BREEDING ECOLOGY OF THE DICKCISSEL

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Polygyny was once thought to have evolved in response to an unbalanced sex ratio in favor of females, but evidence to the contrary accumulated (Orians 1961, Verner 1964, Selander 1965, Zimmerman 1966). A theory developed that took into account the variability possible within habitats for such parameters as food, nest sites, and vegetative cover, and the importance this variability might have to the female choosing a mate (Verner 1963, 1965; Verner and Willson 1966). Polygyny is advantageous to the male so long as the total number of offspring increases with additional mates, but as two females must necessarily receive less help from the male than one could, the advantage for females is less obvious. If the density of the population is high enough to force some males to defend less suitable sites, a female could attain higher reproductive success by pairing with a mated male occupying a good territory than by choosing an unmated male on a poor territory.

Zimmerman (1966) confirmed that the Dickcissel (*Spiza americana*) is regularly polygynous in Kansas. He found that territory size, height of vegetation, and percentage of cover (especially forbs) were less for bachelor males than for mated males. More recently Zimmerman (1971) developed relationships between the volume of vegetation present and number of mates acquired, density of males, and reproductive success at these densities.

The objectives of this study were to determine which territorial features were important to the female in her choice of site and mate and the adaptive value of the polygynous mating behavior as assessed by reproductive success.

Study Areas and Methods

The study areas, hereafter identified as the north and south fields, are located on the University of Illinois Biological Research Area (Phillip's Tract) northeast of Urbana, Illinois. Both fields are abandoned cropland previously in corn. The early successional type of habitat offering both forb cover and grasses is one of several chosen by the Dickcissel in Illinois (Graber and Graber 1963). Other habitats supporting high densities are mixed hay, red clover, and edge shrubs.

The two fields were similar in physiognomy but differed in species composition primarily because of plowing times. *Setaria faberi* was the dominant species on the south field with *Chenopodium album* and *Polygonum pensylvanicum* next in importance. *Lactuca scariola, Aster pilosus, Erigeron canadensis,* and *E. annuus* were the important species on the north field with the exception of the west side in 1971 on which grass species were more common (*Setaria faberi, Andropogon gerardi*, and *Panicum virgatum* in particular).

Field studies were conducted daily when possible from mid-May to early

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August in 1971; observations in 1970 began in early May and ended once territorial boundaries and pair bonds were determined. On both study areas 50-meter grids were laid out to permit plotting the birds' locations on scale maps. Birds were not marked, but sufficient observations were made to be certain of the identity of each pair and the territorial boundaries. The maximum territory occupied was drawn on a scale map and the area in acres determined by a compensating polar planimeter.

Vegetation height was measured early, midway, and late in the nesting season with a pole marked in 1-foot intervals. Vegetation was recorded within each interval if it touched or came within 4 inches of the pole. Plant species were also recorded. Sampling points fell along the grid lines established and were approximately 12 m apart. Percent cover by vegetation at each height was calculated as percent of points having vegetation present. Plant species frequency is the percent of points having those species named. In 1971 nests were checked daily to record progress. Height in cm from the ground to the nest rim and of the vegetation directly above the nest was measured after each nest was located.

Arthropod production was sampled in 1971 on the south field with 20 water pan traps. Peter Price, University of Illinois entomologist, handled the collection and identification.

The t-test of means and a test for the equality of two percentages (Sokal and Rohlf 1969: 607–608) were considered significant at $P < 0.05$ level (two-tailed).

Results

Territory Size and Male Density

There was no direct correlation between size of territory and number of mates acquired (Table 1). Bigamy was the maximum degree of polygyny observed. On the south field, bachelor territories were significantly smaller than those of monogamous males each year, but bigamous males did not have the largest territories.

Zimmerman (1966) found that bachelor males occupied territories significantly smaller than mated males although there were no differences between monogamous and polygynous males (see also Orians 1961, Schartz and Zimmerman 1971). In related studies Verner (1964) found that territory size of Long-billed Marsh Wrens (*Telmatodytes palustris*) increased with each mate acquired, but Martin (1970) found no significant correlation for Bobolink (*Dolichonyx oryzivorus*) territories and Willson (1966) found an inverse relationship for Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*).

Zimmerman (1971) concluded that territory size was inversely correlated with male density. My data (Table 1) compare well with his graph (p. 599) as mean territory size ranged from 0.94 to 1.34 acres when density varied from 67 to 54 males per 100 acres. He also estimated a minimal territory size of about 0.9 acre reached at densities above 70 males per 100 acres. In 1970 when the density on my north field climbed to 119, mean territory size decreased only to 0.86 acre. Individual territory sizes were often less than 0.9 acre.

TABLE 1
TERRITORY SIZE AND MALE DENSITY[1]

	Bachelor	Monogamous	Bigamous	All males	Males per 100 acres	(% bigamous)
1970 North field						
	0.76 ± 0.23	0.84 ± 0.09	0.93 ± 0.06	0.86 ± 0.06	119[6]	(31)
Range (N)	0.53 – 0.98 (2)	0.40 – 1.15 (9)	0.68 – 1.09 (5)	0.40 – 1.15 (16)		
1971 North field						
	1.11 ± 0.00	0.90 ± 0.07	1.04 ± 0.00	0.94 ± 0.05	67[6]	(18)
Range (N)	(1)	0.68 – 1.21 (8)	1.00 – 1.07 (2)	0.68 – 1.21 (11)		
1970 South field						
	0.36 ± 0.10[2]	1.13 ± 0.04[2]	1.08 ± 0.27	1.05 ± 0.08[5]	62	(22)
Range (N)	0.25 – 0.46 (2)	0.89 – 1.41 (16)	0.66 – 2.12 (5)	0.25 – 2.12 (23)		
1971 South field						
	0.73 ± 0.12[3]	1.51 ± 0.10[3, 4]	1.11 ± 0.08[4]	1.34 ± 0.10[5]	54	(15)
Range (N)	0.62 – 0.96 (3)	0.87 – 2.34 (14)	0.95 – 1.24 (3)	0.62 – 2.34 (20)		

[1] Mean acres ± SE of $\bar{X}$.
[2–6] Differences significant between numbered pairs of figures.

Zimmerman (1971) also concluded that in his areas densities of 60 to 70 males per 100 acres forced some males into unsuitable habitats (see also Fretwell and Calver 1969). In 1970 at higher densities, Dickcissels were found in less preferred habitats nearby. One was a mixed forb pasture grazed by cows, another was a lightly wooded area with a groundcover of *Poa pratensis*. With lower densities in 1971, these habitats were left unoccupied.

VEGETATION

Percent cover was calculated for each field (Table 2). By the end of the season in 1970, the north field was significantly greater at all height intervals above 2 feet. This can be correlated with a higher percentage of polygynous males on the north field (Table 1). No consistent trend was established between fields in 1971.

Comparing each field between years during mid-season when sampling dates correspond closely, percent cover on the south field was significantly greater in 1970 than in 1971 at all height intervals above 3 feet. Between-year values were also significantly greater on the north field in 1970 and in this case, at all height intervals above 1 foot. On each field a greater percentage of males were polygynous in 1970.

Percent cover data were averaged at each height interval for groups of territories based on mating type. Differences were rarely significant

TABLE 2

PERCENT COVER BY VEGETATION FOR THE WHOLE STUDY AREA

Height in feet	Early South field	Early North field	Middle South field	Middle North field	Late South field	Late North field
1970	May 15–18		June 20–24		July 19–21	
0–1	100	100	100	100	100	100
1–2	85	79	96	98[d]	98	96
2–3	65	56	60[1]	75[1,e]	61[2]	80[2]
3–4	46	35	37[a]	38[f]	12[3]	54[3]
4–5	28	18	18[b]	22[g]	3[4]	29[4]
5–6	13	5	6[c]	8[h]	0[5]	8[5]
1971	June 3–5		June 26–28		August 8–10	
0–1	100	100	100	100	100	100
1–2	74	80	94	92[d]	100	100
2–3	40	36	53[7]	63[7,e]	98	99
3–4	19	16	21[a]	27[f]	82	75
4–5	7[6]	1[6]	6[b]	6[g]	43[8]	33[8]
5–6	2	0	1[c]	1[h]	10	10

[1–8] Differences significant between numbered pairs of figures.
[a–h] Differences significant between lettered pairs of figures.

and no consistent relationship was found between cover and number of mates acquired.

Plant species frequency on territories categorized by mating success was also analyzed. Success was rated by the number of mates acquired. As forb coverage has been found to be important to mating success (Zimmerman 1966, Martin 1970), the four major forb species, *Aster pilosus*, *Erigeron canadensis*, *E. annuus*, and *Medicago sativa*, were studied as a group.

The frequency of major forbs on bigamist territories was higher than that on both monogamous and bachelor territories on the north field in 1970 and on the south field in 1971 (Table 3).

FOOD AVAILABILITY

Given that the density of available food in marshes and prairies is potentially high but uneven in distribution, interterritorial differences

TABLE 3

FREQUENCY OF MAJOR FORBS ON TERRITORIES OF MALES WITH DIFFERENT MATING SUCCESS

	South Bachelor	South Monogamous	South Bigamous	North Bachelor	North Monogamous	North Bigamous
1970	40[1]	16[1]	23	36[2]	48[3]	69[2,3]
1971	36[4]	30[5]	59[4,5]	76	74	62

[1–5] Differences significant between numbered pairs of figures.

TABLE 4

MEAN TOTAL NUMBER ARTHROPODS ON TERRITORIES GROUPED BY MATING TYPE

Trap session	Bachelor	Monogamous	Bigamous
Early June	342	235[1]	436[1]
Late June	631	666	710
Mid-July	497	539	538

[1] Difference significant.

in food supply could favor selection for polygyny (Verner and Willson 1966, Orians 1969).

Arthropod populations were sampled in three trap sessions: early June, late June, and mid-July. Collections were made every other day each 8-day session. Total number collected per session was averaged for groups of traps categorized by the mating type of the male on whose territory the trap was located. The results showed a tendency for bachelor territories to be slightly lower than mated male groups in mean total arthropods collected in mid- and late season, but the variation within and between daily samples was so great the differences were not significant (Table 4).

NESTING BEHAVIOR

Nesting behavior was studied in 1971. The female alone incubates, broods, and feeds the young (Gross 1921, Crabb 1923, Zimmerman 1966, Fretwell 1967). Information from both fields was divided into three categories to illustrate the seasonal variation in nesting success: (1) females that arrived early on the south field and laid eggs the last week of May, (2) later-arriving females on the south field and early females on the north field that laid eggs June 5–15, (3) second-nestings and July first-nestings (June 20–July 21). The peak in number of active nests was in late June, when arthropod production also peaked.

Location of nests.—The mean heights of the nests above ground and heights of the vegetation above the nests were calculated for successful (fledged at least one young) and unsuccessful nests on both fields. No significant differences were found. Most of the successful nests were late nests when the vegetation had grown taller, but 6 of the 17 successful nests were in tussocks of standing dead *Setaria faberi* and *Polygonum pensylvanicum* and were much lower in both height readings.

Of 33 nests, 61% were located in *Aster pilosus* indicating a preference for this forb as a nesting substrate as aster was found in only 18% of the total sampling points on the south field and 42% on the north field. The percent of aster on individual territories was not significantly different from that on the whole field.

Of the total nests 21% were in dead vegetation, and all of these were

TABLE 5
RELATIVE SUCCESS OF SUBSTRATES (SOUTH FIELD)

	No. nests	% successful	No. females per male	No. young per female
Aster	20	45	1.31	1.52
Grass	7	86	1.00	3.40

on the south field. It is interesting that the females of this group that renested chose dead vegetation again even though the forb cover grew very tall and dense in these areas as the season progressed. Apparently as aster was not abundant on these territories the birds selected an alternative substrate. Of the nests in dead vegetation 86% were successful compared to 45% of the aster nests, which leads one to wonder about the preference shown for aster (Table 5). Table 5 also shows that the average female nesting in dead grass reared more young. Dead vegetation must provide adequate nesting sites, as males defending territories where this cover was dense did acquire mates, but other factors influenced the preference for territories of greater forb density characteristic of polygynous males. All females polygynously paired nested in aster or alfalfa.

Zimmerman (1966) found that forbs were the most frequently used nesting substrate although early in the season more nests were located in grass. On my areas the females appear to select the substrate that is most common on the particular territory.

Clutch size.—The clutch size of 30 nests (Table 6) ranged from 3 to 5 (mean 3.9 ± 0.1) which agrees with the figures in the literature (Gross 1921, Meanley 1963, Long et al. 1965).

Clutches of five were found only during the middle period. Young from those nests hatched during the peak of arthropod abundance (see Table 4). Clutches of three were more common in the early period when food was much less abundant and the weather was cooler. Four-egg clutches were the most frequent, especially late in the season.

Mortality in nests.—Table 7 summarizes nesting data for the two fields combined. Hatching success improved as the season progressed from 0 to 68% of the number of eggs laid. The south field contributed

TABLE 6
SEASONAL VARIATION IN CLUTCH SIZE

	Early	Middle	Late
Mean	3.40	4.09	3.85
Range (N)	3–4 (5)	3–5 (11)	3–4 (14)

TABLE 7
SEASONAL VARIATION IN NESTING SUCCESS

	Early	Middle	Late
No. eggs (No. nests)	17 (5)	45 (12)	54 (16)
% eggs predated	100	44	22
% eggs unhatched	—	28	12
% hatched	—	40	68
No. fledged per female	0.0	1.50	2.47

the bulk of the successful nests, especially in the late period when only 1 of 11 nests failed, while the north field lost 75% of its nests.

The two causes of egg mortality were predation and failure to hatch. The early nests on the south field were all lost to predation. In the middle period 50% of the nests were robbed (44% of the total eggs laid) with nests of the north field suffering the heaviest losses. Predation fell to its lowest level for late nesters (25% of the nests), again taking a greater toll on the north field. For the season as a whole 45% of the nests were lost to predation. Other studies on the Dickcissel also show very high predation losses (Long 1963, Zimmerman 1966).

The greater predation earlier in the season might be a consequence of a low food supply (see Table 4). The female has to spend more time searching for food for herself and thus spends less time protecting the eggs (see Verner 1965).

Even if the nest escaped predation, hatching success was further reduced by the failure of many eggs to hatch. The number of unhatched eggs decreased seasonally from 28% to 12% of the eggs that survived predation. The increased food supply later in the season may have given the female more time on the eggs, which would improve the chances for hatching of all fertilized eggs.

Renesting.—On the south field, 6 of 7 females that lost their first clutch renested. Mousley (1917) found that 70% of the birds he studied renested after losing a clutch. Females on the north field arrived later and thus began nesting later, and only 27% of these females renested after failing in their first attempt.

Fledging success.—Nestlings remained in the nest 8–10 (mean, 9) days before fledging (see also Gross 1921, Long et al. 1965). The fledging success equals the hatching success as no nestling mortality was noted and young were presumed to have fledged successfully if at least 8 days old before disappearing from the nest. Therefore the estimate of fledging success could be too high, and no account of fledgling mortality was attempted As these conditions apply to all nesting data equally, relative success can still be discussed.

The number of young produced per female increased later in the nest-

TABLE 8
SEASONAL VARIATION IN MATING TYPE SUCCESS

	Monogamous			Polygynous		
	Early	Middle	Late	Early	Middle	Late
No. nests	4	10	8	1	2	8
No. successful (%)	0 (0)	5 (50)	5 (63)	0 (0)	1 (50)	6 (75)
No. eggs laid	13	36	23	4	9	31
No. eggs predated (% laid)	13 (100)	16 (44)	4 (17)	4 (100)	4 (44)	8 (26)
No. eggs unhatched (% eggs not predated)	—	6 (30)	3 (16)	—	1 (20)	2 (9)
No. fledged (%)	0 (0)	14 (39)	16 (70)	0	4 (44)	21 (68)
No. fledged per female	0	1.40	2.00	0	2.00	2.62

ing season. In addition to decreasing losses to predation and unhatched eggs, mean clutch size increased as the season progressed.

Relative success of mating type.—Polygynous matings must be advantageous or at least not detrimental. Thus it is essential to compare the breeding success of males and females polygynously paired to that of those monogamously mated. This has been done for Red-winged Blackbirds (*Agelaius phoeniceus*) (Haigh 1968) and Bobolinks (Martin 1970), both regularly polygynous species. Each of these studies demonstrated that polygynously paired males and females increased their reproductive output over those paired monogamously.

Table 8 divides the nesting data into mating type and again into three periods to illustrate the trends. Nesting and hatching (therefore fledging) success increased later in the season for both pair bond groups because losses from predation and unhatched eggs decreased and mean clutch size increased. Most polygynous females nested late and attained higher nesting success than monogamous females in the same period. Comparatively, a greater number of young were produced per polygynously mated male and female.

Grouping data for the season (Table 9) demonstrates that, overall, polygynous females were more successful. As the data often include renestings, the fledging success is given per nest as well as per female. Among the polygynous females, a greater percentage of nests were successful and a greater percentage of eggs hatched, producing a higher fledging success. The differences in fledging success were not found to be significant using a contingency table analysis.

DISCUSSION

The evolution of polygyny depends upon a certain spatial heterogeneity of habitat so that a female might attain greater reproductive success if she pairs polygynously with a mated male on a territory of good quality than if she choses an unmated male on a poor territory (Verner and

TABLE 9
MATING TYPE SUCCESS

	Monogamous	Polygynous
No. females represented	16	9
No. nests	22	11
No. successful (%)	10 (45)	7 (64)
No. eggs laid	72	44
No. eggs predated (% laid)	33 (46)	16 (36)
No. eggs unhatched (% eggs not predated)	9 (23)	3 (11)
No. fledged (%)	30 (42)	25 (57)
No. fledged per nest	1.36	2.27
No. fledged per female	1.88	2.78

Willson 1966). When the male does not help the female in nesting duties a small difference will be enough to favor polygyny (Orians 1969). Potential differences among territories in available nest sites, food abundance, and vegetative cover have been most frequently investigated.

Plentiful food but a restricted number of nest sites is characteristic of many polygynous species (Orians 1969, von Haartman 1969). Type and quality of nesting cover have been related to mating and nesting success (Willson 1966, Zimmerman 1966, Haigh 1968, Martin 1970, Verner and Engelsen 1970). I found that *Aster pilosus* was the preferred nesting substrate, especially by polygynous females, but the frequency of this forb on each territory was not consistently correlated with mating success and nests in aster were not more highly successful.

Verner and Willson (1966) and Orians (1969) felt that an uneven distribution of insects resulting in a differential food supply among territories was quite probable in early successional habitats. Other investigators have discounted food availability as an important territorial parameter because females frequently gather food for nestlings off the territory (Zimmerman 1966, Haigh 1968, Martin 1970). Both males and females were seen foraging on the territory throughout the season; therefore foraging conditions on the territory are still of importance (see also Willson 1966). A female who forages close to the nest on the territory may spend less time foraging and can spend more time incubating the eggs and protecting them from predation while keeping herself in good health. In addition, the percentage of food gathered off the territory has not been documented. Some percentage is probably collected on the territory, especially during inclement weather when nestlings require more brooding time (Haigh 1968), and therefore could be important to reproductive success.

The vegetative structure of territories has also been related to mating success: the percent of emergent vegetation (Verner 1964, Willson

1966), cattail stands (Haigh 1968), bulrush stands (Verner and Engelsen 1970), and forbs (Zimmerman 1966, Martin 1970). In my study forb cover was inconsistently correlated with the male Dickcissels' ability to acquire mates. Major forb density increased greatly over the whole south field from 1970 to 1971 but especially on the north to northeast edge where a zone of dense forb growth (specifically *Aster pilosus*) was distinct. Just as distinct was the greater density of *Setaria faberi* and *Polygonum pensylvanicum* on the southwest corner. These two areas were consistently sites of bigamous and monogamous matings respectively each year, suggesting that the northern zone is of higher suitability to the females. Still forb cover cannot be the only factor, as the east side of the north field in 1971 was covered by a very dense, tall stand of *Aster pilosus* and other major forbs but all males were monogamous.

Zimmerman (1971) concluded that only at high male densities were some males forced to include less suitable habitat in their territories. He found a positive correlation between volume of vegetation and number of mates acquired at all male densities observed. In an earlier paper Zimmerman (1966) found bachelor territories deficient in height and forb coverage but the male density was very low ($<$ 20 males per 100 acres). As Zimmerman found these differences at such a low density, apparently a high density of males is not needed to force some males to occupy unsuitable habitat. The critical density is related to the quality of the specific area.

Perhaps on my study areas high male density reflects the generally high suitability of the habitat and little difference actually exists between territories in height, volume, or type of vegetation. Similarly, low densities indicate a generally poor habitat with some good patches, and some males might occupy territories significantly poorer in vegetative structure. The habitats Zimmerman studied could have been more heterogenous than mine. My study areas could be relatively small but of uniform good quality. Even at a low density Zimmerman (1966) found a much higher percentage of males bigamously mated and some were trigamists attesting to the possibility that this habitat was more heterogenous.

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SUMMARY

Nesting populations of Dickcissels were studied in 1970 and 1971 on two abandoned fields in Illinois. Territorial features and male pairing success were analyzed to determine which factors influence female mate selection. Reproductive success was studied the second season.

Bachelor territories were the smallest in size on the south field each year, but this was not true on the north field. A trend was established for increasing territory size with decreasing male density.

Although no consistent relationship between percent cover by vegetation on the territory and pairing success was found, differences in the percentages of males polygynously paired were correlated with the percent cover values for each field. Some significant correlations were found between mating success and the frequency of major forbs on territories grouped by mating type.

Interterritorial differences in food availability indicated that bachelor territories were somewhat deficient.

Though 61% of the nests were located in *Aster pilosus*, a greater percentage of nests in dead vegetaton were successful and reproductive output per female was higher.

Losses to predation and failure of eggs to hatch decreased while mean clutch size increased seasonally for the whole population. Using reproductive success as a measure of fitness shows that polygyny has adaptive value in the Dickcissel.

It is suggested that the quality of the specific habitat studied influences the critical density at which some males are forced to include unsuitable habitat in their territories. On an area that is quite heterogenous the number of good patches could be very limited and a very low density of males could effectively occupy all suitable habitat. My study areas seem to be fairly uniform in quality so that interterritorial differences were not great enough to be measured by my sampling techniques although male density was fairly high.

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