THE TERRITORY AND ITS DENSITY DEPENDENT EFFECT IN *SPIZA AMERICANA*

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Many species that are territorial during the breeding season are gregarious during the nonreproductive phase of their annual cycle. As Genelly (1955) has shown, this change involves only a shift in the role of aggressive behavior, and Conder (1949) and Guhl (1968) have further suggested that territoriality can be considered simply as a spatial extension of the phenomenon of individual distance under the impetus of an increase in androgens. Such a generalization suggests that the physiological mechanisms leading to the expression of territorial behavior (the hypothalamic-hypophyseal-gonadal axis) and perhaps the proximate environmental factor (i.e. light) may be identical for many bird species. But the ultimate environmental factors selecting for territoriality should not be expected to be the same for all species. Hence the functional roles ascribed to territoriality are various (Nice, 1941).

Recently Fretwell and Lucas (1969) developed models to illustrate several hypotheses of territorial function. One of these states that territoriality is directly involved in population regulation, functioning in a density dependent fashion by forcing some males under conditions of overcrowding into unsuitable habitats in which their productivity would be decreased (see Tompa, 1962). Brown (1969), on the other hand, concludes that territoriality only operates in a density dependent manner if birds are *prevented* from establishing territories as a result of the territorial behavior of resident birds (see Watson and Jenkins, 1968). He argues that if territoriality forces some males to establish their territories in suboptimal habitats and if they reproduce there, the production of the total population will be increased rather than decreased. Yet, it seems to me, that if reproductive rates can be shown to be lower in the birds that are forced into marginal habitats than the level of reproduction of birds in more suitable habitats, then the negative feedback implied in a density dependent effect has been satisfied. Even though these birds in the poorer habitats may have at least some degree of reproductive success, the rate of increase is decreased (Birch, 1960). Furthermore the regulation of population size by density dependent factors can only, by its very nature of operation, affect the local population. Other local populations, as Brown points out, may be at levels where density dependent factors may not be manifest.

The model presented by Fretwell and Lucas (1969) hypothesizes that the departure of males from preferred habitats increases the suitability

of the preferred habitat, enhancing the probability of success for the birds that remain. Thus the density dependent effect of territoriality does give territorial behavior survival value to the individuals exhibiting it.

In this paper I try to show that the structure of the vegetation is the proximate environmental factor affecting habitat selection in the Dickcissel (*Spiza americana*), and that territoriality in this species has a density dependent effect as Fretwell and Calver (1969) first suggested. Furthermore I suggest the hypothesis that the vegetative structure is also an ultimate environmental factor that directly affects reproductive success. Such a coincidence between proximate and ultimate factors involved in habitat selection has been discussed by Hilden (1965).

STUDY AREAS

This work was conducted in Riley County, Kansas mainly during the nesting seasons of 1967 and 1968. Resident Dickcissel populations were measured in several habitats that encompassed the various seral stages occurring in this area: a 51-acre cedar (*Juniperus virginiana*) woodland, two permanent pastures of 27 and 86 acres, a 13-acre overgrazed pasture (the "brushy pasture"), a 41-acre grass-mixed forb stand (the "*Bromus* waterway"), a fallow field of 19 acres (the *Melilotus* field), a 2-year old oldfield (the "*Conyza* field") that was divided into a north portion of 56 acres and a south portion of 37 acres, and a 56-acre young oldfield (the "*Setaria-Rumex* field").

METHODS

In the early spring of 1967 before the arrival of the birds, the *Conyza* field was marked by 80 stakes set in a grid at 200-foot intervals. Fifty of these stakes were chosen at random to be centers of circles, 4 m^2 in area, in which vegetation data would be collected during the middle days of May, June, July, and August of 1967 and 1968. These stakes also served as reference points for the mapping of territorial males and nests.

The vegetational analysis used to determine the height and the percentage cover of grass, forb, and woody vegetation was a modification of the point quadrat method (Greig-Smith, 1964: 7). Depending on the month, at most three levels of vegetation were recognized that generally corresponded to a lower layer of grasses, short forbs, and bushes, a middle layer of medium forbs and bushes, and a third, uppermost layer of tall forbs. If different layers were present at a sampling point, heights and the percentage of cover were determined separately for each layer.

In the other habitats sampled (e.g. pastures), a diagonal transect was run through the field with similarly collected vegetational measurements made at a minimum of 10 randomly chosen points separated by one or more 50-foot intervals along this transect. Additionally the vegetation in territories of selected males was measured by a transect along the longest dimension of their territories, collecting data at every 50-foot interval.

Vegetation data collected from points falling within territories in a given habitat were compared to data collected at points outside of territories. Moreover by summing the products of the average per cent cover and height for each layer of the vegetation of all points within a given habitat or territory, a vegetation index was computed as a representation of the volume of the vegetative cover.

On the *Conyza* field, the *Setaria-Rumex* plot, the *Bromus* waterway, and the *Melilotus* tract census maps were made of territorial males, females, and nests from which weekly composite maps were drawn. From these data, the population of males, females, and nests could be determined as well as the mating relationships of the resident birds. Nest histories on these areas were followed by once-a-week visits to each nest. All population densities computed in late summer exclude birds in the postnuptial molt. The sizes of the males' territories were measured by tracing territory outlines with a compensating polar planimeter. An average of 60 per cent of the territorial males in all the populations and many of the females were color-banded for individual recognition. The population of males and females and the territory sizes were also measured in all the other habitats on a one-trip sample during June.

HABITAT SELECTION

The main nesting population of the Dickcissel extends from the Gulf coast on the south to just over the Canadian border on the north, from the High Plains on the west to the Appalachian Plateau on the east. Although the highest densities of this species are associated geographically with prairie areas (Aldrich, 1948; Robbins and Van Velzen, 1969: 62–63) the Dickcissel is really characteristic of disturbed (subseral) and agricultural habitats (Kendeigh, 1941) and is usually absent from true grassland communities (Cody, 1966) except in certain years.

Figure 1 compares the male density at the height of nesting in June over the range of habitats chosen by Dickcissels. This habitat preference is similar to that Graber and Graber (1963) describe for the Dickcissel in Illinois.

The selection by the Dickcissel of later oldfield habitats in which forbs predominate in preference to the young oldfield stage and more ecologically mature pastures and cedar woodland in which grasses are more abundant appears to be dependent upon two characteristics. First the habitat must provide a properly structured vegetative cover that offers both density and height, since the density of territorial males is dependent upon the volume of the vegetation (Figure 2). The slope of the line that could be drawn through these points is significant ($t_b = 6.887$, df $= 6$, $P < 0.01$). Furthermore it is apparent that the males' density is related to the volume of the herbaceous vegetation, for if the woody vegetation term is subtracted from the vegetation index of the cedar woodland habitat (open circle in Figure 2), the volume is similar to that of the two grassy pastures and is closer to what one would expect from the recorded male density.

The *Setaria-Rumex* field was the same area that was studied the previous year as the north tract of the *Conyza* field. The change that resulted in its reversion down the successional series was severe wind drift in April of aerially applied 2,4-D that eliminated most of the forb seedlings. The
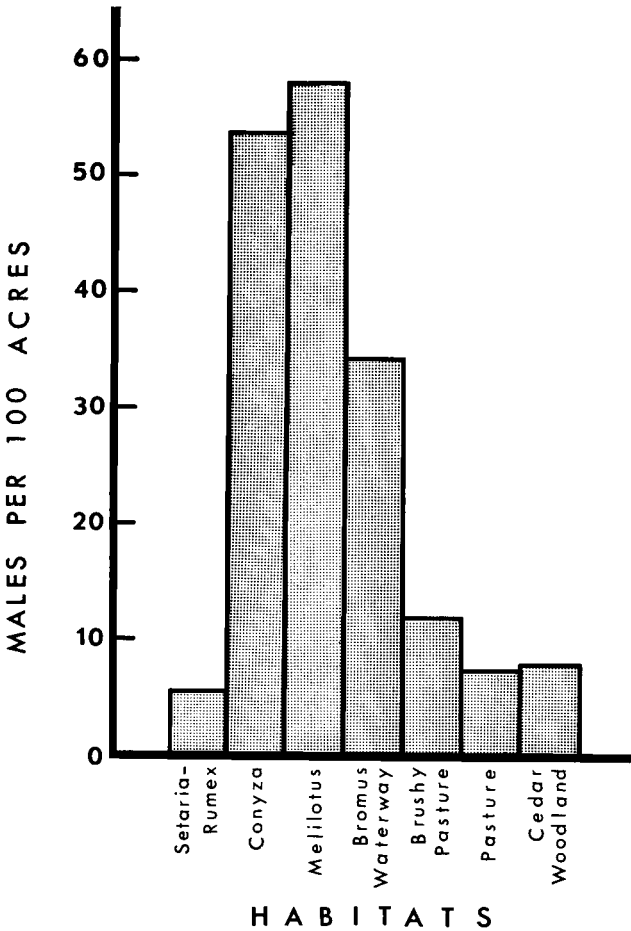
Figure 1. Habitat preferences of males in June.

late development of a resident Dickcissel population in this field the second year further emphasizes the response of males to the volume of the vegetation. Because of the herbicide treatment this field received, the vegetative cover in May was made up mainly of grasses and the dead stems of the last year's forbs and had an average vegetation index of 1,844. As the violent thunderstorm activity that is typical of early June in this region had knocked down most of these dead forb stems, the vegetation index at mid-June was down to 900. In contrast, this same field the previous year had a vegetation index close to 5,000. Although males arrived and exhibited territorial behavior, they did not remain. Two of the six males seen here from mid-May to the first week of June were color-banded
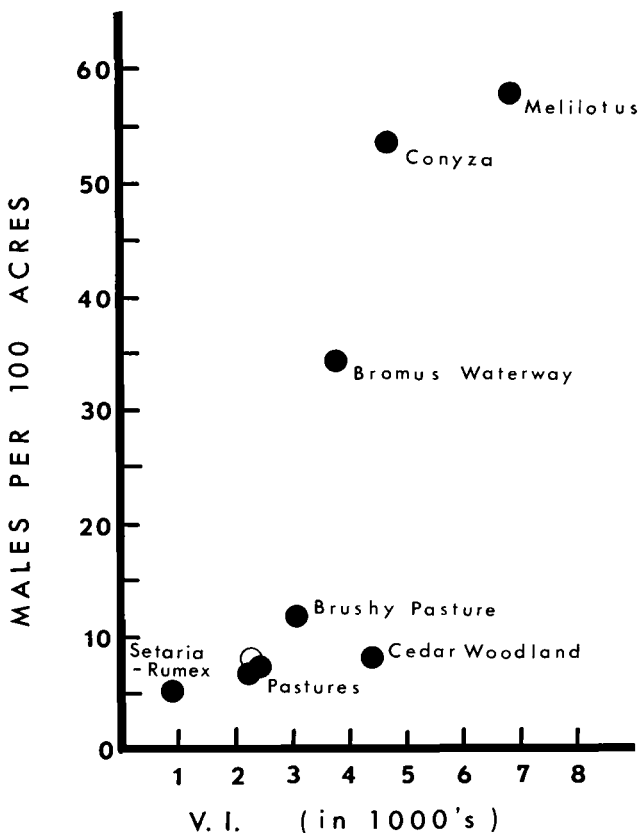
Figure 2. Density of males as a function of the vegetation index (V.I.). See text for computation of this index. Open circle is the value for the cedar woodland with the woody term subtracted from the vegetation index.

birds singing on their last year's territory, but even these birds did not stay. The male density on this field in the second week of June was still zero. Not until the third week of June did males arrive on the field and remain. Although the dominant vegetation in the habitat at this time was annual grass (*Setaria*) and dock (*Rumex*), certain other forbs (*Amaranthus hybridus, Polygonum* sp., and *Chenopodium album*) had begun to grow so that by mid-July the vegetation index had reached 2,534 and the density of males had increased from 5.4 to 20.5 males/100 acres. Responsiveness to the volume of the vegetation has also been shown in forested habitats for chickadees (Sturman, 1968).

The vegetation values shown in Figure 2 are averages for a particular habitat. It is also apparent that within a given field males are responsive
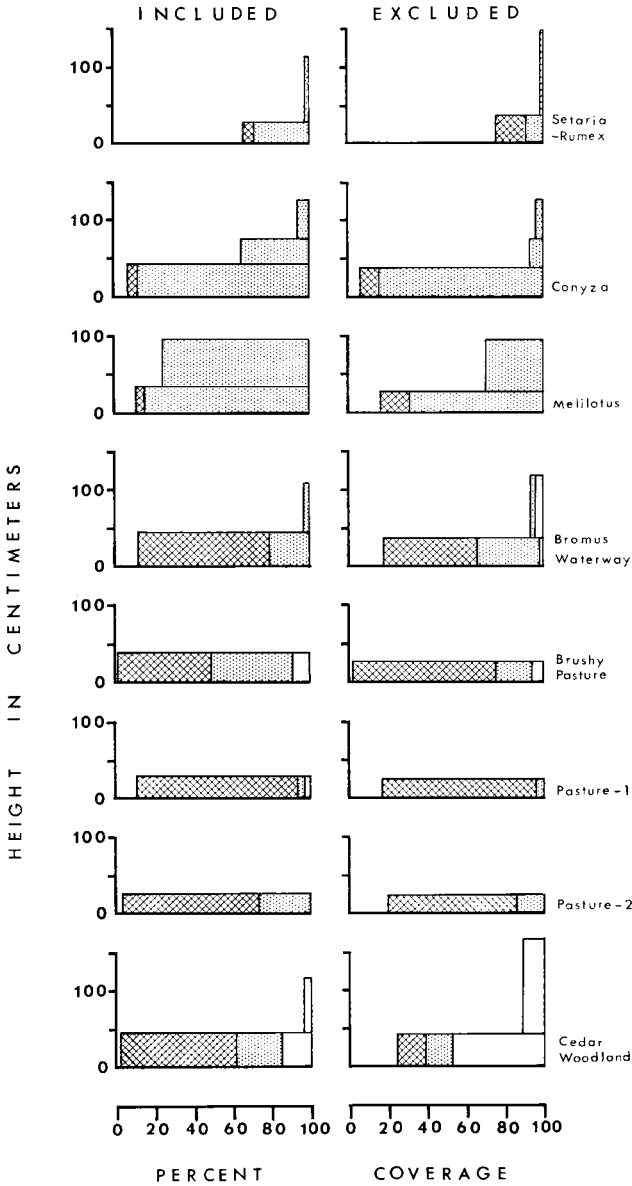
Figure 3.   Structure of the vegetation included within and excluded from territories in the habitats sampled in June. Cross-hatching represents grasses, stippling represents forbs, unmarked portions represent woody vegetation.
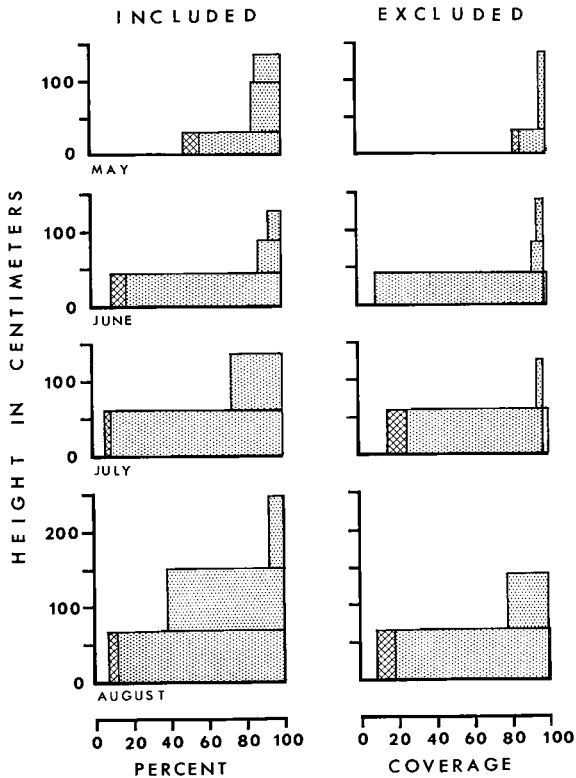
Figure 4. Structure of the vegetation included within and excluded from territories in the months of the nesting in 1967 on the *Conyza* tract. Cross-hatching represents grasses, stippling represents forbs, unmarked portions represent woody vegetation.

to differences in the configuration of the vegetation. Figure 3 compares the composition, heights, and percentage cover of sampling points that were either included or excluded from the territories of males resident in each of the habitats surveyed in Figure 2. In every case the vegetation included within the males' territories is either taller or denser or both taller and denser than that which was not included within their territories. It is also apparent again from this analysis that the male Dickcissel is not responsive to the height and density provided by the cedars in the woodland habitat, choosing instead portions of the habitat containing proportionately larger patches of grasses and forbs.

A more detailed analysis of this within field selection by the male Dickcissel was conducted in the *Conyza* field throughout May, June, July, and August of 1967 (Figure 4). The difference between the June values in this figure and those in Figure 2 results from including data

TABLE 1

COMPARISON OF THE AMOUNT OF FORB COVER BETWEEN POINTS WITHIN TERRITORIES
AND POINTS OUTSIDE OF TERRITORIES

Month	Layer	t	df	P
May	Lowest	3.72	83	$P < 0.01$
	Middle	2.78	83	$P < 0.01$
	Highest	2.44	83	$P < 0.02$
June	Lowest	1.22	94	$P > 0.20$
	Middle	0.96	94	$P > 0.20$
	Highest	1.23	94	$P > 0.20$
July	Lower	2.87	60	$P < 0.01$
	Higher	2.32	60	$P < 0.05$
August	Lowest	0.77	41	$P > 0.40$
	Middle	3.08	41	$P < 0.01$
	Highest[1]			

[1] Not computed.

from the north field in Figure 2 only for 1 week in mid-June. Except for
the presence of tall forbs included within territories in August, the heights
of all layers of the vegetation within territories are similar to the heights
of the vegetation outside of territories for each of the 4 months. The
small percentage of grass is similar between included and excluded averages
for all months. Coverage by forbs, however, shows some significant dif-
ferences between the averages for the vegetation within or outside of
territories (Table 1). For all months but June, male Dickcissels appear
to select the denser vegetation for their territories when sufficient dif-
ferences exist within the total available habitat. The similarities in the
June vegetation between areas within and outside of territories may be
due simply to supply of suitable habitat exceeding demand (see below).

The second requirement of the habitat is the presence of song perches.
Dickcissels have no aerial song, but sing from forb or woody perches that
extend an average of 49 ± 3.5 cm (SE, n = 75) and 235 ± 35.1 cm
(SE, n = 37) respectively above the average level of the vegetation. No
correlation exists between perch heights and density of the males, and
the considerable variation between perch heights selected shows no apparent
preferred perch height. Perches above the general vegetation level must
simply be present. In two parts of the *Conyza* field the alfalfa was har-
vested late the previous year, so no old stems extended above the new
growth. These areas were mostly unoccupied until the last week of June
when other forbs (*Conyza, Ambrosia,* and *Cannabis*) grew through the
dense but lower alfalfa and provided the necessary perches. The absence
of perches in regularly harvested alfalfa may also explain the low densities
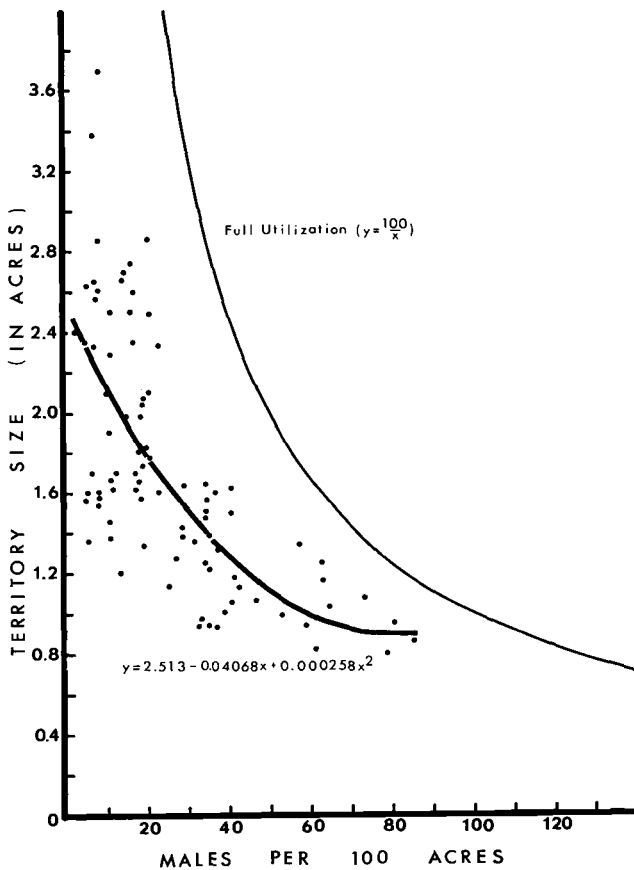Graber and Graber (1963) report in this habitat in Illinois. In my

Figure 5.   Territory size as a function of male density.

experience Dickcissels inhabit such fields only where overhead wires or adjacent fence rows provide perches.

MALE DENSITY AND TERRITORY SIZE

Huxley (1934) describes the territory of a bird as an elastic disc that can be compressed, but only with increasing force until it reaches an incompressable size; this model depicts the territory of the Dickcissel. Figure 5 shows a minimal territory size at approximately 0.9 acres. Territory size decreases as density increases, but the rate of decrease slackens progressively until at densities above 60 males/100 acres the decrease in territory size is quite slight. The quadratic equation for this curve is significant ($t_{b1} = 11.05$, $t_{b2} = 8.19$ with df $= 87$, $P < 0.01$).

The full utilization curve also plotted in Figure 5 relates male density to territory size if all territories were equal and completely contiguous over the whole habitat. As the measured territory size curve flattens out at high densities, it approaches the hypothetical full utilization curve. If territories are nonoverlapping, the territory size curve cannot cross the full utilization curve. Thus the occurrence of a minimal territory size imposes an ultimate limit on the population density of males at approximately 110 males/100 acres on the basis of space alone. One would only expect this maximum density if the habitat were uniformly optimum throughout and the supply of males were superabundant. In the habitats sampled these conditions were not met. As Figures 3 and 4 illustrate, the vegetation was not uniform and males established their territories in the taller and denser vegetation. In June in the *Conyza* field no differences in the vegetation within or outside of territories were detected (Table 1) but the male densities in the north and south fields from which these data were collected averaged 49.1 and 11.0 males/100 acres respectively for the month of June, suggesting that more males could have established territories had they been available.

The energy demands of other activities allow the males to channel only so much time and effort into territory defense (Schartz, 1969). Although not evident in Figure 5 at low population densities, a maximum territory size is thus determined by the economic feasibility of its use. Theoretically one could expect to obtain a cubic regression that would illustrate this maximum over a range of low densities as well as the minimum at high densities. The discrepancy between the actual territory size and what it would be at full utilization at low densities is due then to the effect of this maximum territory size. At moderate densities, once the effect of density on territory size is evident, this discrepancy is probably due largely to the presence of a certain amount of nonsuitable cover (i.e. short and less dense vegetation) within the habitat (see Figures 3 and 4). I believe that at high male densities when the difference between these two curves decreases males must utilize more and more of this unsuitable habitat.

HABITAT SELECTION AT HIGH MALE DENSITIES

A comparison of the vegetation that is either included or excluded from territories in Figure 3 with the density data presented in Table 2 shows that the difference in the vegetation within territories to that outside of territories is more pronounced in fields with the higher male densities. At high male densities all but the least suitable vegetation is included within territories, while at lower densities, although differences in the vegetation exist, apparently some areas of still suitable but perhaps sub-

TABLE 2

DICKCISSEL POPULATIONS AND VEGETATION DURING JUNE IN HABITATS SAMPLED

Field	♂ ♂ /100 acres	♀ ♀ / ♂	V. I.[1]
Setaria-Rumex	5.4	0.67	900
Conyza	53.6	2.02	4691
Melilotus	57.9	1.18	6822
Bromus waterway	34.1	1.07	3795
Brushy pasture	11.7	0.67	3045
Pasture 1	7.5	0.50	2357
Pasture 2	7.0	0.50	2282
Cedar woodland	7.8	0.75	4357(2322)[2]

[1] Vegetation index, see text for calculation.
[2] Figure in parenthesis is the vegetation index computed without the woody plant term.

optimal vegetation are excluded, making the difference between included and excluded less distinct.

It was possible to analyze this suggestion more closely from the situation that developed on the north field of the *Conyza* tract. During June the male densities in this field increased from 37.5 males/100 acres in the first week to 58.9 males/100 acres by the last week. At the latter density territory size was nearing the minimum (Figure 5), but male densities continued to increase and reached a peak in the third week of July at 85.7 males/100 acres. As all these birds were territorial and had not begun to molt, this increase was not caused by postnuptial wandering or migratory influx. In this field seven of the vegetation sampling points were not within occupied territories during June, but with the higher densities reached during July, four of these points became included in territories. In Figure 6 the average vegetation of these four points newly included in July is compared to the average July vegetation of all the other points in this field that were within territorial boundaries during *both* June and July (indicated as "others included") and the average vegetation of the three points that were still excluded during the high population densities of July. The vegetation of the points newly included in July is similar in height and per cent cover to "others included" sample at the lower vegetation layer, but considerably less dense and somewhat shorter at the upper level. They still provide better coverage than the three points not within territories. These results thus suggest that with higher male densities, birds are indeed forced to include less preferred cover within their territories. It is this result of the minimum territory size rather than the ultimate space available that gives territoriality in the Dickcissel its density dependent effect. Although no movement data of individually marked birds from one field to another
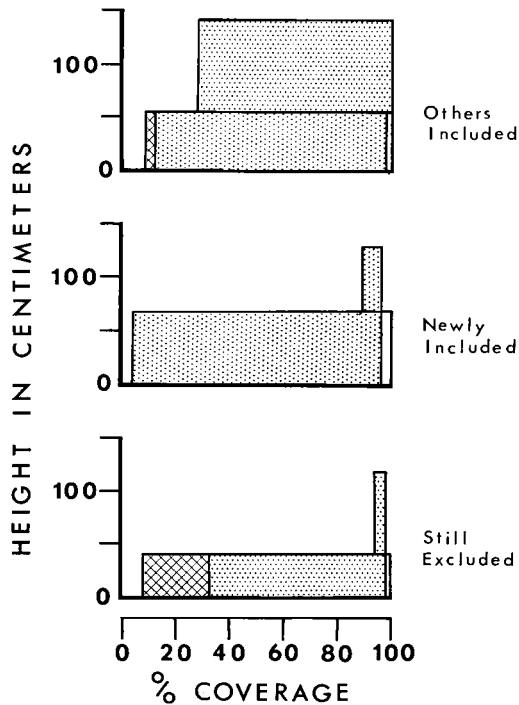
Figure 6. Comparison of the structure of the vegetation at sampling points newly included within territories or still excluded at high male densities with that of others included within territories at both low and high densities. Cross-hatching represents grasses, stippling represents forbs, unmarked portions represent woody vegetation.

were obtained, these results also suggest that males inhabiting less dense, hence less preferred, habitats (e.g. pastures) are similarly forced into this situation by high male densities in habitats with higher vegetation indexes. Just such a response was hypothesized by Svärdson (1949) as a reaction to greater intraspecific competition at high population densities.

SEX RATIO AND THE VEGETATION

I have previously shown (Zimmerman, 1966) that females choose to nest within the territories of certain males on the basis of the structure of the vegetation. Males defending territories that lack suitable nest site vegetation will remain mateless while males holding good territories can be polygynous. Figure 7 relates the vegetation index of the individual males' territories in June with the average number of females to which they were simultaneously mated during this period. The linear relationship between the volume of the vegetation and the number of mates is
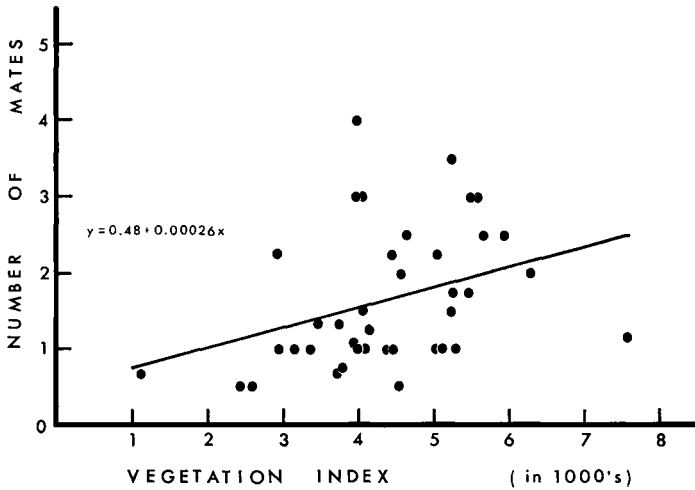
Figure 7. Number of mates of individual males as a function of the vegetation index of their territories.

significant (t_b = 2.52, df = 31, P < 0.02). Thus not only do males defending sufficiently tall and dense vegetation attract mates, the number of mates attracted is directly proportional to the volume of the vegetation. It is therefore apparent that the suitabiliy of a territory in terms of the vegetation is indeed positively related to the potential for successful reproduction.

SEX RATIO AND MALE DENSITY

Only the data for the north portion of the *Conyza* field span a wide range of male densities. If the weekly sex ratio (females/male) is plotted against the weekly male density for this field, a significant parabolic regression is obtained (t_{b1} = 10.97, t_{b2} = 8.81 with df = 7 P < 0.01) (Figure 8). These data include only measurements made up to the end of July, as gonad regression begins in late July (MS) and males stop territorial behavior while nesting females still remain active. The high sex ratios measured in August are due to my not counting males that had started postnuptial molt and abandoned breeding behavior rather than a response to habitat suitability. The other points plotted in this figure are from all other study population. Although they increase the variability, I consider they support this relationship between male density and the sex ratio, but not significantly so.

This curve indicates that the sex ratio increases with an increase in male density up to a peak between 60 to 70 males/100 acres. As it has
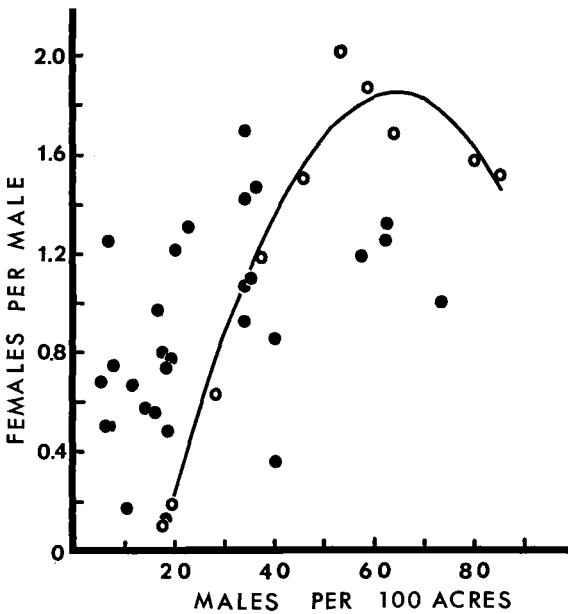
Figure 8. Sex ratio as a function of male density. Open circles are the values obtained from the north field of the *Conyza* tract and upon which the curve was calculated. Solid circles are data from all other populations.

been shown that within this range of increasing male densities the volume of the vegetation increases in the fields inhabited (Figure 2) and that the sex ratio also increases with the volume of the vegetation (Figure 7), this relationship is only to be expected. The decrease in the sex ratio at high male densities, I believe, reflects the forcing of some males into less suitable habitat patches within the same field, decreasing the desirability of their territories to females. The four sampling points in the north field of the *Conyza* tract that were included within territories at these high male densities and which were shown to represent less dense vegetation (Figure 6) were added to the territories of four different males. In the first week of July these males had an average of 3.0 females, but by the end of July their number of mates had steadily decreased by 67 per cent to 1.0. For all other territories in that population over that time span, the average weekly sex ratios were relatively constant at 1.5, 1.5, 1.6, but finally dropping in the last week to 1.2, a decrease of only 21 per cent from the beginning to the end of this period. Similarly the sex ratios in less suitable habitats such as pastures and the cedar woodland are also lower (Table 2), as would be expected from their lower vegetation indices.
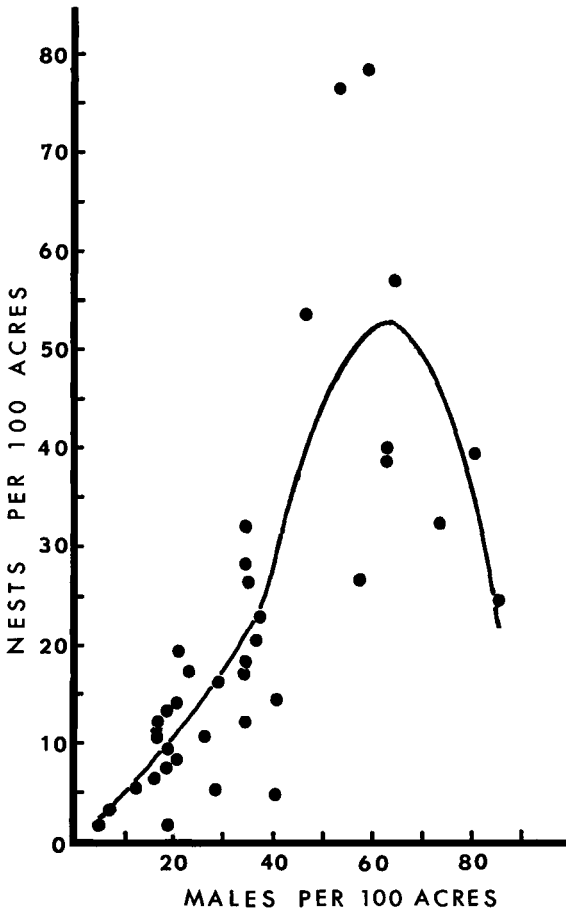
Figure 9.   Nest density as a function of male density.

PRODUCTIVITY

Given this relationship between male density and the sex ratio, the relationship between the male density and the number of active nest/100 acres (Figure 9) was a logical result. This curve is a composite of two separate analyses involving a regression at densities below 35 males/100 acres and a second at higher densities. Together they explain 67 per cent of the variation, although only the regression coefficients for the analysis of male densities above 35 males/100 acres are significant (b_1 = 6.491, t = 2.85; b_2 = –0.053, t = 2.72 with df = 12, P < 0.02). But this is the interesting part of the curve, because it again shows a peak in nest density

at male densities between 60 and 70 males/100 acres, followed by a decrease at higher male densities.

To ascertain any relationship between the density of males and the production of young, the total number of fledglings produced from nests started at various weekly male densities was determined for the four populations in which nesting data were collected (Table 3). Knowing the number of new nest starts and corresponding female density at each male density permitted calculating reproductive rates in terms of fledglings/adult and fledglings/nest started. These productivity measures are relative values and are useful only in comparing the reproductive rates at various male densities of a single population. Total annual productivity rates per adult are presented in Table 4. Although no significant regression relationships are evident between male density and these measures of productivity, there appear to be peaks in productivity at moderate male densities in all but the *Melilotus* field. This is most pronounced in the north field of the *Conyza* tract. Although direct evidence in terms of statistical significance is lacking, these results support Allee's principle (Odum, 1959: 217–218) of an optimum density for survival and the operation of mechanisms to decrease population increase once a critical density in reached (Birch, 1960).

It was also not possible to show a significant relationship between the vegetation indexes of males' territories and the productivity of these territories, but the case of the four males in the north field of the *Conyza* tract that included less dense vegetation in their territories at high male densities provides some indirect evidence. Not only did their number of mates decrease, but only one new nest was started in these territories during the period of high densities in July, and it was not successful. In all other territories in this field during the same period, 15 nests were started, of which 13 per cent were successful.

The major cause of nest failure in the Dickcissel is predation (Table 4; Zimmerman, 1966; Schartz, 1969). Daily predation percentages are not correlated with nest density but rather increase with time (MS). When nest densities are actually decreasing in July and August, the intensity of predation reaches maximum levels. This suggests that as the nesting season progresses, there is an increase in the predator population and/or an increase in the predator's effectiveness. During July of 1967 the average vegetation index of territories in the north field of the *Conyza* tract that suffered any predation loss was 6743.0 ± 605.8 (SE, n = 12), while those territories not losing any nests to predation during the same period had an average vegetation index of 9381.3 ± 2409.0 (SE, n = 6), but the difference between these two means is not significant.

TABLE 3

PRODUCTIVITY AND MALE DENSITY

Month	♂♂/100 acres	♀♀/100 acres	Young fledged[1]	Fledglings/100 acres	Fledglings/adult	Nest starts	Fledglings/nests started
North field of *Conyza* tract							
May	19.6	3.7	0	0.0	0.00	1	0.0
May	28.6	18.0	2	3.6	0.08	4	0.5
June	37.5	44.6	20	35.7	0.44	16	1.2
June	46.4	71.5	28	50.0	0.42	19	1.5
June	53.6	108.3	21	37.5	0.23	16	1.3
June	58.9	110.7	4	7.1	0.04	8	0.5
July	64.3	108.7	0	0.0	0.00	4	0.0
July	80.4	127.0	3	5.4	0.03	9	0.3
July	85.7	130.3	4	7.1	0.03	5	0.8
July	78.6	92.8	0	0.0	0.00	2	0.0
August	60.7	64.3	0	0.0	0.00	0	0.0
August	33.9	51.5	0	0.0	0.00	1	0.0
Setaria-Rumex field							
June	5.4	3.6	0	0.0	0.00	2	0.0
June	7.1	8.9	2	3.6	0.22	1	2.0
July	12.5	7.1	0	0.0	0.00	2	0.0
July	16.1	9.0	4	7.1	0.28	2	2.0
July	20.5	25.0	12	21.4	0.47	6	2.0
July	23.2	30.4	11	19.6	0.37	5	2.2
August	16.1	30.4	3	5.4	0.11	1	3.0

[1] Number of young fledged from nests started at these male densities.

TABLE 3 (Continued)

Month	♂♂/100 acres	♀♀/100 acres	Young fledged[1]	Fledglings/100 acres	Fledglings/adult	Nest starts	Fledglings/nests started
Bromus waterway							
June	40.2	14.5	0	0.0	0.00	3	0.0
June	34.1	36.5	1	2.4	0.04	9	0.1
June	34.1	31.7	0	0.0	0.00	3	0.0
June	40.2	34.2	0	0.0	0.00	5	0.0
July	34.1	36.5	0	0.0	0.00	5	0.0
July	36.6	53.8	10	24.4	0.27	7	1.4
July	34.1	58.1	1	2.4	0.03	7	0.1
July	34.1	48.8	2	4.9	0.06	2	1.0
August	35.4	41.4	0	0.0	0.00	1	0.0
Meliotus field							
May	26.3	–	0	0.0	0.00	4	0.0
June	73.7	73.7	1	5.3	0.04	4	0.2
June	57.9	68.3	0	0.0	0.00	4	0.0
June	63.2	84.1	0	0.0	0.00	5	0.0
June	63.2	79.0	0	0.0	0.00	1	0.0
July	28.9	31.5	0	0.0	0.00	4	0.0
July	21.0	31.5	0	0.0	0.00	2	0.0

TABLE 4
NESTING SUCCESS

Population	Total nests	Fledglings	Percentage predation	Percentage cowbird	Percentage other[1]	Young produced	Young/adult[2]
Conyza field	85	31	49	5	15	82	1.07
Setaria-Rumex field	19	53	37	0	10	32	1.86
Melilotus field	24	4	50	17	29	1	0.05
Bromus waterway	42	14	41	19	26	14	0.45

[1] Includes unknown causes, weather, and desertion other than as a result of cowbird parasitism.
[2] Adult population is the average of the weekly values over the weeks that include any new nest starts.

I believe that predation obscures the relationships between fledgling production and male density (Table 3) and between productivity and the vegetation of territories. Apparently by July and August the predator populations have reached such a level that they find and eliminate even nests built in suitably dense cover. If this is indeed what happens, it decreases the average difference between the vegetation index of non-predatorized and that of predatorized territories as well as obscuring the relationship between productivity and male density or the volume of the vegetation.

Covert nest placement to escape predators may not be the only effect that give dense vegetation survival value. An alternate (or concomitant) hypothesis for the role of the height and density of the vegetation as an ultimate factor in the environment may be its ameliorating effect on the microclimate of the nest site (Blankespoor, 1970).

TERRITORIALITY AS A DENSITY DEPENDENT FACTOR

I contend that territoriality in the Dickcissel has a density dependent effect on the population size in the following way:

1) A minimum territory size that a male will defend exists. Any increase in density within a local population above that density at which this minimum territory size is reached results in utilization by some males of habitats within the area that provide less suitable vegetation (shorter and/or less dense).

2) Furthermore as a minimum territory size means that the most suitable habitats will be close to full utilization, additional males coming into an area must settle in habitats that are less suitable (e.g. pastures).

3) As females are responsive to the height and density of the vegetation, particularly as it relates to nesting sites, males defending less suitable habitats in response to high male densities attract fewer mates.

4) This decrease in the sex ratio is reflected in a decrease in the number of active nests at high male densities and suggests that total productivity is also decreased, although direct evidence relating productivity to the density of the male population or the vegetation index of individual territories lacks statistical significance.

SUMMARY

The Dickcissel is a seral species that is most common in the tall grass prairie region of the grassland biome. Two factors appear to be important in its selection of habitat: presence of song perches and a sufficiently tall and dense cover of herbaceous vegetation. The density of males is proportional to the volume of this vegetation.

The response of its territory size to density of males conforms to Huxley's elastic disc model with a minimum territory size of approximately 0.9 acres, reached at densities of around 60 to 70 males/100 acres.

At male densities greater than this, some males are forced into territories that contain less suitable vegetation, either patches of shorter and less dense cover in the same field or, it is suggested, in less preferred habitats like pastures and woodland. As the number of mates attracted by this polygynous species is directly proportional to the volume of the vegetation, the suitability of the territory in terms of the vegetation is directly related to the potential for successful reproduction.

The density dependent effect of territoriality thus operates through the forcing of males at high population densities into defending territories of less suitable vegetation. This decreased suitability is reflected in a decrease in the sex ratio and a lowered density of active nests. Although direct evidence of statistical significance is lacking, it is suggested that productivity is also decreased at high male densities.

The volume of the vegetation operates not only as a proximate factor guiding habitat selection, but it is hypothesized that it also is an ultimate environmental factor through its effect on protection from predation and/or amelioration of the microclimate of the nest site.

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