Faculty Research & Creative Activity   Biological Sciences

January 2004

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RENESTING DECISIONS AND ANNUAL FECUNDITY OF FEMALE DICKCISSELS (*SPIZA AMERICANA*) IN ILLINOIS

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Abstract.—Renesting decisions and annual fecundity are crucial for interpreting other demographic information, yet are infrequently reported. We used radiotelemetry to monitor female Dickcissels (*Spiza americana*) throughout the 1999 and 2000 breeding seasons in southeastern Illinois. Overall fecundity (regardless of whether females remained in the study area throughout the breeding season) was 0.61 ± 0.13 female fledglings per year. Of females that remained within the study area, 94% fledged young (1.25 ± 0.15 female fledglings per year). Most females (62%) that experienced nest failure emigrated from the study area (moved >10 km) in 2.8 ± 0.6 days; others (36%) initiated subsequent nests in 8.5 ± 0.8 days. After fledging ≥1 young, 95% of females ceased breeding for the season. Successful and failed nest sites were indistinguishable on the basis of vegetative characteristics. Moreover, replacement nests had similar vegetative characteristics and were similar distances from habitat edges, compared with initial nests, which suggests that female Dickcissels do not or cannot "improve" nest-site characteristics in response to nest failure. We observed two behaviors unusual in female Dickcissels: one bird that fledged two broods in one season, and the return of five females banded in 1999 to the study site in 2000. *Received 3 March 2003, accepted 24 June 2004.*

Resumen.—La decisión de anidar más de una vez por estación reproductiva y la fecundidad anual son elementos cruciales para interpretar información demográfica de diversa índole, pero estos datos son reportados con poca frecuencia. Usamos radio-telemetría para monitorear a hembras de *Spiza americana* durante las estaciones reproductivas de 1999 y 2000 en el sudeste de Illinois. La fecundidad global (sin considerar si las hembras permanecieron en el área de estudio durante la estación reproductiva) fue de 0.61 ± 0.13 pichones hembra emplumados por año. De las hembras que permanecieron en el área de estudio, el 94% produjo juveniles (1.25 ± 0.15 pichones hembra emplumados por año). La mayoría de las hembras (62%) que perdieron sus nidadas emigraron del área de estudio (se desplazaron >10 km) en 2.8 ± 0.6 días; otras (36%) iniciaron nidadas subsecuentes en 8.5 ± 0.8 días. Después de emplumar un volantón, el 95% de las hembras cesaron de criar por el resto de la estación. Los sitios de ubicación de nidos exitosos y de nidos que fracasaron fueron indistinguibles con relación a las características de la vegetación. Más aún, los nidos vueltos a instalar presentaron características de la vegetación similares y estuvieron a distancias similares del borde comparados con los nidos iniciales, lo que sugiere que las hembras de *S. americana* no "mejoraron" o no pudieron "mejorar" las características de los sitios de anidación en respuesta al fracaso del nido. Observamos dos comportamientos inusuales en hembras de *S. americana*: un ave que produjo dos nidadas en una sola estación, y el regreso al sitio de estudio en el 2000 de cinco hembras anilladas en 1999.

Annual fecundity is an essential parameter for determining population growth rates, yet it has been directly measured in relatively

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few studies (Nolan 1978, Gavin and Bollinger 1988, Kershner et al. 2004). Empirical data on breeding-season decisions and annual fecundity form the basis for constructing and validating models that can be applied to other species and populations (Pease and Grzybowski 1995, Schmidt and Whelan 1999, Powell and Frasch 2000). Even among well-studied species, such as the Dickcissel (*Spiza americana*), direct measures of annual fecundity are lacking, making it necessary to estimate fecundity levels (e.g. McCoy et al. 1999) that might suggest a role

for reproductive failure in recent population declines (Peterjohn and Sauer 1999).

Nesting birds are expected to use strategies that maximize fecundity (Sandercock et al. 1999). Female birds make a number of decisions during the nesting season that can have important demographic and fitness consequences, including when to initiate and cease breeding within a season; how to select nest sites; whether to abandon parasitized nests; when to terminate care of fledglings; and whether, when, and where to renest. Those decisions are influenced by many factors, such as food availability (Rodenhouse and Holmes 1992), breeding-season length (Sandercock et al. 1999, DeCocco et al. 2000), perceived chances of successful renesting (Jackson et al. 1989), and identity of nest predators (Powell and Frasch 2000).

Many investigations of nest-site selection have compared characteristics of nest sites with available sites, and successful sites with failed sites, but fewer have addressed adaptive site-preference (Clark and Shutler 1999). Nest failure may cue individuals to change or "improve" the characteristics of replacement nest sites (Marzluff 1988). Alternatively, nest-site selection may be genetically constrained so that individuals cannot or do not learn (Howlett and Stutchbury 1997), or nest failure may be unrelated to nest-site characteristics, in which case there is no advantage to changing nest sites (Filliater et al. 1994).

We used radiotelemetry to measure annual fecundity and looked for evidence of adaptive nest-site placement among female Dickcissels in southeastern Illinois from 1999 to 2000. We followed radiotagged birds experiencing natural nest failure (predation) and those subjected to experimental clutch removal to better understand "renesting decisions." Our objectives were to (1) determine how female Dickcissels respond to nest failure (dispersal, renesting, and time to make those decisions), (2) measure demographic success of initial nests as compared with that of replacement nests, and (3) compare physical characteristics of replacement nest sites to those of initial nests.

METHODS

We conducted the study within six grassland tracts (24–120 ha) of Prairie Ridge State Natural Area (PRSNA) in Jasper County, Illinois. Consisting of ~800 ha of restored grassland managed for grassland wildlife, PRSNA is embedded in an agricultural matrix (see Walk 2001 for a detailed description of PRSNA, including its vegetation, management, and landscape context). Soon after Dickcissels arrived at the site in early May in 1999 and 2000, we located their nests by watching females carrying nest materials or by flushing females from nests by walking haphazard paths; we searched ~200 ha among the six tracts.

Radiotelemetry.—To ensure that female Dickcissels were monitored from their first nest of the season, in both years we captured the earliest returning females at the study site, rather than attempting to monitor most or all of the females that would eventually settle within a grassland tract. As soon as females initiated egg laying and incubation, we captured birds by flushing them from nests into nearby mist nets. We banded females with individually numbered federal bands and a unique combination of colored bands, recorded mass and wing chord, and attached a radiotransmitter. We used a modification of the attachment procedure described by Rappole and Tipton (1991), whereby a cotton thread harness, with loops of thread under each leg, held the transmitter in place on the bird's synsacrum, with the antenna trailing along the bird's tail. Transmitters (Sparrow Systems, Champaign, Illinois) had an expected operating period of 60 days; their total length was ~90 mm; and their mass was 0.96 to 1.05 g (including harness), representing a mean of 3.96% (range: 2.9–4.5%) of the female's body weight. Female Dickcissels were released 5–10 min after capture.

We assumed that radiotelemetry did not significantly alter breeding behavior of Dickcissels, and that we captured each female at her first nest attempt of the breeding season on the study site. It is possible but unlikely that the females nested elsewhere before arriving at our site; earliest-reported nests were in the first week of May in Missouri (Winter 1999) and the second week of May in Texas (Basili 1997).

We tracked female Dickcissels using programmable receivers and three-element yagi antennas. We located birds three times per week when they had active nests or recently fledged young, using handheld antennas that gave us detection ranges of <400 m. When females did not have active nests, we located them more frequently by searching with truck-mounted antennas that could be raised to a height of ~4 m, allowing us to detect radio signals to 1 km; we followed up with handheld antennas to determine the birds' precise locations and locate renest attempts. About every two weeks, we searched via fixed-wing aircraft for birds that could not be located from the ground, searching as far as ≥10 km from the individual's last known location. From aircraft, signals could be detected to 6 km. If radiotagged birds could not be relocated within 10 km of their last known location, we classified them as having emigrated from the study area.

Nest monitoring and experimental clutch removal.—
Nest contents were visually inspected every 3 to 4
days to record numbers and development of eggs and
nestlings. Within one grassland tract, we removed the
entire clutch from initial nests ("experimental" nests
hereafter; unaltered nests and females are referred to
as "controls"). We removed eggs near sunrise on the
morning after radiotagging the incubating female. In
some cases, eggs hatched prior to intended experi-
mental removal, and young were not disturbed. In
other cases, natural predation had already occurred.
Following experimental clutch removal, radiotagged
females were tracked intensively to determine behav-
ior and movements (Wentworth 2001). We did not
remove any eggs from replacement nests.

*Nest productivity and fecundity measures.—*We used
several measures to compare productivity of initial
nests with that of replacement nests, including clutch
size, egg hatchability, hatchlings per nest, nestling
survival, fledglings per nest, and fledglings per suc-
cessful nest. "Egg hatchability" was the proportion of
fully incubated eggs that hatched and was intended to
measure egg infertility and embryo mortality. We cal-
culated nestling survival as the proportion of hatch-
lings that survived to fledging in successful nests,
indexing nestling mortality attributable to factors
such as starvation and inclement weather. Initial nests
with experimental clutch removal were not consid-
ered in productivity measures, except in calculations
of clutch size; if we had incorrectly classified initial
nests (i.e. if we captured birds at very early renests),
our comparison of reproductive parameters between
initial and replacement nests could have been biased.

Although we assumed that we located every nest
attempt by every radiotagged female in the study
area, nests destroyed prior to onset of incubation
may not have been detected. That error could lead
to underestimation of nest attempts and eggs laid
through the season. We calculated annual fecundity
by two methods: considering all females, regardless of
whether they remained in the study area; or consider-
ing only females that remained within the study area
for the entire breeding season. We assumed an even
gender ratio among fledglings, and express fecundity
as female fledglings per adult female per year.

*Nest-site characteristics.—*Within one week of each
nest's fate (fledge or fail), we measured vegetation at
nest sites and at random points 20–30 m away. Nest
height was measured from soil surface to rim of nest
bowl. We estimated nest concealment at a height
and distance of 1 m from nests in four directions.
Vegetation composition was determined by center-
ing a 0.25-m^2 frame—modified from Daubenmire
(1959)—on nests and estimating the percentage of
grasses, forbs (including scarce woody plants), lit-
ter, and bare soil. Litter and bare-soil coverage were
minor and unimportant in nest fate (Walk 2001) and
are not considered further. Average vegetation height

was also determined within the Daubenmire frame
centered on nests. To determine vegetation density,
we placed a pole banded in 1-dm increments at nest
sites and measured visual obstruction in four direc-
tions (Robel et al. 1970). Distance from nests to nearest
agricultural and wooded edges was recorded.

*Statistical analyses.—*We used the first two axes
from principle components analysis (PCA) to dis-
criminate fecundity and vegetative characteristics
of groups of Dickcissel nests (McCune and Mefford
1999). Descriptive statistics for variables considered
in each grouping are provided. First, we compared
fecundity of initial and replacement nests, using the
variables clutch size, egg hatchability, and nestling
survival, to determine if nest productivity changes
predictably across nesting seasons. Only nests that
survived to fledging were included, to avoid consid-
ering nests with missing data values for egg hatch-
ability or nestling survival. Second, we considered
vegetative characteristics to attempt to distinguish
successful nests (producing ≥1 fledgling), depre-
dated nests, and random points. Only initial nests
of the season and random points paired with those
nests were considered, to reduce seasonal variation
in vegetative measures. Where available, data from
initial nests of females that shed radiotransmitters
were included to increase sample sizes. Finally, we
contrasted characteristics of initial nests and replace-
ment nests to examine if female Dickcissels altered
nest-site characteristics in response to nest failure.
Differences in fecundity estimates between years and
in productivity measures of initial and replacement
nests were tested using multivariate analysis of vari-
ance on SPSS, version 11.0 (SPSS, Chicago, Illinois).
All values are presented as mean ± standard error (SE)
unless otherwise noted.

RESULTS

We captured and radiotagged 26 female
Dickcissels in 1999 and 35 females in 2000
($n = 61$ birds). All nests of captured females had
been initiated (first egg laid) prior to 25 May
(within the earliest 10% of Dickcissel nests initi-
ated at the site each year; Walk 2001, J. Walk and
E. Kershner unpubl. data) and within one week
of observed arrival of female Dickcissels in the
nesting area, which suggests that we followed
each female from her first nest of the season at
the site.

Capture and radiotelemetry appeared to
have little influence on breeding behavior. After
capture, we observed each female returning to
her nest in <30 min, often <15 min. Fifty-nine
of 61 females (97%) continued incubation and
brood-rearing until fledging, nest predation,

or experimental clutch removal. Most of the females we captured (79%) accepted the harness and transmitter. One bird abandoned the eggs she was incubating two days after being captured. Rate of nest abandonment (1.6%) is lower than the rate observed in Dickcissels that were not captured (3.7%; Walk 2001). We were unable to gather data by radiotelemetry for the remaining 12 females, because of transmitter–harness failure (20%). In all cases, telemetry failure occurred during or after initial nest attempts, but prior to subsequent nesting. In 10 of those cases, the female was able to cut the harness and shed the transmitter. One transmitter ceased functioning shortly after attachment (though we observed the transmitter and harness still attached to the female), and one female died. We found no evidence that the transmitter–harness harmed any other bird.

Although we were able to follow some color-banded females after telemetry failure, we considered only numbers of eggs, hatchlings, and fledglings produced from initial nest attempts of those females (Table 1). We excluded them from other analyses, because those results are strongly biased toward individuals that remained in the same area for the remainder of the nesting season. Therefore, we considered 49 female Dickcissels with known behavior following initial nest attempts.

Transmitters began to expire ~55 days after being attached to birds (after 15 July). Less than 10% of Dickcissel nests at the study site are initiated after 10 July (Walk 2001). All birds carrying transmitters to expiration had fledged young or had not initiated new nests (or both), and had moved <2 km over ≥3 weeks. Females that remained in the study area until transmitter

expiration probably did not emigrate and renest elsewhere in the same year; latest nests are initiated in early August, range-wide (Basili 1997).

Initial control nests. — The majority of initial nest attempts by radiotagged females failed (68%; Fig. 1). In 24 of 25 cases, nest loss was attributed to predation. In one instance, an eastern garter snake (*Thamnophis sirtalis*) was observed eating the three-egg clutch (see Olson and Warner 2001 for documentation of this and eight other instances of *T. sirtalis* preying on eggs and young grassland birds at the study site). One nest was abandoned. Although that female was observed returning to incubation after radiotagging and release, the nest was abandoned within two days, and capture may have contributed to nest desertion.

Replacement nests. — We located 18 replacement nests (14 second attempts, 4 third attempts). Eight replacement nests fledged one or more young (44%). Clutch size tended to be smaller in replacement nests than in initial nests (Table 1). However, successful initial and replacement nests fledged similar numbers of young, because nestling survival (proportion of hatchlings that fledge from successful nests) was greater for initial than for replacement nests (Table 1). Although PCA did not produce two clear clusters, initial nests tended to plot high on axis 1 (factor loading indicating larger clutch size and lower nestling survival) and axis 2 (factor loading for greater egg hatchability). Subsequent nests plotted low on axis 1 (smaller clutch size and greater nestling survival) and axis 2 (lower egg hatchability) (Fig. 2).

Dispersal distances from previous to subsequent nest sites were highly variable, ranging from 22 to 806 m (222 ± 63 m). One female built

TABLE 1. Reproductive parameters of initial and subsequent Dickcissel nests at Prairie Ridge State Natural Area, Illinois, 1999–2000. Initial nests with experimental clutch removal are excluded from all parameters except clutch size.

Parameter	Initial nests (Mean ± SE)	n	Subsequent nests (Mean ± SE)	n	Factor loadings PC1	PC2
Clutch size	4.21 ± 0.08	61	3.47 ± 0.19	15	0.644	0.263
Egg hatchability [a]	0.858 ± 0.034	29	0.798 ± 0.070	12	−0.431	0.901
Hatchlings per nest attempt	2.32 ± 0.29	48	1.83 ± 0.38	18	–	–
Nestling survival [b]	0.731 ± 0.071	14	0.959 ± 0.042	8	−0.632	−0.345
Fledglings per nest attempt	0.77 ± 0.20	48	1.06 ± 0.34	18	–	–
Fledglings per successful nest	2.64 ± 0.32	14	2.38 ± 0.26	8	–	–
Variance explained (%)	–	–	–	–	57.3	27.9

[a] Proportion of eggs that hatch in a fully incubated clutch.
[b] Proportion of hatchlings that survive to fledging within a successful nest.
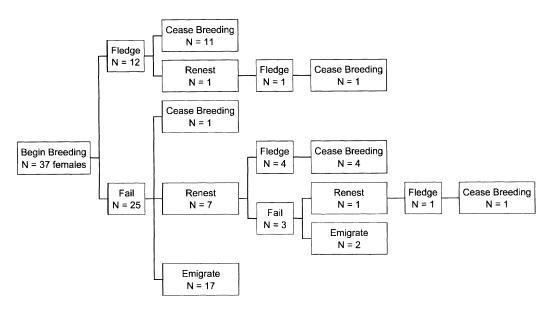
FIG. 1. Decision tree for 37 female Dickcissels during the breeding season at Prairie Ridge State Natural Area, Illinois, 1999–2000. Females exposed to experimental clutch removal are not included.

a second nest 788 m from the first, and a third nest 806 m from the second. However, her first and third nests were only 29 m apart.

Nest-site characteristics. — Characteristics of initial nests that were depredated (*n* = 27, including nests of 3 females that shed transmitters) and successful (*n* = 15, including nests of 3 females that shed transmitters) were similar (Table 2). With PCA, successful nests, failed nests, and random points were indistinguishable on the basis of vegetation height, visual obstruction,
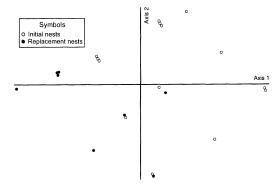

FIG. 2. Ordination of initial and replacement Dickcissel nests, based on clutch size, egg hatchability, and nestling survival. Axis 1 has positive loading for clutch size and negative loading for nestling survival. Axis 2 has positive loading for egg hatchability. (Some points are staggered to avoid overlap.)

percentage of grass coverage, and percentage of forb coverage (Fig. 3).

Similarly, we noted few changes in vegetative characteristics at replacement nests as compared with initial nests. However, many replacement nests, but not all, clustered low on axis 1 (Fig. 4). On the basis of factor loadings, we describe that space as representing nests with greater percentage of forb coverage, lower percentage of grass coverage, greater visual obstruction, and greater vegetation height (Table 3). Females tended to build replacement nests higher above ground in vegetation of greater average height, visual obstruction, and forb composition and somewhat lower grass composition. However, vegetation at associated random locations exhibited the same trends toward greater average vegetation height, visual obstruction, and forb composition later in the season (Table 3). Females did not alter nest concealment or distance to habitat edges among nest attempts (Table 3).

Response to failure. — Female Dickcissels responded similarly to natural predation and experimental clutch removal in proportions of females ceasing breeding, emigrating, and renesting; in days to emigration or renesting; and in distance to renesting locations (*P* > 0.18). Therefore, we pooled natural and experimental nest failures (*n* = 47) for describing female Dickcissels' responses.

TABLE 2. Characteristics of failed nests (n = 27), successful nests (≥1 young fledged; n = 15), and random points (n = 41) paired with Dickcissel nests at Prairie Ridge State Natural Area, 1999–2000. To reduce seasonal variation in vegetative characteristics, only initial nests of the season were considered.

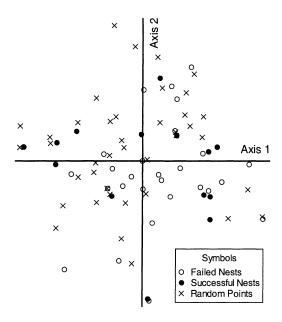| Characteristic	Failed nests (Mean ± SE)	Successful nests (Mean ± SE)	Random points (Mean ± SE)	Factor loadings	
				PC1	PC2
Nest height (cm)	17 ± 1.8	17 ± 3.1	–	–	–
Vegetation height (cm)	65 ± 3.6	59 ± 6.1	66 ± 4.1	0.290	−0.642
Visual obstruction (cm)	45 ± 3.1	40 ± 5.2	36 ± 2.8	0.319	−0.629
Nest concealment (%)	85 ± 3.0	85 ± 4.2	–	–	–
Grass coverage (%)	34 ± 4.9	39 ± 7.2	37 ± 4.6	−0.616	−0.358
Forb coverage (%)	53 ± 5.1	47 ± 8.1	43 ± 4.5	0.659	0.252
Agricultural edge (m)	152 ± 12	137 ± 23	–	–	–
Wooded edge (m)	392 ± 25	332 ± 49	–	–	–
Variance explained (%)	–	–	–	46.7	39.7

FIG. 3. Ordination of successful and failed Dickcissel nests and random points, based on vegetative characteristics. Axis 1 has positive loading for percentage of forb coverage and negative loading for percentage of grass coverage. Axis 2 has negative loading for visual obstruction and average vegetation height.
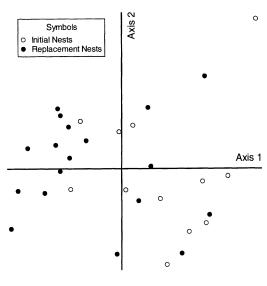

FIG. 4. Ordination of initial and replacement Dickcissel nests, based on vegetative characteristics. Axis 1 is characterized by positive loading for percentage of grass coverage and negative loading for percentage of forb coverage, visual obstruction, and average vegetation height. Axis 2 is characterized by positive loading for percentage of nest concealment and percentage of forb coverage and negative loading for percentage of grass coverage and nest height.

After nest failure, females made the decision to emigrate (62%), renest (36%), or cease nesting (2%). Each of the females that emigrated from the study area was located at least once after nest failure, which suggests that all survived nest failure with a functional transmitter. Emigrating females were last detected by telemetry within the study area 2.8 ± 0.6 days after nest failure (range: 1–15 days). One emigrant

was relocated 13 km from her nest site, 5 days after nest failure; another was relocated 32 km away, 28 days after failure. Stage of nest at time of failure had no apparent effect on emigration; 60% of females (18 of 30) with nests failing during incubation emigrated and 65% of females (11 of 17) emigrated when nestlings were depredated. Birds that decided to renest did so rather quickly; first eggs were laid in

TABLE 3. Vegetative characteristics of initial and replacement nest attempts by female Dickcissels, Prairie Ridge State Natural Area, Illinois, 1999–2000.

Characteristic	Initial nests Mean ± SE	Replacement nests Mean ± SE	n	Factor loadings PC1	PC2
Nest sites					
Nest height (cm)	22 ± 2.0	29 ± 3.4	17	–0.232	–0.405
Vegetation height (cm)	85 ± 7.4	99 ± 5.9	17	–0.382	–0.269
Visual obstruction (cm)	61 ± 5.3	75 ± 4.5	17	–0.411	–0.120
Nest concealment (%)	87 ± 5.1	86 ± 4.7	12 [a]	0.252	0.482
Grass coverage (%)	28 ± 5.8	18 ± 5.5	17	0.420	–0.462
Forb coverage (%)	60 ± 7.7	75 ± 7.0	17	–0.461	0.397
Agricultural edge (m)	113 ± 20	113 ± 23	12 [b]	0.229	0.332
Wooded edge (m)	288 ± 46	296 ± 42	16	0.355	–0.186
Variance explained (%)	–	–	–	35.9	23.0
Random sites					
Vegetation height (cm)	52 ± 8.4	78 ± 9.2	7 [b]	–	–
Visual obstruction (cm)	59 ± 8.7	73 ± 7.2	17	–	–
Grass coverage (%)	31 ± 6.2	27 ± 6.7	17	–	–
Forb coverage (%)	45 ± 8.4	58 ± 7.9	17	–	–

[a] Concealment measures were not meaningful for some nests destroyed by predation (i.e. nests were shredded or removed from supporting vegetation).

[b] Data missing for some initial nests; data are then omitted from replacement nests for the same females.

replacement nests 8.5 ± 0.8 days (range: 4–15 days) after nest failure. Only one female ceased nesting and remained in the study area without having fledged young.

Response to success.—Radiotagged females produced 20 successful nests. In response to fledging young from nests, 95% of females ceased breeding attempts for the season (i.e. they did not renest prior to expiration of the transmitter; Fig. 1). One female initiated a second nest attempt 24 days after fledging young from her initial nest and successfully fledged a second brood. All females with successful subsequent nests ceased breeding for the season.

Although we did not attempt to monitor fledgling survival, we observed all successful females feeding fledged young within 50 m of nest sites for 8–18 days after fledging. One female was observed feeding a juvenile 43 days after fledging.

Annual Fecundity.—Only 49% of control females remained within the study area throughout a breeding season and had known nesting histories. Those birds fledged 1.25 ± 0.15 female young per season from 1.4 ± 0.1 nest attempts (Table 4). Seventeen of 18 females (94%) fledged young within the breeding season. All control females, many of which emigrated after nest failure and may have nested successfully elsewhere, had annual fecundity of 0.61 ± 0.13 female young per year (Table 4).

Return of banded females.—Five of 25 females (20%) emigrating from or remaining in the study area in 1999 were recaptured or resighted in 2000. Two females that emigrated after initial nest failure in 1999 were resighted in 2000, 1.1 km and 5 km from their 1999 nest sites. The former's initial nest in 2000 also failed, and the latter was found dead next to a nearly complete nest bowl. Three recaptured females fledged young in both years at nest sites <200 m from the previous year's nests. Each of the five returning birds had shed their transmitter between the end of the 1999 breeding season and the beginning of the 2000 breeding season. Of the 1999 cohort, in 2000 we resighted or recaptured 3 of 6 females with successful initial nests, 2 of 15 females that failed to fledge young and emigrated, and none of 8 females that renested. Note that some females are considered twice in this accounting (e.g. one female renested after fledging young from her initial nest; others renested, then emigrated following a second nest failure), and some females are not considered at all (e.g. those that renested successfully).

DISCUSSION

Almost all the female Dickcissels that remained within our study area nested until they fledged young and built replacement nests similar to initial nests, given available

TABLE 4. Annual fecundity of female Dickcissels at Prairie Ridge State Natural Area, Illinois, 1999–2000. Estimates are made for all radiotagged females (except those with experimental clutch removal), many of which emigrated following a nest failure (all females; $n = 37$), and for those females that remained within the study area for the duration of the nesting season (full-season females; $n = 18$). Annual fecundity measures did not differ between 1999 and 2000 ($P > 0.17$).

Parameter (per year)	All females		Full-season females	
	(Mean ± SE)	Range	(Mean ± SE)	Range
Eggs	4.9 ± 0.3	3–11	5.7 ± 0.5	4–11
Hatchlings	2.7 ± 0.4	0–7	3.8 ± 0.4	0–7
Female fledglings [a]	0.61 ± 0.13	0–2.5	1.25 ± 0.15	0–2.5
Nests	1.2 ± 0.1	1–3	1.4 ± 0.1	1–3
Successful nests	0.47 ± 0.09	0–2	1.0 ± 0.1	0–2

[a] One-half the total number of fledglings produced.

vegetation. The complete nesting history of 51% of the radiotagged females, which emigrated following nest failure, is unknown. It is possible that those birds renested >10 km from previous nests and eventually fledged young.

Annual fecundity of females that remained in the study area was 1.25 female young per adult female per year. That may be a liberal measure of annual fecundity, because all successful females remained within the study area. Considering all control females, fecundity was 0.61 female young per female per year. That annual fecundity measure may be conservative, given that many birds with failed nests dispersed long distances and likely renested outside the study area. McCoy et al. (1999) estimated that, in order to maintain stable populations, Dickcissels required annual fecundity of 1.39 and 0.90 female young per adult female per year, on the basis of adult survival rates of 0.59 and 0.69 for Bobolinks (*Dolichonyx oryzivorus*), a similar-sized Neotropical migrant, and the assumption that juvenile survival is one-half of adult survival. However, adult and juvenile survival of Dickcissels has not been measured, and fecundity levels that might indicate source or sink status of a population (*sensu* Pulliam 1988) can not be reliably estimated at this time.

Although few projects have studied marked females, most investigators have reported Dickcissels to be single-brooded (i.e. they do not initiate additional nests after fledging young; e.g. Zimmerman 1982). Thus, it was unexpected when one female in the present study attempted and succeeded in raising a second brood. Bollinger and Maddox (2000) also reported a double-brooded Dickcissel ~50 km from our study area.

They hypothesized that double-brooding is rare in Dickcissels because of time and energetic constraints imposed by postbreeding molting and Neotropical migration. We add that single broodedness is consistent with extended postfledging parental care. We observed an instance of postfledging care extending 43 days. Male Dickcissels typically contribute little, if anything, to provisioning nestlings and fledglings (but see Maddox and Bollinger 2000). If double-brooding is not feasible, extended care of fledglings may be a prudent investment for female Dickcissels if it is energetically inexpensive, does not delay molting and preparing for migration (Evans Ogden and Stutchbury 1996), and improves survival and condition of fledglings. The trade-off between extending parental care and forgoing additional nest attempts is made more favorable when nest predation rates are high and the chance of successfully fledging a second brood is low.

After failed nest attempts, factors that may influence renesting decisions include stage at which the previous nest failed, perceived likelihood of successful renesting, perceived availability of resources, and anticipated effects on survival. Dickcissels were equally likely to renest when eggs or nestlings were destroyed. Females may have used nest success of conspecifics within grasslands as a renesting cue. In 1999, we observed 42% nest success, whereas nest success was 27% in 2000 (Walk 2001). In 1999, 50% of females renested following failures, and one bird successfully produced a second brood. In 2000, 27% of females renested following failures, including one bird that ceased breeding before fledging young, the

only individual observed to do so. Bollinger and Gavin (1989) provide evidence that female Bobolinks used reproductive success of conspecifics, in addition to their own, in choosing whether to return to breeding sites.

Females that decided to renest initiated subsequent nests (i.e. laid first eggs) in as little as 4–5 days after nest failure, whereas others delayed renesting for up to 15 days. Rapid renesting may be typical of small passerines, with means of 5.05 days for Gray Catbirds (*Dumetella carolinensis*) and 5.53 days for Northern Cardinals (*Cardinalis cardinalis*) (Scott et al. 1987), 5.5 days for American Pipits (*Anthus rubescens*; Hendricks 1991), and 6.9 days for American Goldfinches (*Carduelis tristis*; Middleton 1979). Four to five days is suggested to be the shortest physiologically possible interval for passerines to renest (Scott et al. 1987).

Female Dickcissels renested 22–806 m from previous nest sites within our study area. Distances from failed nests to replacement nests averaged 37 m in American Pipits (Hendricks 1991) and 85 m in Prairie Warblers (*Dendroica discolor*; Nolan 1978), and ranged from 4 to 160 m in Hooded Warblers (*Wilsonia citrina*; Howlett and Stutchbury 1997). About one-third of Gray Catbirds abandoned territories, usually after nest failure, and moved ≤450 m (Darley et al. 1971). Zimmerman (1982) reported that 27% of female Dickcissels with failed nests renested in the same or nearby territories, but most disappeared and were not seen again.

When building replacement nests, female Dickcissels made little change in relation to initial nests sites. They did not attempt to move nearer or farther from agricultural or wooded edges. Subsequent nests were placed in taller, denser vegetation than initial nests; however, that placement paralleled seasonal growth of vegetation at paired random locations. Nests of unmarked birds were also placed in progressively taller and denser vegetation later in the 1996–2000 nesting seasons (Walk 2001). Our findings support several of the predictions made by Filliater et al. (1994) regarding passerines nesting in habitats with rich predator guilds: simple rules for nest placement, rapid renesting following failure, and little or no pattern of success or failure related to nest-site selection. Dickcissels place nests in tall, dense vegetation and renest or emigrate rapidly following nest failure. At our study site, the predator guild includes avian, mammalian,

and reptilian species. Additionally, prey within grasslands are concentrated in a narrow vertical band of vegetation, decreasing the likelihood that nest-site characteristics can reliably provide protection from all predators.

Subsequent nests contained fewer eggs than initial nests, but had greater nestling survival and therefore fledged similar numbers of young from successful nests. Judging from 512 nests, decreasing clutch size and increasing nestling survival are robust seasonal trends of Dickcissel nesting in the study area (Walk 2001). Clutch sizes, including those of Dickcissels, frequently decrease through the breeding season (Zimmerman 1983, Winter 1999). However, we could not discern whether changing clutch size was a replacement-clutch effect or time effect: are replacement clutches smaller because they are later, or are later clutches smaller because they are replacements (Arnold 1993)? Improving nestling survival may be related to warmer weather later in the season, because females are able to brood nestlings less and increase provisioning time, and nestlings allocate less energy to thermoregulation.

Fretwell (1986) and Basili (1997) speculated that Dickcissels nested within breeding seasons at widely spaced geographic locations. Indeed, half our marked population may have renested tens of kilometers or farther from initial nest sites. Based on peaks of nest initiations rangewide, Basili (1997) noted that Dickcissels that successfully fledged young in the southern part of the species' range (e.g. Texas) could conceivably move and renest again later in the breeding season in the northern portion of the range (e.g. Wisconsin). Nest initiations peaked in Texas and at our site on similar dates (late May; Basili 1997, Walk 2001). However, all birds that fledged young from nests in Illinois remained in the study area until at least 15 July–20 August (when transmitters expired), well past the late peak of nest initiations observed in Wisconsin (early July; Basili 1997). Our results suggest that many female Dickcissels likely renest at widely spaced locations after nest failure. However, it is improbable that female Dickcissels are double-brooded within different portions of the breeding range within a season.

Why did most females experiencing nest failure emigrate rather than renest nearby? Female Dickcissels were twice as likely to emigrate as renest within the study area. After nest failures,

emigrating Dickcissels left the study area in an average 2.7 days. Darley et al. (1971) found that a greater proportion of female Gray Catbirds that remained faithful to their mate and territory, as compared with females that abandoned their mate or territory, were ultimately successful in fledging young.

Several hypotheses have been presented to explain why birds disperse to different breeding sites despite costs and risks associated with finding suitable, alternative locations, mates, and resources. Dispersal may be motivated by avoidance of factors associated with nest failure (Jackson et al. 1989, Powell and Frasch 2000) or attraction to better sites (e.g. Clark and Shutler 1999). Dickcissels that emigrated effectively avoided predators, mates, and territories of previous nest failures and locations they may have depleted of resources, though dispersing >10 km was likely not necessary to achieve those objectives. However, birds that renested nearby did not appear to suffer from proximity to those factors. Dispersing birds also risk settling in other predator-rich, resource-poor sites and pairing with other failed mates.

Several lines of evidence suggest that long-distance dispersal is not based on attraction to better sites. First, vegetative characteristics are weakly related to Dickcissel nest fate (Hughes et al. 1999, Winter 1999, Walk 2001). Second, 40% of marked birds found suitable sites for successful nesting within the study area. Renesting birds did not alter nest-site characteristics in response to differences in available vegetation. Finally, although 71% of female Dickcissels emigrated or ceased nesting after initial nest attempts, we found that 55% of nests at PRSNA were initiated after 5 June (>10 days after first nests of marked females were initiated; Walk 2001). It is likely that female Dickcissels initially unsuccessful at other sites immigrated into our study area later in the breeding season. Zimmerman (1982) reported increasing density of female Dickcissels after the peak of nest initiations in Kansas, presumably because of birds immigrating after earlier nests failed elsewhere or delaying nest initiation.

Dispersal may have been related to site fidelity. Half of the females with successful initial nests in 1999 were recaptured in 2000, and each of those birds fledged young at proximate locations in both years. Females in their first breeding season may continue to disperse until they succeed in fledging young, and then develop fidelity to the successful site.

At least 20% of the 1999 cohort (successful and unsuccessful) returned in 2000. That is similar to the 24% return rate of female Bobolinks to low-quality sites in New York; 49% of females returned to a high-quality site (Bollinger and Gavin 1989). In contrast, Zimmerman and Finck (1989) reported that no banded females had ever returned in years of banding Dickcissels in old fields and prairies in Kansas. We did not attempt to capture most or all of the females occupying any grassland tract and could not search all nesting habitat (because of site restrictions). Therefore, we may have failed to resight or recapture other marked females that did return to the study area. We may have recorded returning female Dickcissels, whereas Zimmerman and Finck (1989) did not, because our population of Dickcissels is constrained to a relatively small amount of available nesting habitat surrounded by intensive row-crop agriculture, as compared with more-abundant nesting habitat in Kansas.

Identification of an adaptive function of dispersing >10 km within nesting seasons remains enigmatic. Dickcissel nest success can vary significantly among geographic regions (Basili 1997) and among years (Walk 2001). Long-distance dispersal may reflect female Dickcissels' attempts to locate and renest within "hotspots" of nesting success; but time, energetic costs, and mortality risks associated with such behavior must be great.

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Associate Editor: S. G. Sealy