

## GENERAL NOTES

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**Male Dickcissel behavior in primary and secondary habitats.**—The Dickcissel (*Spiza americana*) is an early successional species nesting in weedy oldfields (Zimmerman, *Auk* 83:534-546, 1966; *Auk* 88:591-612, 1971; Harmeson, *Auk* 91:348-359, 1974). Fretwell and Calver (*Acta Biotheoretica* 19:37-44, 1969) suggested that Dickcissels have an ideal dominance distribution because habitat suitability, as indicated by female/male sex ratio, is higher in oldfield habitat where the density of individuals is higher, than in prairie where density is lower. Using nest survival rate and fledgling production, Zimmerman (*Auk* 99:292-298, 1982) demonstrated the existence of the ideal dominance system for male Dickcissels, but found an ideal free distribution for females, since female fitness did not differ between habitats.

Females invest more energy per gamete than males, therefore females should be more selective of mates than males (Trivers, pp. 136-179 in *Sexual Selection and the Descent of Man 1871-1971*, E. C. Campbell, ed., Aldine Press, Chicago, Illinois, 1972). Females maximize their fitness by making optimum choices of male characteristics and territorial qualities, if these factors are assessable when they choose their mates (Searcy, *Am. Nat.* 114:77-100, 1979a). The selective pressure of female choice on males of polygynous species results in the males evolving to choose and defend optimum habitat and/or to behave in a manner that would attract more females. Both territory quality and male quality may determine the reproductive fitness of the males (Wittenberger, *Am. Nat.* 110:779-799, 1976). Males defending territories of less than optimum quality may either compensate for this by emphasizing the displays in their repertoire that attract females, or may seek other territories of better quality.

In this paper I document the difference in habitat quality between primary oldfield habitat and secondary prairie habitat and its relationship with arrival times of males and females and female/male sex ratios. Primary habitat is defined as higher quality habitat where individual density is high, while secondary habitats have lower quality habitat and low individual density.

In addition, the behavior of male Dickcissels is analyzed to test predictions related to differences in habitat quality and selective pressures on males caused by female choice. I predict that Dickcissel males in primary habitat will spend more time defending their territories than those in secondary habitat, because there should be intense competition among males to obtain territories that will allow them to increase their fitness by sustaining higher levels of polygyny (Zimmerman 1982). Since female densities are higher in primary habitat, pressure to attract a mate is less than in secondary habitat. Therefore, I predict that secondary habitat males will spend more time in display behaviors that attract females, since territories in secondary habitats are generally of inferior quality and they are more dispersed within the habitat, while the pool of available females is small (Zimmerman 1966, 1971; Harmeson 1974). Scharzt and Zimmerman (*Condor* 73:65-76, 1971) suggested that males on inferior territories spend more time away from their territories than those on superior territories because those males with inferior territories have a higher probability of locating territories more suitable than their own for attracting females than do males on superior territories. Therefore, I predict that secondary habitat males should spend more time in distant flight, a behavior in which a male temporarily leaves his territory, than primary habitat males; secondary habitat males might increase their fitness as a result of

such behavior if they could obtain better territories elsewhere. A male in an inferior territory would more likely switch territories if possible. Therefore, I predict that between-year site fidelity and within-year site tenacity should be lower in secondary habitat males than in primary habitat males.

*Study sites and methods.*—Four study sites were selected: an oldfield located approximately 15 km SW of Manhattan, in Riley Co., Kansas, on the eastern edge of the Fort Riley Military Reservation (Sec 30 T 10S R 7E) and three prairie sites about 11 km S of Manhattan in Riley and Geary counties within the boundary of the Konza Prairie Research Natural Area (KPRNA) (Secs 30 and 20 of T 11S R 8E). The study areas were marked with a 75-m square grid, corner positions being indicated by surveyor flags and/or 1-m wooden stakes. The study was conducted from the first week of May through the last week of August 1979.

The oldfield consisted of 30.4 ha of weedy forbs, grasses, and scattered woody species bounded on the north, west, and south by tree rows and on the east by a milo field. The area was dominated by sweet clover (*Melilotus officinalis* and *M. alba*), sunflower (*Helianthus* spp.), milkweed (*Asclepias* spp.), and lespedeza (*Lespedeza capitata*), with patches of daisy fleabane (*Erigeron strigosus*) and field bindweed (*Convolvulus arvensis*). Some patches of Canada wild rye (*Elymus canadensis*) were also present. Scattered woody species included small elms (*Ulmus americana*), American plum (*Prunus americana*), and smooth sumac (*Rhus glabra*).

The prairie sites consisted of 78.8 ha characterized by limestone shelves and dry creek beds. Big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), and Indian grass (*Sorghastrum nutans*) were the dominant grasses. Common forbs included lead plant (*Amorpha canescens*), New Jersey tea (*Ceanothus ovatus*), Baldwin ironweed (*Vernonia baldwinii*), and Atlantic wild indigo (*Baptisia leucophaea*).

Dickcissels were mist-netted and individually marked with colored leg bands. For all birds captured, flattened wing length was measured in mm as the distance from the bend of the wing to the tip of the longest primary (Baldwin et al., Sci. Publ. Cleveland Mus. Nat. Hist., No. 2, 1931). Bill length was the distance from the front of the nares to the tip of the bill. Bill depth was measured as the widest distance between the lower edge of the lower mandible to the upper edge of the upper mandible. The throat patch size was taken as the continuous length of the black throat patch, when the bird's neck was extended to a point just prior to spreading the neck feathers. Additional markings on the breast were also noted, but not measured. Mist-netting and visual identification were used to identify males banded the previous year.

Territory size was determined by flushing the males and recording their locations on grid maps (Wiens, Ornithol. Monogr. 8, 1969). Territorial boundaries were determined by observing interactions between neighbors as well as the location of perches used before and after flushing. Territory size was determined weekly by tracing the mapped territorial outlines with a compensating polar planimeter (K & E model 62-0000) and converting this reading to ha. Since Dickcissel territory size is affected by male density (Zimmerman 1971), all territories were adjusted to the same density for comparisons between males using the relationship  $Y = 0.73627 - 0.1035X + 0.0005X^2$ , where Y is the adjusted territory size and X is male density per 40 ha.

During June–August 1979, time budgets of 12 prairie and 21 oldfield males, randomly selected for this study, were recorded using the behaviors listed by Schartz and Zimmerman (1971): foraging, resting, singing, territorial defense, courtship, maintenance of the female, distant flight, and interspecific aggression. In addition, feeding young was also recorded. Observations were made using binoculars and a spotting scope. Behaviors were recorded at

TABLE 1  
MEAN ( $\pm$  SE) FOR VEGETATION VARIABLES IN OLDFIELD (N = 36) AND PRAIRIE (N = 71)

		May	July	August
Vegetation vol.	Oldfield	1623 ( $\pm$ 208.2)	3414 ( $\pm$ 508.4)	5240 ( $\pm$ 361.3)
	Prairie	621 ( $\pm$ 45.9)	1926 ( $\pm$ 106.4)	3133 ( $\pm$ 110.0)
	<i>t</i>	6.22*	3.81*	7.04*
% grass	Oldfield	20.4 ( $\pm$ 3.00)	16.1 ( $\pm$ 2.61)	25.7 ( $\pm$ 4.10)
	Prairie	26.7 ( $\pm$ 1.68)	39.4 ( $\pm$ 1.77)	50.3 ( $\pm$ 1.71)
	<i>t</i>	1.97*	7.52*	6.52*
% forb	Oldfield	33.2 ( $\pm$ 4.35)	38.6 ( $\pm$ 3.84)	43.0 ( $\pm$ 4.35)
	Prairie	12.4 ( $\pm$ 1.27)	35.8 ( $\pm$ 15.11)	23.5 ( $\pm$ 1.64)
	<i>t</i>	5.84*	0.14	5.07*
Height	Oldfield	25.9 ( $\pm$ 2.46)	53.6 ( $\pm$ 5.94)	64.8 ( $\pm$ 4.01)
	Prairie	14.7 ( $\pm$ 0.51)	30.7 ( $\pm$ 1.31)	41.7 ( $\pm$ 1.35)
	<i>t</i>	5.76*	4.98*	6.74*

\*  $P < 0.05$ .

10-sec intervals at the instant a beep was heard from a metronome timer (Wiens et al., Ecology 51:350-352, 1970). Behaviors were observed over 45-min periods, starting on the half hour from 06:30 until 20:30 CDT. There were 30 observation periods on the prairie and 75 in the oldfield.

Vegetation analysis was conducted in mid-May, early July and mid-August by using a modified point quarter technique (Greig-Smith, Quantitative Plant Ecology, 2nd ed., Butterworth, Washington, D.C., 1964). Randomly selected grid posts were used as sample sites. Ten randomly selected azimuths were used to obtain percent cover of forbs, grasses, and woody vegetation and the height of vegetation. Vegetation volume was calculated by multiplying percent vegetation cover by vegetation height.

Since data for particular behaviors were compiled as percent of total activity, they were transformed to arcsine (Zar, Biostatistical Analysis, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974; Barr et al., SAS. User's Guide, SAS Institute Inc., Raleigh, North Carolina, 1979) for analysis of covariance in order to adjust the observations for variations in time, date, and temperature (see Schartz and Zimmerman 1971). The field season was divided into 2-week intervals for adjusted date and the day was divided into 2-h intervals for adjusted time.

The Spearman rank correlation was used for testing the association between male behaviors and the average number of females per week attracted to each territory (as determined by weekly censuses and nest counts). The relationship between the average number of females and the wing length, bill length, bill depth, and throat patch size of the territorial males was assessed using the Pearson product-moment correlation test. Differences in vegetation and the morphology of the males between oldfield and prairie habitats were analyzed by Student's *t*-test. The G-statistic was used to find differences between site fidelity and site tenacity for the males in the primary vs the secondary habitat.

*Results.*—Except for the coverage of forbs in July, there were significant differences between the vegetation in the oldfield and prairie sites throughout the breeding season (Table 1). Since the greater vegetation volume and the higher coverage by forbs in the oldfield is

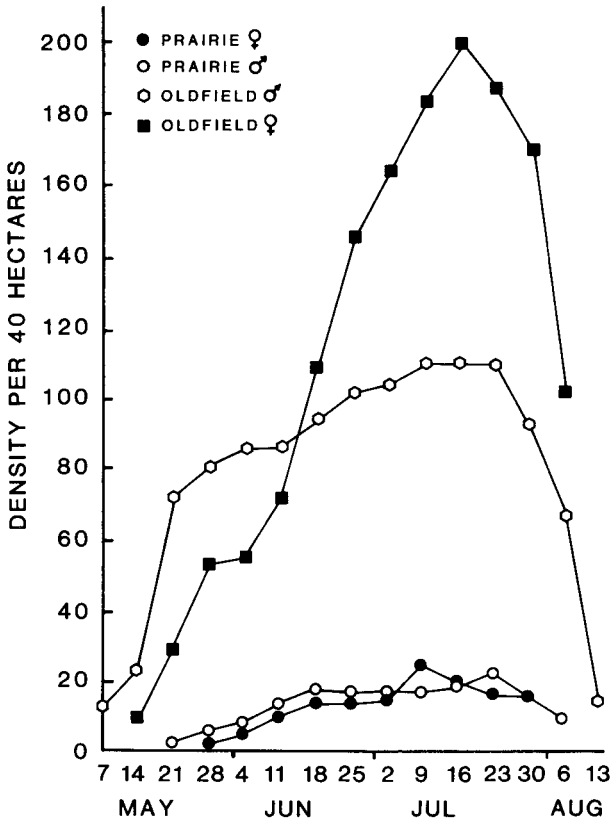


FIG. 1. The number of males and females per 40 ha in oldfield and prairie habitats for summer of 1979.

positively correlated with the incidence of polygyny (Zimmerman 1971), the oldfield habitat is preferred (primary habitat) more than the prairie (secondary habitat).

This difference in preference was reflected in the earlier arrival of Dickcissels in the oldfield (Fig. 1). Wittenberger (Condor 80:355-371, 1978) also found differential arrival for Bobolinks (*Dolichonyx oryzivorus*) in preferred vs other habitats, as did Carey and Nolan (Evolution 33:1180-1192, 1979) for Indigo Buntings (*Passerina cyanea*). Males arrived in the oldfield the first week of May and on the prairie during the third week of May. Females arrived during mid-May and late-May on the oldfield and prairie, respectively. Dickcissel density was also much higher on the oldfield than the prairie (Fig. 1). In the prairie, male density leveled off by the third week of June, whereas oldfield male density continued to increase until early July. Prairie female density remained constant from mid-June until late July, while oldfield female density sharply increased in early July before dropping off. Female/male sex ratio (Fig. 2) was higher in the oldfield than in the prairie at all times even with higher density in the oldfield, a pattern similar to that found by Fretwell and Calver (1969).

Oldfield males attracted a higher average number of females per week than prairie males

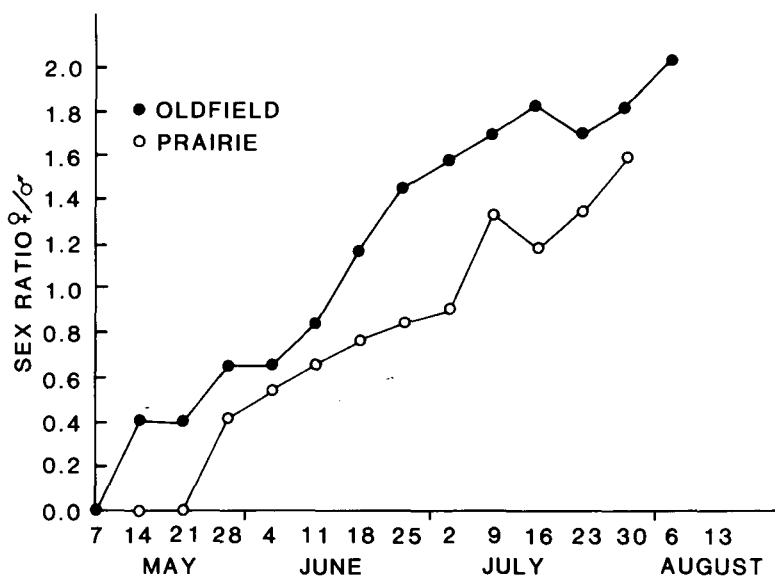


FIG. 2. The sex ratio (female/male) in oldfield and prairie habitats for summer of 1979.

( $\bar{x} = 1.1$ ,  $SE = \pm 0.06$ ,  $N = 140$  and  $\bar{x} = 0.8$ ,  $SE = \pm 0.05$ ,  $N = 56$ , respectively; Student's  $t = 3.51$ ,  $P = 0.006$ ). The average number of females was positively correlated with adjusted territory size on both the prairie and the oldfield ( $r = 0.412$ ,  $N = 56$ ,  $P = 0.001$  and  $r = 0.193$ ,  $N = 140$ ,  $P = 0.02$ , respectively), but adjusted territory size did differ between the two habitats with adjusted territories on the prairie significantly larger than in the oldfield ( $\bar{x} = 0.50$ ,  $SE = \pm 0.036$ ,  $N = 56$ , and  $\bar{x} = 0.45$ ,  $SE = \pm 0.007$ ,  $N = 140$ , respectively; Student's  $t = 1.98$ ,  $P = 0.05$ ).

Male morphology was not different between the two habitats with respect to wing length, bill length, bill depth, and throat patch size (Table 2). Since wing length is a measure of size (Connell et al., *Auk* 77:1-9, 1960), larger males did not occupy primary habitats to the exclusion of smaller males. The fact that bill length and depth were similar between habitats, suggests that the food types eaten in the two habitats may be similar.

Prairie males were present on their territories less than oldfield males, spending significantly more time in distant flight (Table 3). Prairie males also spent more time in courtship display, despite the fact that there were fewer females on the prairie, but less time in territorial defense, which is expected since male density was lower on the prairie. No other significant behavioral differences were observed between prairie and oldfield males. Male Dickcissels do not typically feed their young and the feeding observed in this study occurred rarely and then only in the oldfield late in the season when territorial drive had waned.

On the prairie, the only male behavior significantly correlated with average number of females attracted to a territory per week was resting (Table 4). This may reflect the fact that resting males sit on exposed perches and are conspicuous to females flying over the habitat. On the oldfield there was a negative correlation between time spent foraging by males and average number of females, which may be related to food density, which is higher on the oldfield than on the prairie. It may also reflect the fact that foraging males are less conspicuous

TABLE 2  
MORPHOLOGICAL COMPARISONS OF DICKCISSEL MALES IN OLDFIELD AND PRAIRIE HABITATS

	Oldfield		Prairie		<i>t</i>	<i>P</i>
	$\bar{x} \pm SE$	N	$\bar{x} \pm SE$	N		
Wing length (mm)	82.6 $\pm$ 0.69	53	82.9 $\pm$ 1.25	8	0.36	NS
Bill length (mm)	10.43 $\pm$ 0.103	51	10.96 $\pm$ 0.109	8	1.69	NS
Bill depth (mm)	8.93 $\pm$ 0.003	42	8.97 $\pm$ 0.043	4	0.44	NS
Throat patch size (mm)	23.03 $\pm$ 2.236	50	19.58 $\pm$ 2.035	8	0.92	NS

\*  $P < 0.05$ .

to females flying over and hence, fewer females are attracted to the territory. There was a positive correlation with throat patch size and average number of females only on the prairie (Table 4). In poorer habitats females may use male morphological qualities as selection cues in addition to behavioral ones.

There were no differences in site fidelity ( $G = 0.156$ ,  $df = 1$ ,  $N = 28$ ,  $P > 0.05$ ) or site tenacity ( $G = 1.30$ ,  $df = 1$ ,  $N = 196$ ,  $P > 0.05$ ) between resident males in the two habitats. Eleven of 18 (61.1%) oldfield males marked in 1979 returned in 1980, while 6 of 10 (60.0%) prairie males returned. Thirty-eight of 56 (67.9%) prairie males remained on their territories for more than two-thirds of the breeding season, while 81 of 140 (57.9%) oldfield males remained.

*Discussion.*—As predicted, primary habitat males did spend more time in territorial display than prairie males, which reflects the difference in male density between the two habitats. Since territorial display was not correlated with the average number of females attracted to the territory in either the oldfield or the prairie, this suggests that territorial display in Dickcissels functions in male-male competition for habitat rather than to attract females. When Dickcissel territory holders disappeared, replacement occurred within a couple of

TABLE 3  
MALE DICKCISSEL BEHAVIORS\* IN OLDFIELD AND PRAIRIE HABITATS

Behaviors	Oldfield %	Prairie %	<i>F</i> value ( $df = 1,102$ )
Distant flight	3.09	7.97	5.61*
Interspecific aggression	0.18	0.11	0.78
Resting	35.33	32.06	0.70
Singing	18.52	19.54	0.18
Territorial displays	1.42	0.68	2.90
Courtship	0.32	1.00	3.65
Foraging	35.35	34.44	0.21
Maintenance of females	5.73	4.20	0.08
Feeding young	0.02	0.00	0.42

\* Adjusted for temperature, time, and date.

\*  $P < 0.05$ .

TABLE 4  
SIMPLE CORRELATION OF AVERAGE NUMBER OF FEMALES/WEEK ATTRACTED TO TERRITORIES  
AND MALE PHENOTYPE

	Oldfield		Prairie	
	N	$r_s$	N	$r_s$
<b>Morphology</b>				
Wing length	53	-0.039	8	-0.461
Bill length	51	-0.096	8	-0.172
Bill depth	42	-0.235	4	0.800
Throat patch size	50	-0.060	8	0.730*
<b>Behavioral</b>				
Distant flight	21	0.001	11	0.161
Interspecific aggression	21	0.060	11	0.031
Resting	21	0.308	11	0.596*
Singing	21	0.212	11	-0.018
Territorial defense	21	-0.241	11	-0.375
Courtship	21	-0.245	11	-0.282
Foraging	21	-0.477*	11	0.156
Maintenance of females	21	-0.101	11	-0.510

\*  $P < 0.05$ .

days, which is another observation that supports the argument for intense competition for territories. By experimentally lowering male density, Orians (Ecol. Monogr. 31:285-312, 1961) demonstrated intense competition for territories in Red-winged Blackbirds (*Agelaius phoeniceus*). High intensity of territorial competition is also indicated by defense of sub-optimal territories within primary habitat of Red-winged Blackbirds (Orians 1961), Dickcissels (Zimmerman 1966, 1971; Harmeson 1974; this study), and Bobolinks (Wittenberger 1978).

There was a negative correlation between foraging time and average number of females in the primary habitat, while in the secondary habitat there was a positive correlation with resting and average number of females; it appears therefore that male visibility may be important in attracting passing females even though the number of females a male attracts is not based on specific display behaviors (e.g., singing). Males on the prairie did not spend more time in behaviors that would attract more females. So this prediction was not met, yet prairie males compensated for their poorer territory quality and lower density of females by spending more time courting when the females were present. Because there were no differences in morphology between the males in the two habitats, these behavioral differences could be related to the demonstrated differences in habitat quality and associated with differences in female choice.

There are weak correlations with male behaviors and female choice in Red-winged Blackbirds (Weatherhead and Robertson, Wilson Bull. 89:583-592, 1977; Searcy, Auk 96:353-362, 1979b; Yasukawa, Ecology 62:922-929, 1981), as well as with Dickcissels (Finck, Ph.D. diss., Kansas State Univ., Manhattan, Kansas, 1983; this study). Verner (Evolution 18:252-261, 1964), Wittenberger (1976), Searcy (1979a), and Yasukawa (1981) suggested that it is

a combination of male quality and territory quality that forms the basis for female choice. Elsewhere (Finck 1983) I have shown that this is true in Dickcissels.

There was no greater site fidelity in oldfield males with better quality territories than prairie males with poor quality territories between years nor was there a difference in site tenacity between oldfield and prairie males. This may indicate that prairie males can not obtain better territories in more preferred habitats and instead maintain their fitness by increasing courtship and long distant flight. As the greater amount of distant flight in prairie males indicates, they still may spend more time looking for better territories during the breeding season on the chance that one is open.

The number of females on territories was positively correlated with adjusted territory size. However, Zimmerman (1966) and Harmeson (1974) found no correlation with unadjusted territory size and number of females in Dickcissels. Since territories in Dickcissels change with male density (Zimmerman 1971, Harmeson 1974, this study), unadjusted territory size is weighted by the density of males rather than being a true measure of territory size, which therefore masks the relationship between female numbers and territory size. The correlation of female numbers and adjusted territory size can not be accounted for by more available nest-sites alone, since adjusted territories are larger on the prairie, but prairie males have fewer females than oldfield males even though the number of females obtained by prairie males is still positively related to the adjusted territory size.

Dickcissel males must be able to assess the habitat quality of their territories, since prairie males spend more time off their territories than oldfield males and poor territory quality is correlated with increased distant flight (Schartz and Zimmerman 1971). They may do this by assessing density of males via the frequency of territorial song within a habitat or the intensity of encounters with territorial males that fly up to chase males intruding on distant flight.

Orians (1961) hypothesized that distant flight provided a means for increased foraging for male Red-winged Blackbirds. Yasukawa (Condor 81:258-264, 1979) showed that Red-winged Blackbird males who successfully occupied territories spent less time in distant flight than unsuccessful males. He attributed this to increased foraging off the territories by unsuccessful males because distant flight and foraging equaled the foraging on territories by successful males. However, it is possible that these unsuccessful males obtained territories elsewhere. In this study there was no difference between the amount of time spent foraging by the oldfield males and that spent by the prairie males. The prairie males spent more time (42.4%) in the combination of distant flight and foraging than oldfield males did in foraging (35.5%). This suggests that other factors may influence distant flight in Dickcissels.

Schartz and Zimmerman (1971), Martin (Am. Zool. 14:109-119, 1974), and Nolan (Ornithol. Monogr. 26, 1978) hypothesized that distant flight functioned as a mechanism for exploring potential territories. This could be very important for an early successional species such as the Dickcissel. Schartz and Zimmerman (1971) suggested that during distant flight males evaluated population densities. In support of this idea they found a correlation with poor quality territories, as measured by the number of females on territories, and increased distant flight. In this study I have demonstrated that individuals in poor habitat are in distant flight more than individuals in good habitat. Zimmerman (1982) has shown that male fitness is higher in habitats with higher male density.

A male Dickcissel that leaves his territory may find a better site and/or a potential mate. He may lead that mate back to his territory, copulate with her at the new site or switch territories. Many male passerines have been seen singing off of their territories and copulating with females (Ford, pp. 329-356 in *Current Ornithology*, Vol. 1, R. F. Johnston, ed., 1983). I have seen three instances of male Dickcissels singing off their territories and a non-resident



male displaying towards a receptive female in another male's territory. Also, territory switches occur during the season. There was also an instance in which a male Dickcissel left his territory for 3 weeks and returned with a female. Some female Red-winged Blackbirds on territories of vasectomized males have still been known to produce young (Bray et al., *Wilson Bull.* 87:195–197, 1975). Keller (M.S. thesis, Univ. North Dakota, Grand Forks, North Dakota, 1979) suggests that in Chipping Sparrows (*Spizella passerina*) an alternative strategy to holding a good territory could be to sneak copulations, provided that the male does not spend much time off his territory or his female may be inseminated by other wandering males. The role of distant flight and switching territories needs further investigation. In birds such as the Dickcissel, both strategies could increase fitness.

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**Passage rate, energetics, and utilization efficiency of the Cedar Waxwing.**—The Cedar Waxwing (*Bombycilla cedrorum*) is noted for its intensive foraging on fleshy fruits (Nice, *Condor* 43:58–64, 1941; Tyler, *U.S. Natl. Mus. Bull.* 197:79–102, 1950). Flocks of Cedar Waxwings have been reported to deplete entire fruit crops of red cedar (*Juniperus virginiana*) over a period of 2 days (Parker, Ph.D. diss., Duke Univ., Durham, North Carolina, 1949). In summer the diet of the Cedar Waxwing is composed largely of insects and fleshy fruits and in winter their food consists almost exclusively of fruits (Beal, pp. 197–200 in *Ann. Rept. Dept. Agric.* 1892, and *Farmer's Bull.* 54:38–39, 1904; Nice 1941; Tyler 1950; Martin et al., *American Wildlife and Plants*, Dover Publ. Inc., New York, New York, 1951). The Cedar Waxwing is therefore considered a major frugivore (Thompson and Willson, *Evolution* 33:973–982, 1979; Stiles, *Am. Nat.* 116:670–688, 1980). However, the extent to which the Cedar Waxwing can subsist on fruits alone has not been investigated.

Nutritional studies of fruit-eating passerines in Europe have shown that all species except the Bohemian Waxwing (*Bombycilla garrulus*) rapidly lose weight and die in captivity if supplied only with fruits (Berthold, *J. Orn.* 117:145–209, 1976a; *Experientia* 32:1445, 1976b; *Ardea* 64:140–154, 1976c; *J. Orn.* 118:202–203, 1977). Therefore, Berthold (1976b) considered the Bohemian Waxwing a fruit specialist, as opposed to an opportunistic frugivore. A similar adaptation to a frugivorous diet may be expected from the Cedar Waxwing, since this bird closely resembles the Bohemian Waxwing in its food habits (Bent, *U.S. Natl. Mus. Bull.* 197:62–79, 1950; Tyler 1950).