NESTING SUCCESS OF DICKCISSELS (SPIZA AMERICANA) IN PREFERRED AND LESS PREFERRED HABITATS

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ABSTRACT.—Habitat selection in the Dickcissel (*Spiza americana*) was evaluated by a comparison of over 500 nest histories from the preferred oldfield and the less preferred prairie communities in Kansas. Females are equally successful in either habitat, and their productivity is not adversely affected by their being mated to polygynous males. Thus, these two habitats are similarly suitable for females, and females are distributed simply according to the availability of adequate nesting environments and not in any density-dependent manner or in response to density cues. No differences exist in survival rates of nests associated with individual males or in the males' individual productivities between prairies and oldfields when monogamous and bigamous males are compared. The oldfield habitat is more suitable for males, however, because the potential for sequestering more nesting sites is greater in this more heterogeneous habitat. This permits higher levels of polygyny, which increases the productivity of individual males, even though densities of birds in oldfields are greater. *Received 3 February 1981, accepted 23 October 1981.*

GRASSLANDS and variously aged oldfields are the two major habitats selected by Dickcissels (*Spiza americana*) for establishment of territories by males and nests by females. The density of males is higher in oldfields than in prairies, and the frequency of polygyny and the average number of females per male is also greater in oldfields (Zimmerman 1971). The greater suitability of preferred oldfields over other habitats appears to be a function of the vegetation, which is more heterogeneous and taller in oldfields, with greater coverage by forbs. The density of males in a particular habitat and the number of females per male in this polygynous species are significantly and positively related to the amount of vegetation present there (Zimmerman 1971). I do not know which attribute of the vegetation structure particularly enhances the attractiveness of oldfield habitats. It could be food. Even though female Dickcissels regularly forage beyond the boundaries of the territory of their mate (Zimmerman 1966), Wittenberger (1980) has suggested several reasons why the proximity of high-quality food resources to the nest still may be crucial. The vegetation probably does not protect the nest from loss to predators (Wittenberger 1976), but the importance of vegetation for nest sites may be through the improvement of the microclimate surrounding the nest and the critical impact of this mitigation on the growth of the young (Blankespoor 1970). Pleszczynska (1978) also has demonstrated the importance of nest-site microclimate for the Lark Bunting (*Calamospiza melanocorys*), the short-grass plains counterpart of the Dickcissel.

Using the predictions based on the models developed by Fretwell and Lucas (1969), which differentiate between the three notions relating territoriality to population regulation (i.e. Huxley 1934, Kluyver and Tinbergen 1953, Lack 1964), one may infer that oldfield habitats are more suitable, even though densities are higher there, because females prefer oldfield males to prairie males. Male Dickcissels thus illustrate the "ideal dominance" distribution (Fretwell and Calver 1969). K. L. Petersen (MS) has shown that the temporal sequence of utilization of different habitats by male Dickcissels follows the pattern expected from the ideal dominance model. Early in the season, when male densities in oldfields are low, no birds settle in grasslands, but, as densities increase in the more preferred oldfields, Dickcissels invade upland prairies, peaking in density a week or so after the oldfield populations have reached maximum numbers but never attaining the high densities characteristic of oldfields.

The ultimate measure of habitat suitability, of course, is the productivity of birds. As Fretwell and Lucas write (1969: 33), "If a species has an ideal territorial (dominance) distribution, then the success rate in habitats with

higher densities of residents will be higher." Whitham (1980) has pointed out that the Fretwell-Lucas hypotheses have been largely untested because of the difficulty of measuring fitness in habitats of known quality. The purpose of this paper is to use the Fretwell-Lucas hypotheses to identify the habitat distribution systems of male and female Dickcissels through a comparison of nest survival rates and the production of young from over 500 nests in oldfields and prairies, habitats clearly differing in quality.

METHODS

Nest data were gathered from 1965 through 1979 from populations on the Ft. Riley Military Reservation and the Konza Prairie Research Natural Area in Riley and Geary counties, Kansas, deep within the center of the area with highest breeding densities of this species in North America (Robbins and Van Velzen 1969). Except for a few populations for which nests were visited every 3 or 4 days, most data were obtained by checking nest contents once a week. The fates of nests in which young were expected to fledge during the intervening period and that were found empty at the next visit were easily determined by the behavior of the females. A female with fledged young gives agonistic displays and continues to feed the young in the vicinity of the nest for several days before moving further away with the brood. A female whose nest has suffered predation immediately disappears. In some populations birds were color-banded, so that male territories and the densities and mating patterns of males and females could be determined weekly. In these situations, then, it also was possible for me to relate the success of individual nests to the specific male presumed to be genetically involved, by observing either copulation or the companionate behavior of the pair during the early days of nesting. Although "stolen" copulations among marked birds have not been observed, they may occur from time to time. For the purpose of this analysis, however, I have assumed that the observed mate is probably the biological parent, so that these nests could then be used to measure the success and productivity of males as well as of females according to the polygynous status of the male.

Johnson (1979) has validated the efficacy of the Mayfield (1961, 1975) nest-exposure method of estimating nesting success and has effectively answered the critics of this procedure. Furthermore, he has provided a formula by which confidence limits for survival rates may be calculated, thus permitting unbiased comparisons between the probabilities of nest survival in different populations. Accordingly, daily nest survival rates were determined for the separate stages of the nesting cycle in oldfields and prai-

ries. Additionally, daily survival rates of nests were computed on a per-male basis for males with differing levels of polygyny by summing all days of nest exposure for all nests of males with just 1 nest on their territories (including the monogamous males involved with several single nests sequentially during a single season) and of polygynous males with 2–6 nests active on their territories. This number of nests is not exactly the same as the male's harem size, because not all nests for a given male were simultaneous. Rather, this value is used as a measure of the suitability of a male's territory, as reflected by the use of his area for nesting by different females. This procedure compensates for differences in reproductive effort among males with different levels of polygyny and isolates the effect that differences in the numbers of nests might have on the assessment of males' nesting successes. In all analyses, samples for males with 5 and 6 nests were pooled to make the total sample size similar to that of the other nest categories.

While recognizing Mayfield's (1961) caveat regarding the biases inherent in determining the numbers of fledglings produced per nest found, I have calculated this value for nests in both habitats as a measure of the average productivity per female and have also converted this value into an average per male by summing the production for all nests present in a male's territory.

RESULTS

Nesting phenology.—The week of initiation of nest construction was known or, in most cases, estimated for 397 oldfield nests and 130 prairie nests. Nesting begins earlier in oldfields than in prairies and spans a longer season (Fig. 1). The peak week of nest starts, however, is the same for both habitats (15–21 June), but 50% of all prairie nest starts occur in the 3-week period from 15 June to 5 July, while 50% of all nest starts in the oldfield span a broader period, 8 June–5 July. The difference in the variance of these two populations is significant ($F = 1.65$, $df_1 = 396$, $df_2 = 129$, $P < 0.01$). These data are consistent with the population data gathered by Petersen (MS) and parallel the difference in settlement dates of Indigo Buntings (*Passerina cyanea*), another polygynous species, in high-density and low-density habitats (Carey and Nolan 1979).

Clutch size.—A total of 149 nonparasitized nests was known to have complete clutches. The 15 prairie nests in this total contained from 3 to 5 eggs with a mean of 4.0 (SE = 0.14), and the 134 oldfield nests contained from 2 to 6 eggs with a mean of 4.0 (SE = 0.07).

Although it is not possible to determine with certainty the number of Dickcissel eggs actually laid in nests parasitized by the Brownheaded Cowbird (*Molothrus ater*), due to host egg removal by the cowbirds, there is no significant difference between habitats in the number of Dickcissel eggs present in parasitized nests at the beginning of incubation. For 193 oldfield nests the mean was 2.4 eggs (SE = 0.09), and for 96 prairie nests the mean was 2.5 eggs (SE = 0.12).

There is, however, a significant difference in the mean number of cowbird eggs per nest in parasitized oldfield nests (2.3, $n = 201$, SE = 0.10) compared to those in the prairie, (2.9, $n = 96$, SE = 0.16) (Student's $t = 3.28$, df = 295, $P < 0.01$). The higher intensity of cowbird parasitism in the prairie (Elliott 1978) results in the total clutch of Dickcissel and cowbird eggs in prairie nests ($\bar{x} = 5.2$, SE = 0.16, $n = 111$) being significantly different from the total clutch in oldfield nests ($\bar{x} = 4.5$, SE = 0.08, $n = 330$) (Student's $t = 4.34$, df = 439, $P < 0.01$). The larger combined clutch size of prairie nests, however, does not in itself decrease the chances for survival of the young; within the same habitat there is no significant relationship between clutch size and survival rate (Zimmerman MS).

Female success.—Female Dickcissels are single-brooded. For all the nest histories of marked individuals, no two nests that successfully fledged young were produced by the same female in the same year. The length of nest life (average 26 days) and the postfledging care of the brood (about 2 weeks), when compared with the period during which reproduction is energetically feasible (Zimmerman 1965), precludes second successful broods. Indeed, I have never observed a successful female initiate a second attempt.

Females do renest after the failure of an earlier attempt. This sometimes occurs within the territory of the same male (17% of the time) or with another male in the same local population (10% of the time), but most frequently the female disappears and is not seen again. These unsuccessful females may seek out other fields of the same habitat type, or perhaps they select different habitats. Thus, population data from preferred oldfield study plots show a continued increase in female density until mid-July, as females enter the habitat after presumed failures elsewhere or for some reason have de-
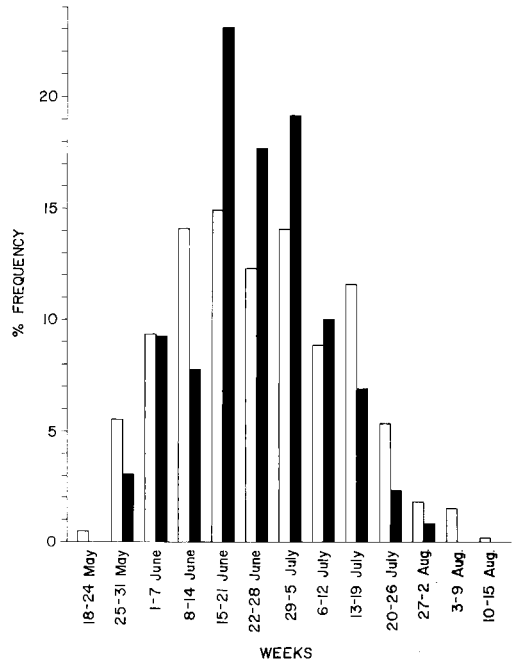

Fig. 1. Percentage frequency distribution of oldfield nest starts (open bars) and prairie nest starts (shaded bars) with the weeks of the nesting season.

layed initiation of nesting. For the purpose of this analysis, therefore, I have considered the probability of nest survival and the productivity per nest attempted to approximate the success of the average individual female in each habitat.

The daily survival rates computed for 137 prairie nests and 413 oldfield nests are presented for each phase of the nesting cycle (Table 1). The daily survival rates in each habitat were not significantly different among phases of nesting. The overall probability for survival can be calculated by raising the probability of each phase to the power equal to the number of days in that phase and then multiplying these separate probabilities together. Thus, oldfield nests have a 14.3% chance of being successful, while prairie nests have a similar value of 15.2%. Although female densities are higher in oldfields than in prairies (Zimmerman 1971), the estimated survival rate of nests of individual females in each of these two habitats is the same.

Even though the survival rates are similar, during the nest-building and egg-laying periods the values for prairie nests are lower than those for oldfield nests, while during the in-

TABLE 1. Daily survival rates of nests.

	Building		Egg-laying		Incubation		Brooding	
	Oldfield	Prairie	Oldfield	Prairie	Oldfield	Prairie	Oldfield	Prairie
Mean days in phase	2	2	3	3	12[a]	12[a]	9[b]	9[b]
Total days of nest exposure	185	23	405	81	2,117	624	1,056	534
Number of nests lost	13	2	49	15	164	34	53	25
Daily survival rate	0.930	0.913	0.879	0.815	0.922	0.946	0.952	0.955
±95% C.L.	0.04	0.12	0.03	0.09	0.01	0.02	0.01	0.02

[a] Incubation starts with day the last egg is laid.
[b] Includes the day of hatching.

cubation and brooding phases they are higher. This is explained by the greater impact of cowbird parasitism in the prairie, which leads to nest abandonment during construction and egg laying, and the higher incidence of predation in the oldfield (Zimmerman MS).

Production of Dickcissels per nest attempted is similar in oldfield ($\bar{x} = 0.72$, $n = 396$, SE = 0.068) and prairie ($\bar{x} = 0.87$, $n = 115$, SE = 0.122). There is, however, a significant difference in the total numbers of Dickcissels and cowbirds fledged per nest attempted between oldfield ($\bar{x} = 0.94$, $n = 396$, SE = 0.081) and prairie ($\bar{x} = 1.42$, $n = 125$, SE = 0.171) (Student's $t = 2.774$, df = 519, $P < 0.01$). This result is related to the significantly larger clutch size in prairie nests due to the heavier cowbird parasitism.

For a subset of these nests, mating relationships were known. It is therefore possible to compare the mean production of fledglings per nest in both habitats according to different levels of territory suitability as indicated by the numbers of mates attracted by the males (Table 2). No significant association occurs between the number of mates a male attracts, that is, the quality of his territory, and the average

productivity of females involved, nor is there a significant difference between habitats in the productivity of females mated to males with equivalent numbers of mates. It should be noted that the number of mates used for this comparison is not strictly equivalent to the harem size of the males, but, as in other polygynous species (Holm 1973, Weatherhead and Robertson 1977, Carey and Nolan 1979), the success of the female is not lessened by her being mated to a polygynous male.

Male success.—Some polygynous males were involved with as many as five simultaneous mates in oldfields, while two were the maximum in the prairie (Table 3). The survival rates of a male's nests were analyzed according to the total numbers of females he attracted (Table 4). Again, this ranking is not exactly the same as the harem size. The probability of survival of a male's nests, if he has just one or two, is the same regardless of habitat. Furthermore, no difference exists between the daily survival rates of nests according to the number of nests per male in either habitat, nor does a significant association occur between the number of nests per male and the daily survival rates for the nests of these males.

TABLE 2. Production of fledglings/nest attempted ($\bar{x} \pm SE$) according to the number of females attracted to the territory.

	Oldfield			Prairie		
Number of mates	Number of nests	Dickcissel	Dickcissel + Cowbird	Number of nests	Dickcissel	Dickcissel + Cowbird
1	83	0.84 ± 0.16	1.01 ± 0.18	22	1.18 ± 0.31	1.73 ± 0.45
2	52	0.92 ± 0.22	1.31 ± 0.26	20	1.10 ± 0.38	1.45 ± 0.46
3	75	0.88 ± 0.16	1.08 ± 0.19			
4	72	0.50 ± 0.14	0.67 ± 0.18			
5 and 6	46	0.63 ± 0.21	0.72 ± 0.22			

Table 3. Numbers of males according to maximum number of simultaneous mates/male (percentage within each habitat).

Number of females	Prairie	Oldfield
One	23 (74.2)	75 (51.0)
Two	8 (25.8)	43 (29.2)
Three	0	24 (16.3)
Four	0	4 (2.7)
Five	0	1 (0.7)

The mean number of Dickcissel young/male, or the total number of Dickcissel and cowbird young/male, is not significantly different when males with one or two nests are compared between habitats, nor do any significant differences exist among prairie males in the numbers of Dickcissels or Dickcissels plus cowbirds produced. In the oldfield, on the other hand, there are significant differences between the mean numbers of young produced by males with just one nest and males with two nests, both for Dickcissels fledged (Student's t = 3.194, df = 94, $P < 0.05$) and for Dickcissel and cowbird young together (Student's t = 3.194, df = 94, $P < 0.01$). Males with 3 or more nests also produce significantly more young than males with 1 nest, but the numbers of young produced by males with 2, 3, 4, 5, and 6 nests are not significantly different from each other. Furthermore, there is a significant positive association between the number of nests of a male and the numbers of both Dickcissels

and total young fledged/male in the oldfield habitat (Spearman $r = 0.9$, $n = 5$, $P < 0.05$).

Discussion

The female Dickcissel most certainly has a set of criteria that she uses to select an appropriate nesting location. As they arrive during spring migration and presumably are attracted by the singing and other displays of territorial males, females discover suitable nest sites and begin to build. I do not know what involvement the male has in nest-site selection, but I do know that the behavioral interaction of the male with the female during this critical period is intense (Schartz and Zimmerman 1971). It is also not known whether the female chooses a territory on the basis of male phenotype (Weatherhead and Robertson 1979), and thus incidentally obtains access to a suitable nest site, or selects the nesting situation directly using criteria of microhabitat quality (Searcy 1979). Of course, it could be both, as Weatherhead and Robertson suggest. Yet, if females were choosing solely on the basis of the quality of the male rather than that of the nesting habitat, some females would certainly end up with unsuitable nest sites as harem size increased, assuming a limited number of nest sites, and there would be a decline in nesting success. This does not happen, however (Tables 2 and 4).

Because there is no significant difference between survival rates of oldfield and prairie nests (Table 1) nor any difference between

Table 4. Daily nest survival rates (±95% C.L.) and production of fledglings/male ($\bar{x} \pm SE$) according to the number of females attracted to the territory.

	Number of different females/male				
	1	2	3	4	5 and 6
Oldfield					
Number of males	70	26	25	18	8
Survival rate	0.930 ± 0.02	0.940 ± 0.02	0.944 ± 0.02	0.913 ± 0.02	0.912 ± 0.03
Dickcissel young	1.00 ± 0.19	1.85 ± 0.45	1.64 ± 0.50	2.00 ± 0.48	3.62 ± 1.13
Dickcissel and Cowbird young	1.20 ± 0.21	2.62 ± 0.47	3.24 ± 0.57	2.67 ± 0.62	4.12 ± 1.12
Prairie					
Number of males	22	9			
Survival rate	0.954 ± 0.03	0.931 ± 0.04			
Dickcissel young	1.18 ± 0.31	2.44 ± 0.82			
Dickcissel and Cowbird young	1.73 ± 0.45	3.22 ± 1.23			

these two habitats in the number of Dickcissel young produced by each female, the two habitats have equal suitability for the female. Any individual nesting location in the prairie is just as good as a nesting site in an oldfield. Females fill up the habitat or, more precisely, occupy adequate nest sites according to their availability. The distribution of females is not determined by the territory boundaries of the males nor in any density-dependent manner by the numbers of females themselves (for example, female-female aggression has never been observed).

An important corollary to this conclusion is that females mated to polygynous males are not at a disadvantage (Tables 2 and 4). Such a relationship is to be expected from the threshold model for the evolution of polygyny (Verner 1964, Verner and Willson 1966, Orians 1969).

If females spread themselves across the landscape simply as a function of the distribution of suitable nesting sites, it is important for the male to include as many suitable sites as possible in his territory. Prairie males do just as well at this as oldfield males when they are monogamous or bigamous (Table 4). The enhanced suitability of the oldfield habitat for males, however, lies in its providing for higher orders of polygyny, which augment male productivity (Table 4) even though male density is greater. These data support the ideal dominance model for the distribution of male Dickcissels (Fretwell and Lucas 1969).

Thus, three different patterns interact in the distribution of Dickcissels across the available habitat space. The heterogeneity of the vegetative substrate results in an uneven distribution of potentially suitable nesting situations within habitats as well as between habitats (Zimmerman 1971). The males' territories are then superimposed upon the habitats, but suitable nesting sites are not equitably apportioned among the males. Not all the territories in the same habitat are equal in quality, and territories in different habitats also differ in quality (Zimmerman 1971). A male that controls a high-quality territory with multiple nesting situations will attract more mates and gain greater fitness. The male's size, the signalling value of his plumage, the aggressiveness of his behavior, his experience, and other attributes have been suggested as possible factors that might explain observed differences in the abilities of polygynous Red-winged Black-

bird (*Agelaius phoeniceus*) males to obtain numerous mates (Searcy 1979, Yasukawa 1979), but supporting data are weak or lacking. Similar factors may assist male Dickcissels in obtaining good territories, and they are being tested (Finck MS).

Females, on the other hand, simply distribute themselves as a function of the availability of nesting situations, with nests built in any habitat and in any territory being equally suitable to the female as long as the site is adequate for nesting. She loses nothing by choosing a nest site within the territory of a male that is already mated. She only loses if she chooses to mate with a male that is defending an area lacking a suitable nesting environment. The regular occurrence of bachelor males (Zimmerman 1966) suggests that females do not make this mistake very often.

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