POLYGYNY IN THE DICKCISSEL[1]

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ALTHOUGH monogamy is the most common type of pairing system among passerine birds, the concurrent mating of a territorial male with two or more females occurs regularly in species of several families (von Haartman, 1954; Verner and Willson, 1966). As Selander (1965) has illustrated, such polygynous matings (as well as promiscuous systems) are not a result of a greater number of females than males in the breeding population. Counts that I made of wintering flocks of the Dickcissel (*Spiza americana*) in the Republic of Panama indicated that the sex ratio was equal, at least at that season. My observations of summer populations in Illinois revealed that polygyny might exist, even though the few reports on breeding biology of Dickcissels provided no concrete evidence of its occurrence (Crabb, 1923; Gross, 1921; Meanley, 1963). Recent work by Long *et al.* (1965) further suggests, however, that such matings do take place.

Since the assumption that polygyny results from an unbalanced sex ratio is not tenable, I undertook studies in Kansas from the middle of May to the end of August, 1965, to determine the mating patterns of the Dickcissel and the possible adaptive significance of polygyny in the populations being investigated.

STUDY AREA

Two separate areas located approximately one mile apart in Riley County, Kansas, were used in this study. The Schruben tract of 128 acres in section 31, T8S, R6E, contained the following types of cover: 60 per cent of the area was in brome grass (*Bromus inermis*) and sweet clover (*Melilotus alba* and *M. officinalis*) with fairly extensive stands of sunflowers (*Helianthus* sp.) and ragweed (*Ambrosia trifida*) in the damper areas; 25 per cent was wheat stubble, sweet clover, and a variety of annual forbs; and 15 per cent was mixed grasses (*B. inermis*, *B. secalinus*, *Bouteloua curtipendula*, *Sporobolus clandestinus*, *Andropogon scoparius*). The 34-acre Springer tract, located in section 29, T8S, R6E, was covered over approximately 60 per cent by very dense brome (*B. inermis*), while the remaining 40 per cent was an old field community of grass (*B. inermis* and *B. secalinus*), alfalfa (*Medicago sativa*), ragweed, sunflowers, elms (*Ulmus* sp.), and box elder (*Acer negundo*).

METHODS

Dickcissels were captured with mist nets, banded, and individually marked by a combination of colored leg bands and spray enamel applied to the primaries and the tips of the rectrices. A total of 58 birds (37 males, 14 females, and 7 fledglings) were marked in this way, although not all remained on the study area. Nor were all the birds resident on the study area marked. Unbanded males could be distinguished by song and the individualistic pattern of black on the throat and breast.

[1] Serial 399, Department of Zoology, Kansas State University.

TABLE 1

SEX RATIOS AND PAIR BONDS OF THE DICKCISSEL

Ten-day period	*Average daily sex ratios*				*Average daily percentage of ♂ ♂*		
	Number of ♂ ♂	*Number of ♀ ♀*	*♂ ♂ / ♀*	χ^2	*Mate-less*	*Monoga-mous*	*Polygy-nous*
31 May–9 June	17.6	8.4	2.22	3.26	70.6	26.2	3.1
10 June–19 June	18.8	15.0	1.26	0.42	43.6	38.7	17.7
20 June–29 June	19.0	15.1	1.26	0.44	45.4	42.1	12.6
30 June–9 July	17.4	12.7	1.40	0.73	50.9	36.1	12.9
10 July–19 July	16.5	16.0	1.05	0.08	30.1	44.7	25.3
20 July–29 July	15.9	17.4	0.95	0.07	26.8	48.0	25.2
30 July–9 August	9.3	12.3	0.69	0.50	19.4	49.5	31.1
All dates	16.4	14.2	1.22	0.15	41.9	40.3	17.8

A few of the unbanded females could be satisfactorily identified as individuals on the basis of the amount of ventral yellow and the extent of the less distinct black throat patch.

On 63 days between 17 May and 23 August, censuses of the study population were conducted during which the locations and numbers of males, females, and active nests with their contents were recorded on scale maps of the study area drawn from aerial photographs. Only on 15 of these days were such counts made on the Springer tract, but these were sufficient to ascertain the territorial limits of the males and whether the males were mated. Most of the data reported below were collected on the Schruben property. Territory size was calculated by tracing the outline of the scale drawing of the territory with a compensating polar planimeter.

An analysis of the vegetative structure of 17 territories in the Schruben tract and 7 territories in the Springer tract was made in the last week of June and the first week of July. The life forms, the percentage of area they covered, and the height of the vegetation were measured on square meter plots located every 25 feet along the longest dimension of the territory. The average number of square meter samples per territory was 13.

The criteria used to determine the presence of an established pair bond between a male and female were similar to those used by Ryves and Ryves (1934*a*). A pair was considered mated if at least one of the following was observed: 1) copulation followed by the female's building within the male's territory, 2) nest building by a female with the territorial male closely in attendance, or 3) the male's moving about with a female during her inattentive periods from an established nest located in that male's territory.

RESULTS

Sex ratio.—The numbers of males and females on the study area were compiled from the day construction began on the first nest (31 May) to the last day on which males were still present on their territories (9 August), although the last active nest did not fledge young until 28 August. These data are presented as averages for ten-day periods in Table 1 and are based on the Schruben population since such a day-to-day analysis was not conducted on the Springer tract. At no time during

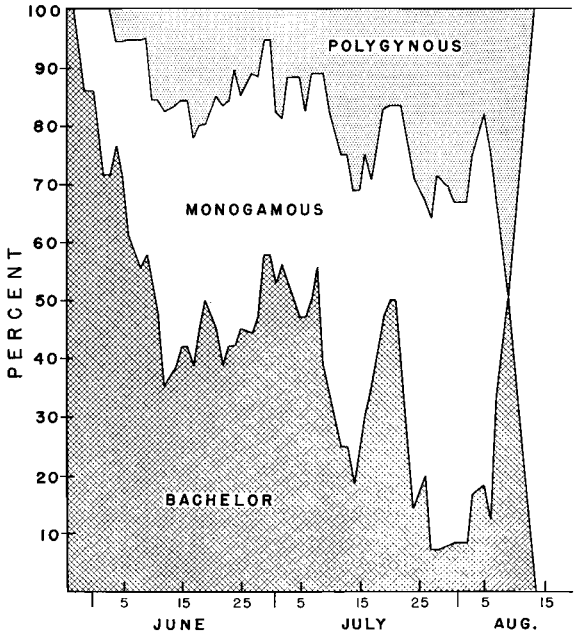

Figure 1. Daily proportions of bachelor, monogamous, and polygynous males on the Schruben tract.

this period was the ratio between the sexes significantly different from unity, using a Chi-square test ($P > .05$).

Mating patterns.—The pair bonds established by 22 males on the Schruben tract were known with certainty. Of these, 3 (14 per cent) remained mateless, 8 (36 per cent) never had more than one mate at any one time, 9 (41 per cent) were bigamists at least once, and 2 (9 per cent) had three mates concurrently at least once during the course of the breeding season. Of the 9 males that maintained territories on the Springer tract, 3 remained bachelors and all the rest were monogamous. Tabulation of the existing pair bonds of the males on the Schruben area for ten-day periods shows, however, that although 50 per cent of these males were polygynously mated, never were all these polygynous males involved in multiple pair bonds at the same time (Table 1). The proportion of bachelor, monogamous, and polygynous males on a day-to-day basis is illustrated in Figure 1.

The male Dickcissel is very attentive to the female but not to the nest. From the female's first arrival on his territory until the nest is completed, the male is with the female whenever he is not involved in singing or more proximal territorial defense encounters. Nest site selection by the

female spans a period of several days during which she moves about the territory closely attended by the male. They forage together, the male usually following after her as she flies from place to place within the territory. It is during this period that sexual chasing and frequent copulations occur. The sexual chase is a rapid flight by the male in pursuit of the female which ends abruptly on the ground, occasionally with a puff of body feathers being seen, which are pulled as the male makes some sort of physical contact with the female. Since the end of the chase is concealed within the vegetation, I do not know if this flight terminates in copulation. It seems unlikely, however, since copulation usually occurs at exposed perches and involves an invitational display by the female. The female begins carrying nesting material between courtship, copulation, and feeding bouts, occasionally taking dried grasses to sites which are then abandoned by the following day, but eventually selecting a site in which the nest is completed in two to three days. The male still accompanies the female as she gathers nesting materials, and he returns with her to the nest site. During egg laying and incubation the male continues his attentiveness to the female whenever she is off the nest, but during the brooding phase his companionate behavior decreases. This may be partly because she regularly flies outside the territory to collect food for the nestlings; it is not because the male is involved in the care of the young. There are a few reports of male Dickcissels feeding young (Bellrose, 1936; Purdie, 1878), and one of the males in this study did bring food to the nest. Yet, as a rule, the male is not at all attentive to the eggs, nestlings, or fledglings. Similar attentive behavior toward his mate as well as his inattentiveness to the nest is described by Ryves and Ryves (1934*a*) for the regularly polygynous male Corn Bunting (*Emberiza calandra*).

The male's intense attentiveness to the female during their early mated days apparently precludes his obtaining an additional mate at that time. Never did a male successfully acquire a second mate while a female was still building, although on several occasions unattached females were on the territory and received some attention from the male. Of the new mates, 22 per cent were obtained while the previously acquired female was laying eggs, 61 per cent during the incubation phase of the prior female, 6 per cent when the previous female was brooding, and 11 per cent during the first two days after the fledging of the brood of the last acquired female. The average time lapse between the first day of egg laying of one female and the subsequent initial egg deposition of the next additional female was 8.8 days. Similar data for the Pied Flycatcher (*Muscicapa hypoleuca*) compiled by von Haartman (1951: 261) averaged 7.9 days, and for the Corn Bunting (Ryves and Ryves, 1934*a*: 21–24) averaged 9.0 days. The females of polygynous Red-winged Blackbird males

TABLE 2

TERRITORY SIZE (MEAN ACRES ± S.E.) AND DENSITY OF MALE DICKCISSELS[1]

Dates	*Mateless*	*Monogamous*	*Polygynous*	*All males*	♂ ♂/100 acres[2]
5–12 June	1.70±0.218 (8)	2.34±0.208 (8)	2.35±0.231 (3)	2.04±0.143 (19)	18.7
14–17 June	1.50±0.197 (6)	1.62±0.191 (7)	1.77±0.204 (4)	1.61±0.111 (17)	17.8
18–24 June	1.14±0.152 (8)	1.76±0.191 (9)	2.07±0.225 (3)	1.56±0.133 (20)	18.7
25–30 June	1.72±0.253 (8)	1.65±0.089 (8)	2.50±0.654 (2)	1.77±0.141 (18)	20.6
1– 5 July	1.78±0.204 (9)	1.96±0.139 (5)	2.57±0.225 (3)	1.97±0.137 (17)	18.9
6–10 July	1.85±0.283 (7)	2.23±0.289 (8)	2.10±0.068 (2)	2.06±0.177 (17)	18.9
12–15 July	2.55±0.372 (3)	2.20±0.212 (7)	2.44±0.415 (5)	2.35±0.176 (15)	16.7
16–22 July	2.62±0.218 (7)	2.75±0.363 (6)	2.29±0.510 (3)	2.60±0.182 (16)	16.7
24–31 July	—	2.55±0.091 (7)	2.86±0.460 (4)	2.66±0.169 (11)	14.0
All dates	1.79±0.096 (56)	2.10±0.080 (65)	2.34±0.126 (29)		

[1] Numbers in parentheses are sample sizes.

[2] Density data include males occasionally on study area and exhibiting territorial behavior but whose territory sizes were not accurately determined. These data also take into account changes in the area of suitable habitat resulting from agricultural practices.

(*Agelaius phoeniceus*) have been reported to be similarly out-of-phase with each other (Nero, 1956: 8).

Territory size.—As is true for several other passerines (Lanyon, 1957: 28; Stenger and Falls, 1959; Weeden, 1965; Zimmerman, 1963: 147), the size and shape of the Dickcissel's territory is not fixed throughout a single breeding season. The sizes of maximum territories (see Odum and Kuenzler, 1955) were computed from daily census data compiled over four- to eight-day periods. These data were further segregated according to the mating situation the particular male had established for that period (Table 2).

For all birds changes in territory size with time show a significant inverse correlation with the density of the males ($r = -0.756$, $n = 9$, $P < .05$). Territory size is also related to the presence of a mate. The smaller area of the territories of bachelor males is significantly different from that of both monogamous ($t = 2.45$, $df = 119$, $P < .02$) and polygynous males ($t = 3.38$, $df = 83$, $P < .01$). As with the Red-winged Blackbird (Orians, 1961: 292), there is no significant difference in territory size between monogamous and polygynous males.

Vegetative structure of the territory.—The vegetation in grasslands produces a two-dimensional environment, since there are no stratal communities as in forested habitats. In the vegetative analysis of 24 Dickcissel territories, however, three heights were recognized which correspond generally to the tops of the grasses and smaller forbs, the tops of the forbs of medium height (e.g., ironweed [*Veronia* sp.] and sweet clover), and the tops of the tallest forbs (e.g., ragweed, prickly lettuce [*Lactuca scariola*], and sunflowers). Although woody vegetation was present on many ter-

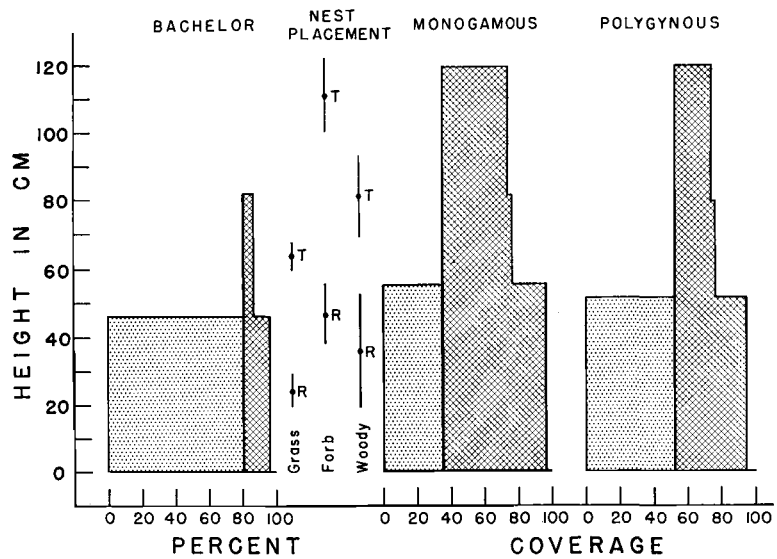

Figure 2. Average height and per cent coverage by the vegetation on territories of bachelor, monogamous, and polygynous males, and the mean heights of the nest rim (R) and of the vegetation directly above the nest (T), with their respective 95 per cent confidence intervals. Stippling indicates grasses; cross-hatching indicates forbs.

ritories, its density averaged less than one per cent when these data were compiled. The data were grouped according to the type of pair bonds that the males had established during the course of the breeding season and are presented in Figure 2.

There was a marked difference in vegetational structure between the territories of bachelor and mated birds. In the former's territories, the vertical development of the vegetation was restricted both in height and per cent coverage, and the coverage by forbs was also less there than in the territories of mated males. Figure 2 also illustrates the average heights of the nest rim in grass, forb, and woody substrates and the average heights of the vegetation above these nests. From these data it is apparent that the territories of unmated males lacked suitable nesting sites; particularly were they deficient in vegetative cover above the nest. Dickcissel nests are characteristically well concealed, usually deep within the vegetation. This covert placement, however, does not exempt them from heavy nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) or predation (see below). The adaptive value of such placement may lie in the moderated microclimate which is produced by the vegetation of the nest site (Horváth, 1964; Kendeigh, 1934: 348), although I have made no mea-

surements of the climatic elements involved for the Dickcissel. The lower abundance of forbs in mateless males' territories may also be a factor in their failure to provide suitable nest sites. Most nests were placed in forbs, while grass substrate was used mainly for nests constructed before the middle of June, prior to the fullest development of the forbs. Among mated males I found no relationship between the vegetative structure of their territories and their number or retention of mates.

The heights of at least the three most frequently used song perches of the males were also measured (Figure 3). Grasses were seldom used as song perches. Several males whose territories bordered along a road regularly used the telephone wires, but I eliminated these since such perches are not a regular feature of most Dickcissel territories (although a drive along any road in the midwest might bias one against this assumption). There is no significant difference in the heights of the song perches between mated and bachelor males for woody or forb song posts.

Nesting success.—Of the 55 nests observed, 29 were of monogamously mated females and 26 were nests of females mated to polygynous males. Nest parasitism by the Brown-headed Cowbird was heavy; 72 per cent of the monogamous nests and 86 per cent of the polygynous nests (78 per cent of all nests) contained at least one cowbird egg. Of the 43 parasitized nests, 14 per cent received one cowbird egg, 33 per cent had two, 21 per cent contained three, 16 per cent held four, 9 per cent had five, 2 per cent contained seven, and 5 per cent held eight cowbird eggs. In one of the nests with eight cowbird eggs, five of them were laid during a single day! This high intensity of social parasitism as compared to published levels (53 per cent [Hergenrader, 1962], 33 per cent [Wiens, 1963], 31 per cent [Overmire, 1962]) may have been due to the late breeding by other cowbird hosts such as the Red-winged Blackbird, Eastern Meadowlark (*Sturnella magna*), and Western Meadowlark (*S. neglecta*), since the cowbird burden of a single species is inversely related to host availability (Scott, 1963: 128). Nest failure (Table 3) from cowbird parasitism resulted twice from the desertion by the female of a nest in which cowbird eggs had been deposited before the nest was completed, and in seven cases from removal of Dickcissel eggs and apparent replacement of them by one or more cowbird eggs. I do not know the reason for the lower incidence of nest failure due to cowbird parasitism in polygynously mated birds; this difference may not be real. Armstrong (1955: 109) suggested that polygyny would give selective advantage to the most vigorously competing males, but even if this were true with the Dickcissel, and I do not know if it is, it is not manifest interspecifically, since there was very little aggression toward the cowbird or any other species. In fact, a greater percentage of polygynous nests than monogamous nests were parasitized.

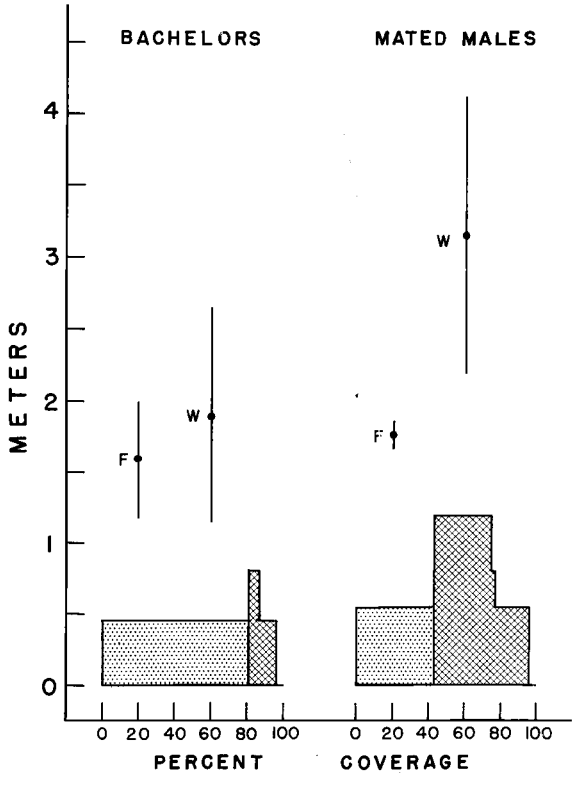

Figure 3. Mean heights and 95 per cent confidence intervals of song perches in woody (W) and forb (F) vegetation of bachelor and mated males with the average height and coverage of vegetation of their territories. Stippling represents grasses; cross-hatching indicates forbs.

This difference is not related to territory size, since there was no significant difference in the amount of defended area between monogamous and polygynous males.

There is little difference between the two mating systems in the degree of nest failure from other causes. No actual instances of nest predation were observed; in 22 cases the nest was empty, the contents probably having been removed by avian or reptilian predators, and in 6 instances the nest had been torn up, presumably by mammals. Two cases of desertion resulted from an unexplained disappearance of the female, while the remaining five involved nests that were disturbed by agricultural practices. Weather losses resulted from the nests either being washed out, flooded, or blown down.

TABLE 3
NESTING SUCCESS OF DICKCISSELS

Nests according to mating pattern of male	*Nests fledging young*[1]	*Nests failing and causes*			
		Cowbird parasitism	*Predation*	*Desertion*[2]	*Weather*
	Numbers				
Monogamous	1 (3D)	8	13	4	3
Polygynous	5 (6D, 9C)	1	15	3	2
	Percentages				
All nests	11[3]	16	51	13	9

[1] Numbers of Dickcissels fledged indicated by D, numbers of cowbirds fledged, by C.

[2] Other than as a result of cowbird parasitism.

[3] Only 7 per cent of the nests produced at least one Dickcissel, since two nests of females mated to polygynous males fledged only cowbirds.

DISCUSSION

The occurrence of polygyny in a population with an equal sex ratio produces a surplus of unmated males. The survival value of polygyny might then lie in the ready availability of mates to replace males lost in the breeding season. Yet in the several instances when a territorial male disappeared, the vacated territory was subdivided by the adjacent males, irrespective of whether they were currently mated or not. Bachelors from non-contiguous territories did not move in to take over the undefended area. Furthermore, in view of the lack of participation by the male Dickcissel in the care of the eggs and young, his presence on the territory, once egg deposition begins, may be superfluous with respect to that particular mating. On two occasions this contention was borne out. In one case a male disappeared from his territory on the seventh day of incubation by his mate. Part of the vacated territory, but not the area containing this nest, was taken over by an adjacent male who was already polygynously mated. The female continued to be attentive until the fourth day of brooding, when the young were taken by a predator. In the other instance, the male left the territory on the first day of incubation and, since territorial activity was waning, no male took over the area, but three young were fledged 19 days later through the continued parental care of the female. The male Pied Flycatcher (von Haartman, 1951: 260–263) regularly leaves his first female by the time egg laying begins and moves to another territory to mate with an additional female. After the second female begins laying, he then returns to aid in the feeding of the first brood.

Verner (1964) hypothesized that the selective advantage of polygyny is in allowing males holding the better territories to accommodate more than one female, while, if monogamy were the only permissible mating

pattern, some females would have to nest in marginal habitats and perhaps have a lower reproductive success. Verner and Willson (1966) have discussed the possibility that the availabilities of nest sites and food are the important factors differing between territories. These authors have pointed out that polygynous mating systems most commonly exist in environments where food is readily available (i.e., not only where primary production is high, but also where the food sources are concentrated). They suggest that in such situations (savannahs, prairies, and marshes), large differences between territories in the production of food are more likely to exist than in habitats where food production is low.

Crook (1964: 104) has related seasonal rains and the concomitant peak of food as factors allowing the development of polygyny in weaver finches; since the females alone can rapidly find sufficient amounts of food, males are freed from parental care "and have thus been able to increase their productivity through polygamy and the construction of successive nests." While the productivity of the environment may indeed be a permissive factor in the case of the Dickcissel, there is little support for the notion that a difference in food supply between territories has operated as a proximate selective factor in the evolution of polygyny, since females regularly forage beyond the territory boundaries when feeding nestlings. In the polygynous Corn Bunting, which uses a common feeding area separate from the individual males' nesting territories (Ryves and Ryves, 1934*b*), food supply also appears not to be the factor responsible for one territory being more efficacious than another in terms of reproductive success.

It appears that the distinctive environmental factor from which the selective advantage of polygyny accrues in the Dickcissel is the difference between territories in the availability of nest sites. As has been shown, the territories of mateless males do not provide sufficient nesting substrate. Since nest sites are selected by the female, even though a bachelor may attract a female, she does not remain to nest if his territory lacks the proper cover, moving on instead to a territory where a suitable nest site is available. Since she is not affected by another female's already being mated to the male holding such a territory, she is not prevented from reproducing. Long *et al.* (1965: 252) report such an instance of choice by a female Dickcissel between the territories of unmated and mated males. The availability and height of song perches may be of primary importance in territory selection by the male, and with respect to these factors there was no difference between the territories of mated and mateless birds. Yet selection by the male of the kind of substrate required by the female for nest placement should be selected for, since his territory must meet with her requirements if he is to contribute to the future gene pool of the population. Exclusion of some males from reproducing as a result of a

lack of nest sites also has been observed in the Red-winged Blackbird (Linsdale, 1938: 141).

Since reproductive success is the ultimate measure of fitness, I had hoped that a comparison of fledgling production between monogamously and polygynously mated birds could be used to illustrate the selective advantage of one mating system over the other. Yet, only 0.29 fledglings were produced for every adult on the Schruben tract, and none was fledged on the smaller study area. Of the four nests with fledgling Dickcissels, three were of females mated to three different polygynous males and produced a total of six young, while the nest of the single successful monogamously mated female fledged three young. No valid comparison between these relative successes can be made. It need not necessarily be expected that a difference in reproduction between the two mating systems will exist. A single female, whether the sole mate or one of several simultaneous mates of a male, can rear a brood unaided and she is not limited by the food resources of the particular territory in which she nests. Polygyny has adaptive value in the Dickcissel because it permits *all* available females to select suitable nest sites.

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SUMMARY

The mating patterns established in a color-marked population of Dickcissels were investigated during the summer of 1965 in Kansas. There was an equal number of males and females in the breeding population. Day-to-day censuses during the period from 31 May to 9 August revealed that there was an average of 42 per cent bachelors in the population, while 40 per cent of the males were monogamously mated and 18 per cent had established polygynous pair bonds.

The male Dickcissel is characteristically very attentive to the female during the early days of the nesting cycle, but he is not at all attentive

to the nest or fledglings. Additional mates are obtained by polygynous males most often during the incubation phase of the previously acquired female.

The territories of mated males are significantly larger than those of mateless males, but there is no difference in size between the territories of monogamous and polygynous males. The territories of bachelor and mated males also differ in that the vertical development of vegetation is restricted in the territories of unmated males, and the per cent coverage by forbs is less. There is no difference between their territories, however, in the height or availability of song perches.

Of all Dickcissel nests, 78 per cent contained eggs of the Brown-headed Cowbird, and this social parasitism was directly responsible for failure of 16 per cent of all nests. Predation, however, caused the greatest proportion of nest loss.

The adaptive advantage of polygyny in the Dickcissel seems to be based upon the differential availability of nest sites among the territories of the males; polygyny allows all available females the chance to reproduce.

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