with survival may indicate that these variables provided fledglings with more protection from predators (Mullin and Cooper 2000, Stake et al. 2005). Several unexplained deaths of both marked and unmarked birds were associated with periods of extreme heat (L. I. Berkeley pers. obs.); dense vegetation may also mitigate extreme temperatures by providing fledglings with shadier or cooler microhabitat.

There were no relationships between habitat and fledgling survival at the larger field level, even though fledglings move across this spatial scale. This may be because most mortality occurred during the first few days of the monitoring period, when individuals were usually within 10 m of their nests or because older fledglings were able to select better resting places regardless of the average quality of a field.

Fledgling Movement and Habitat Use

The mean distances that fledglings moved from their nests were different between the two years; the distance moved was always greater in 2004 than in 2003. The latter year was warmer and drier than 2004, which may have affected food supply or the degree of heat stress. West Nile virus was also widespread in the study area for the first time in 2003, and several of the fledglings appeared to be sick, which may have reduced mobility (L. I. Berkeley unpubl. data). Within years, we did not detect any effects of the habitat variables we measured on fledgling movements from their nests.

In both years, the distances fledglings moved were small enough for us to reject our hypothesis that the habitats used by fledglings differed from those used for nesting. Even after several weeks out of the nest, most fledglings were in their natal fields or fields adjacent to them, and usually in the same fields that adults used for nesting. All nestlings that left their natal fields were still being fed by adults, so it is unclear whether fledglings were selecting habitats or simply following adults who were selecting habitats. Fledglings were found in habitats such as wetlands and crop fields that adults did not use for breeding (Fig. 3). However, fledglings or their parents showed significant selection for grasslands, whereas they used cropland less than expected judging from its prevalence in the environment.

Dispersal patterns at other sites are likely to be a function of how large and isolated grassland fragments are at those sites. In the present study, most nests were within 100 m of the fragment edge, so birds could leave the site with limited mobility. Also, other grassland fragments were adjacent to almost all our natal sites. The limited mobility of fledglings may restrict their ability to move from more isolated fragments. In larger fragments, we predict that individuals would not even be capable of leaving their natal sites until they were out of the nest for at least three weeks.

Within grasslands, our results suggest that fledgling Dickcissels survive well under the conditions recommended to encourage adult settlement in eastern Nebraska and western Iowa. Dechant et al. (2003) report several studies showing that adults in this region are often associated with habitat that includes dense vegetation and forbs. Our results show that habitat with dense vegetation and forbs may also be beneficial for fledglings because fledgling survival increased in dense grasses and forbs at our study sites, at least over the lifetime of the radiotransmitters used. A key remaining question is what happens once fledgling Dickcissels become independent of their parents (which never occurred while radiotransmitters were still active during our study).

Conservation Implications

Our results suggest that the fledgling life stage is a vulnerable time for Dickcissels and, thus, may be an important factor affecting recruitment into Dickcissel populations. Current guidelines for grassland management in central North America that focus on increasing the density of native forbs will likely increase survival of fledglings and increase adult settlement. Both vertical and horizontal vegetation densities were beneficial to fledgling survival, with patchily distributed vegetation having a negative effect. Therefore, incorporating a diversity of grasses and forbs into restorations that become dense at a variety of heights and that provide consistent cover over areas where Dickcissels nest may improve fledgling survival in eastern Nebraska and western Iowa.

Most noteworthy is the observation that fledgling Dickcissels remain dependent on their parents for several weeks after fledging and that their mobility is limited for much of this time. In grasslands where mowing or other management activities occur in the summer, we suggest that guidelines minimize disturbance to natal fields and adjacent areas not just during the time when Dickcissels are nesting, but that managers also be aware of the importance of the first few weeks of the postfledging period for the survival of young grassland birds.

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