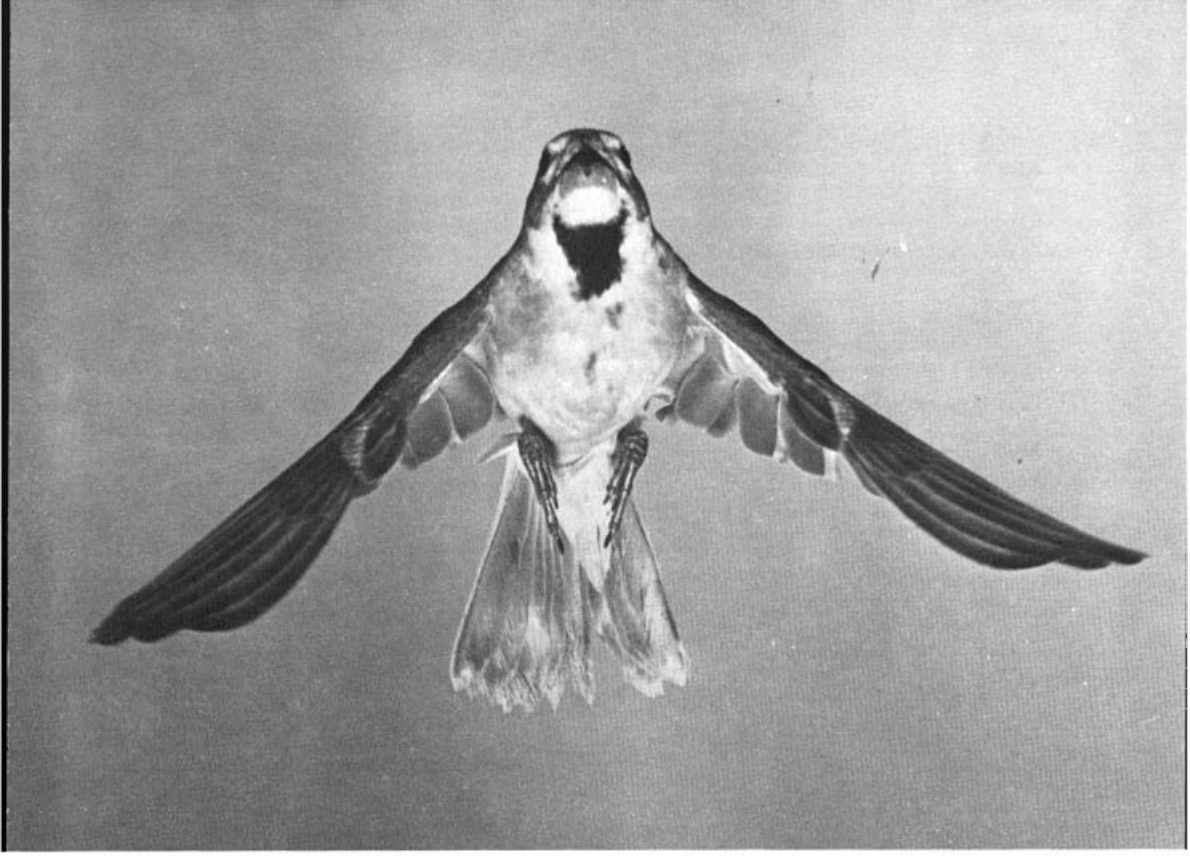

Dickcissel. Photo by G. Ronald Austing from the Audubon Collection/PR

Is the Dickcissel a threatened species?

Does what the males and females eat on wintering grounds affect the breeding success of the species?

by Stephen Fretwell

Introduction

THE DICKCISSEL (*Spiza americana*) is one of the most ubiquitous and abundant summering bird species of the tall and mid-grass prairie states. In Illinois, it would appear to breed in every clover field in the central part of the state. In Missouri, timothy hayfields are the typical habitat. In Iowa, Nebraska, Kansas, Oklahoma, and Texas, Dickcissels occur in weedy roadside edges where those edges border wheat, corn, or soybean fields. They also occur in substantial colonies in alfalfa and clover hayfields, in patches of ragweed near river bottoms,

and in ungrazed patches of prairie. On the edges of its range, the species is rather erratic and unpredictable in abundance. In this article I want to show that in spite of its apparent abundance, the Dickcissel could well be a threatened species. Some species that have become extinct in the past typically have been common, but erratic in winter occurrence, as is the Dickcissel.

Introduction to the species—Breeding Biology

THE DICKCISSEL BREEDS from May through August. Its nest site usually involves some dead or woody vegetation from the previous year, unless a clover or hayfield is the nesting habitat. The nest is sited in a crotch or clump of this old material, concealed by this year's green foliage, but not tied to the vegetation in any way. The eggs are pale blue.

Both the eggs and young are the sole responsibility of the female. The male is polygynous, and is mated to up to eight females in a season. The mated females in the territory of any one male are always dissynchronous by about 4–5 days in their nesting schedule (Zimmerman, pers. comm.); evidently the male takes his many mates one at a time, attending each one until she is well into her nesting cycle, and then seeking another.

Male Dickcissels are both more brightly colored and larger than the female: 30 grams for the males, 25 for the females.

Sexual selection and sex ratio

THE DICKCISSEL at first glance appears to fall into a group of species with polygynous mating systems (Zimmerman 1966), discussed by Selander (1965) and Orians (1969). These species breed in single layer environments (Verner and Willson 1966, 1969), the males provide little or no food to the young, and the males are substantially bigger than the females. Selander (op cit.) argued that this difference in size was due to the polygynous mating system. Males evolve a larger size because of size advantages in the aggressive interactions between males for mates, and in spite of the ecologic disadvantage of being too big for the species' niche. This is presumed to result in fewer males surviving than females, leaving more females than males.

Applying this aspect of the hypothesis to the Dickcissel reveals a discrepancy. In almost every observed situation, there appears to be more male than female Dickcissels present. Richard ffrench found this to be true in Trinidad (1967), and I verified it there (Figure 1); I also found from 2 to 2.5 males per female in Panama and in Acariqua, Venezuela. John DeGrazio of the Denver Fish and Wildlife Center found similar ratios in Mexico (pers. comm.), and in various places near Acariqua, Venezuela. In Calabozo, Venezuela, our data suggested that males and females might be about equally abundant, but these data were likely to be biased (Fretwell ms a.).

UNMATED MALE DICKCISSELS are also very common in the breeding season (Fretwell ms a.; Fretwell and Calver, 1970) Only in Texas in May are there more females than males, but this is not the case later in the season. In sum, it seems that overall there is about one female for every two males in the total population; contrary to the prediction of Selander's sexual selection hypothesis.

Why are there so many male Dickcissels? There may be a simple answer to this question. Dickcissels wintering in the tropics are similar to the polygynous blackbirds in North America in other respects besides sexual dimorphism and polygyny. Like the blackbirds, Dickcissels form giant wintering roosts of several million birds. Great flights leave these roosts in the morning for nearby feeding grounds. Often, these feeding grounds are rice and grain sorghum fields.

Dickcissels on their wintering grounds indicate a preponderance of males in crop habitats (Fretwell and Shane, 1975). Sex ratios in crops averaged 3 to 5 males per female, while natural grasslands had either an equal number of males and females, or more females than males. Crop seeds are generally bigger than weed seeds (they are bred for size), and it is known that larger sparrows eat larger seeds (Newton 1967). My hypothesis is that recent increases in plantings of these crops have provided an in-

Table 1. North–south trends in Dickcissel nesting success.

Rates of cowbird parasitism (per cent of nests affected)	*Rates of nest survival*	*Location*	*Author*
47%	0	Nebraska	Von Steen (1965)
52%	—	Nebraska	Hergenrader (1962)
60%	25%	Kansas	Zimmerman (1971)
31%	30%	North Oklahoma	Overmire (1962)
20%	45.5%	South Oklahoma	Wiens (1963)
5%	50%	North Texas	Fretwell, Francis, and Shane (1974)

creased food supply for the larger male Dickcissels. If females are too small to eat these seeds, these crop increases will not expand the females' resources and may actually reduce them. Thus, the males, instead of being food stressed because of their larger size, now find *more* to eat than the smaller females. The postulated resulting high survival of males leads to a sex ratio skewed heavily in favor of males. This may well have serious implications for the breeding success of the species.

Breeding success and sex ratio

A NUMBER OF STUDIES of Dickcissel nesting success in the central areas of the species' range have produced alarming data. Von Steen (1965), working in Nebraska, found zero nesting success. Zimmerman found similar results in eastern Kansas in 1965 and 1966, but found 1967 to be a more successful year. Even in good years, Dickcissels succeeded in fledging only about 20 to 30% of eggs laid, sometimes losing whole nests, but often losing part of a clutch, owing to cowbird parasitism.

Farther south, Dickcissels are moderately successful (Table 1).

In an attempt to account for the failures in the northern part of the range, I noted that in Kansas in 1967, when success was not zero, the sex ratio was considerably higher. Males seemed not to be especially abundant, but females were quite common, and most males were mated. In fact, most were polygynous. Also, in Texas, where success is consistently higher, there are, as noted, more females than males. So, where there are more females, the nesting success is higher Yet, how could the sex ratio affect nesting success?

The Allee effect and the sex ratio

FRETWELL AND LUCAS (1970) considered the case of a species with an Allee effect in its breeding success. They demonstrated that at certain lower densities, increases in density resulted in an increase in nesting success. We found that such species should have an erratic breeding distribution Thus, certain habitats or geographic regions are predicted to be unoccupied in some years, but densely occupied in others, owing to very slight changes in population size Tabor (1947) and Emlen and Wiens (1965) have documented the "erratic breeding range fluctuations" of the Dickcissel, suggesting that this species might well be under the influence of an Allee effect. This is consistent with the observation that females are more successful in nesting where they are more densely distributed. It remains to relate this to the sex ratio.

Zimmerman (1971) has brilliantly shown that male Dickcissel densities are set by the territorial behavior of the males. As the male densities are set at levels that do not vary much, variations in the overall population sex ratio (females/male) owing to differential winter survival of the sexes leads to extensive variations in the densities of breeding females in a particular field. If there are 3 females/male, and 1 male per hectare, there will be 3 females per hectare, but when the sex ratio drops to 1 female/3 males, still with one male per hectare, there will be only 1 female in 3 hectares, or 0.33 females/

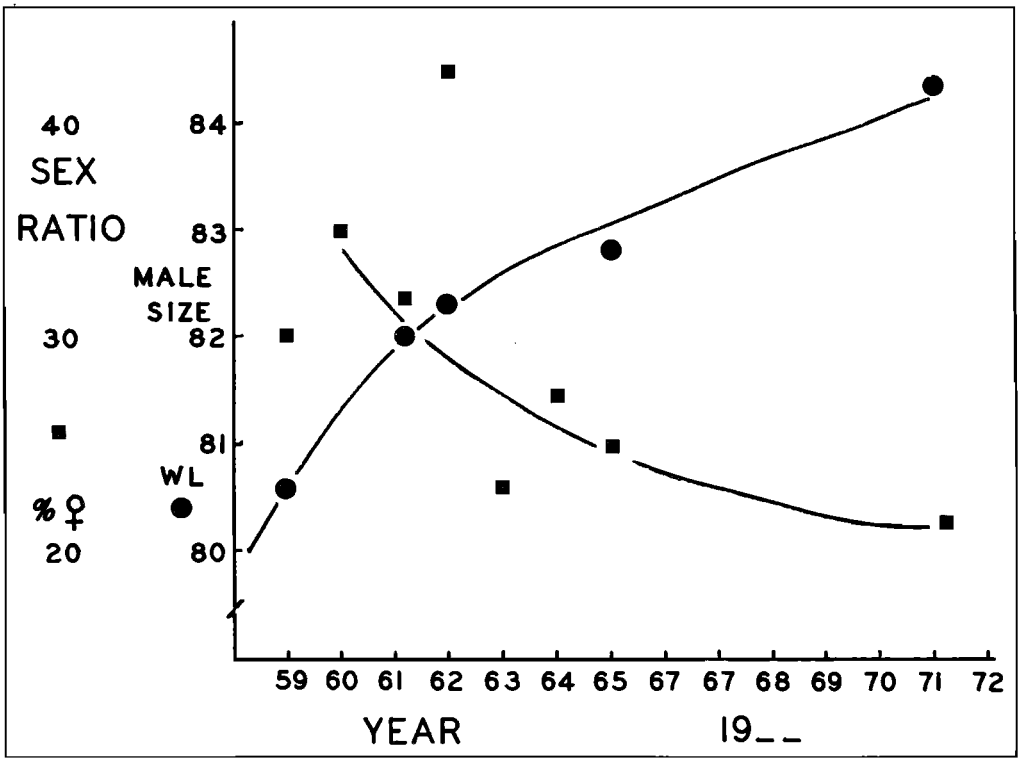

Figure 1. Sex ratio and male size. The data on this figure were largely gathered by R. ffrench in Trinidad, I measured the last point. They show sex ratios averaging 30 per cent females and declining with years. Also, male wing lengths increase over the same period.

hectare. This is a nine-fold drop in female density. Thus, the lower the sex ratio (females/male), the lower the female density.

But the evidence suggests that the lower the sex ratio, the lower the nesting success. This seems to imply that lower densities of females have lower rates of success, which is the critical aspect of an Allee effect. Thus, the Allee effect predicted from the distribution theory and the erratic distribution appears to be confirmed, and is consistent with the sex-ratio, nesting success correlation. There also appears to be an Allee effect in male Dickcissels (Zimmerman, 1971, p. 606, Fig. 9).

I wanted to further confirm the Allee effect in females. As an index to nesting success, I recorded the per cent of females seen that were carrying food in nesting colonies. As an index to density, I took the number of females seen per acre. I obtained samples from south Texas to South Dakota, and from western Kansas to Indiana, all in 1971. The results are plotted in Figure 2. They fit in well with the hypothesized Allee effect, and seem to further confirm that at low densities female Dickcissels are not as successful at breeding.

Mechanisms for breeding failure

THE DISTRESSING ASPECT of my tour about the Dickcissel range in 1971 was the almost uniform nesting failure throughout 40% of the area covered. In all the northern states, females were much scarcer than males (about one male in three was mated) and, apparently due to the Allee effects, females were only rarely found feeding young. What has affected the female Dickcissels in the north? Could it spread to Oklahoma and Texas where success was still high?

Zimmerman conducted his detailed studies on the evolution of the breeding activity in Dickcissels (1966, 1971; also an unpub-

lished A.O.U. presentation, 1969). He found that the major sources of nesting failure in Dickcissels were cowbird parasitism and nest predation. Zimmerman found that cowbird parasitism was a major source of loss early in the breeding season and that predation was a major source of loss later. His evidence suggested that mid-June, when Dickcissels start more nests than any other time, was a relatively safe period, falling between the times of cowbird parasitism and nest predation.

I have found that nest predation in the Field Sparrow and in other old-field species is density dependent, so that when densities rise, nest predation rises also (Fretwell 1972b). A summary plot of data from the literature on Dickcissels (Figure 3) confirms the density dependent effect. Therefore, nest predation cannot produce an Allee effect, and female Dickcissels should not group together to escape predation.

COWBIRD PARASITISM, on the other hand, is a likely candidate for Allee effects. It is well known about the Red-winged Blackbird that nests in colonies are much less parasitized by cowbirds than isolated nests (Friedman 1963: 128). If this effect is owing to density, and not to habitat differences, then it clearly implies an Allee effect. A colony of birds may be able to harass female cowbirds (and Friedman reviews some

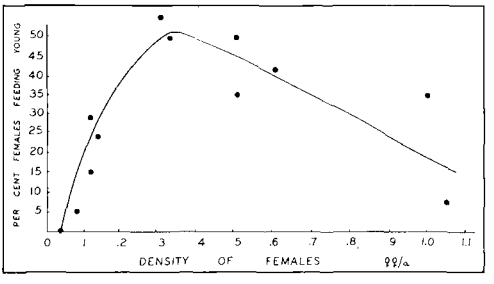

Figure 2. Visits to breeding areas were made three weeks after the females had arrived and had started nesting. Each female seen was scored for the stage of the nesting cycle that she had reached. Females were scored either as feeding nestlings or fledglings, or being in some other stage of nesting. The density was estimated from the number of females per acre. The per cent females that were sufficiently successful to be feeding young was computed, and compared to the density. Females at low densities appeared to be least successful in rearing young. (From Fretwell, 1972b).

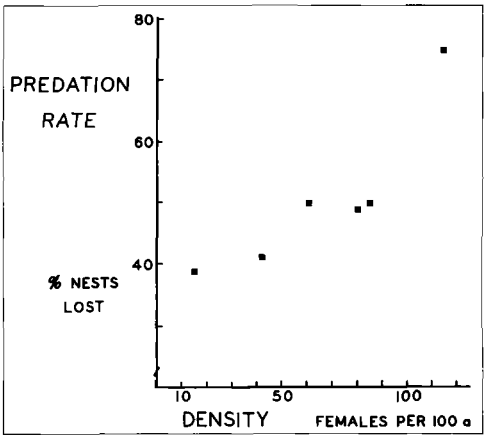

Figure 3. Density dependence and nest mortality The points on this graph are from published studies of Dickcissels, where both densities and predation rates were measured. Four of the six points are from John Zimmerman's studies (1966, 1971) with one by Fretwell, and one by Janet Harmeson (*Auk* 91: 348–359, 1974).

anecdotal evidence to this effect in the Red-winged Blackbird literature), so that the cowbirds are unable to lay. Or the density of female cowbirds may be constrained by other than the availability of nests, so that where there are many nests, the cowbirds present are simply too few to parasitize them all

That cowbird parasitism causes extensive nest failure in Dickcissels is shown in Figure 4, where losses owing to other factors (mostly unknown) average much higher in studies where cowbird related losses were high. When cowbirds are such a serious parasite that some female Dickcissels are driven to desert their nests, then other problems are more severe as well.

Thus it appears that cowbird parasitism could produce an Allee effect in Dickcissels At low densities, excessive numbers of cowbird eggs are deposited in Dickcissel nests (Zimmerman 1966, noted five cowbird eggs in one day in one nest, and eight eventually), leading directly to desertion (about 19% of the time) or to other sorts of failures (about 25% of the time). As 50% of the nests fall to predators, a population with heavy cowbird parasitism should lose 93% of all nests, as opposed to 50% without parasitism This is similar to the values in Figure 2

In more detailed studies (Fretwell ms b) I have confirmed these effects in both Red-winged Blackbirds and Dickcissels, and in the

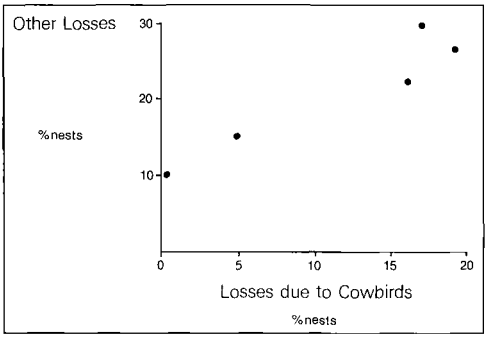

Figure 4. Effect of excessive cowbird parasitism on accidental nest losses. The data are from Zimmerman (1971, 1966) and plot losses of unknown cause against per cent nests deserted due to excessive cowbird parasitism.

process have discovered a competitive effect between these two species, where Red-wingeds attract both cowbirds and predators to Dickcissel nests. These studies confirmed that density is a major factor in cowbird parasitism, quite capable of producing an Allee effect. They also introduce another factor, however, the presence of Red-winged Blackbirds. When Dickcissels nest with Red-wingeds, they are heavily parasitized by cowbirds and they suffer high rates of nest predation.

Prognosis for the future—factors determining the distribution of nesting success

LET US ACCEPT that the sex ratio of Dickcissels has been distorted by planting of sorghum, which feeds males but not females, and that this distortion in sex ratio has led to the observed nesting failures through a low-density Allee effect. The breeding female density is lowered by the poor winter survival of females, which leads to high cowbird parasitism and other associated nesting failures.

I have noted that these failures and the associated sex ratio problems are largely confined to the northern tier of states in which the Dickcissel breeds; Texas and Oklahoma populations appear to have more successful nestings (Table 1). I am concerned about whether this pattern of failure could spread to the southern part of the range. This concern is fostered by the recent nature of the present situation. Sorghum and rice plantings have increased substantially in the tropics in the last decade. In Figure

Table 2A. Geographic variation in wing lengths in wintering populations, after food movements in mid-January. (See Figure 5)

	Western edge of range		Center range	Eastern edge of range	
	Panama	Acariqua, Venezuela	Calabozo, Venezuela	Trinidad (ffrench)*	Trinidad 1972
Males					
(n,x̄)**	10 86.00	79 83.03	28 81.19	141 82.8	132 84.35
(SE)	.63	.22	.38	.17	.17
Females					
(n,x̄)	5 77.9	37 76.10	74.05	74.7	32 76.34
(SE)	.89	.33	.4	.23	.35

Table 2B. Geographic variation in wing lengths (mm) in breeding males.

	$\bar{x}$	n		$\bar{x}$	n		$\bar{x}$	n
Western Kansas	84.0	(10)	South Dakota	85.1	(8)	Missouri	82.67	(6)
			Kansas Upland	83.3	(10)			
			Kansas Lowland	82.6	(9)			
			Oklahoma	81.5	(5)			
			North Texas	81.2	(7)			

* ffrench and I checked for bias in measurements by both measuring the same bird; we found no difference.

** n = sample size; x̄ = mean wing length in mm; SE = standard error of mean.

1, I plot the sex ratio estimates in Trinidad since 1959, showing the trend for more and more males in recent years.

In order to know whether the distorted sex ratio in the north might appear in the south, we need to know what causes such a difference in the distribution in the first place. Why are the northern populations and not the southern ones affected?

Winter distribution

We find an answer on the wintering grounds. Dickcissels leave the United States by the first of October (except for vagrant lingerers), and appear in Central America through October. By November the birds seem to have disappeared; very few are reported in that month. Those records that do exist which are representative of the large numbers typical of the wintering grounds are from southeastern Venezuela, but this area has not been studied adequately for Dickcissels. By mid-December the Dickcissels are back on the move, and grain depredations in western Venezuela are reported then. Also, Richard ffrench describes some December arrivals in Trinidad, to the east. These movements do not appear to be migrations, but are probably wonderings searching for food (Fretwell ms. c).

I saw no birds in Panama until early January, and no big flocks until mid-January. Local birdwatchers noted that this was the time that the birds normally arrived in this region in late winter food flights. Pacora, Panama is a thousand miles west of Acariqua, Venezuela, in western Venezuela (see map, Figure 5).

But where are the Texas males in winter? I believe that many are in central Venezuela, near a town called Calabozo (map, Figure 5), where there is a large reservoir with irrigated rice plantings. Local people say that Dickcissels abound there all winter. Our Calabozo sample was in late March, and was probably of the birds that apparently never made much of a food flight. Shane measured some birds there (Fretwell and Shane, 1975), and we found that the males had much shorter wings than males caught elsewhere. In fact, Calabozo male wing lengths were the same as those of Texas males while wing lengths of food movement birds (Panama, Trinidad, or Acariqua) are more like those of males that breed in the northern United States (Table 2). Also, the sex ratio in Calabozo (females per male), was higher than elsewhere (about 1:1). This may have been owing to a biased sample, since no birds were taken at a roost where the sexes are randomly mixed. As noted earlier, females occur more frequently in weeds, but males occur more frequently in crops. Shane, who collected the Calabozo data, had difficulty finding mature crop habitats, and saw most birds in "green" fields. Only samples from watering areas or roosts are unbiased, and we lack such data from Calabozo, so that we are less sure of the sex ratio there. It seems possible, however, that Texas-Oklahoma Dickcissels winter in central Venezuela, are smaller, and do not make extensive food flights.

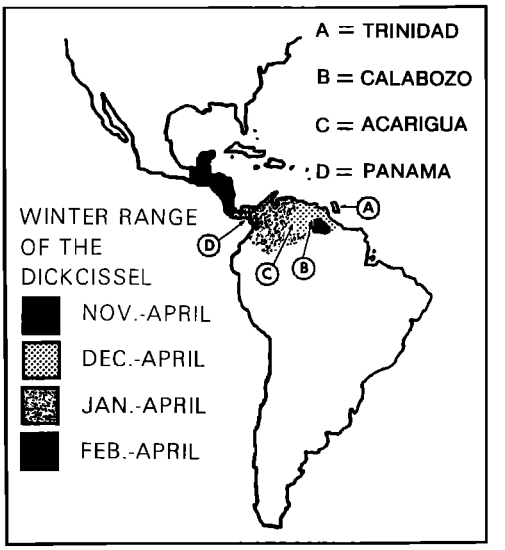

Figure 5. Winter range of the Dickcissel. The species is localized until mid-December somewhere in eastern Venezuela. From this region, it spreads out as winter progresses with reports from as far north as Mexico. Most of the information is anecdotal, and refers to major population movements. Isolated Dickcissels are reported from all regions north of Venezuela into the United States all winter long (A.O.U. 1957).

Apparently in fall most Dickcissels wintering in the tropics migrate to Calabozo, or points to the southeast in Venezuela. By December, some, but not all,

of the birds are somehow motivated to fly out of this region. Probably food is the motivating factor in these movements. In any case, it is mostly long-winged males and females (see Table 2) that leave. Those birds that leave apparently wander east or west from Calabozo. No one knows how far these birds eventually move; some seem to wander all the way to Mexico. In early April, some, perhaps all, the Dickcissels fatten, and in mid-April migrate to the breeding grounds. It seems that the birds that never left Calabozo breed in Texas, while the males that had wandered off on foraging travels migrate on to Nebraska, Iowa, South Dakota, and other northern mid-western states. The Calabozo population seems not so crop dependent, and so the sex ratio is not so skewed. Hence, when they breed in Texas, they are successful. Only the wandering ecotypes that feed on crops have too many males and dispersed females.

We do not have very many measurements of females from these northern states because females are so scarce. So we cannot confirm the trends that we see in males. Texas females are similar in size to Calabozo females somewhat smaller than either Trinidad or Panama or western Venezuela females. The females in the outlying regions of the wintering grounds do not show increases in size nearly as much as the males (Table 2).

Stability of the system

APPARENTLY, THE SEX RATIO distortion is rather recent (Fig. 1), and is likely to be getting worse as more and more crops are planted. A mitigating factor is the clearing of forest land in the tropics. Such cleared land, as it grows up in weeds and grass, apparently is beneficial to female, but not to male, Dickcissels. However, much land is cleared for grazing, and I have not found Dickcissels wintering in grazed habitats (Fretwell, 1972a).

How stable is the present breeding situation? The winter-eruptive population goes on north to breed but fails at breeding, while the winter-stable (Calabozo) population stops in Texas and Oklahoma, where it breeds successfully. Can this imbalance persist?

We may reasonably suppose that when sorghum and rice first became widely available the Dickcissels that were able to take advantage of it were the northern breeding birds. First, the northern breeders are probably bigger birds, obeying Bergmann's rule They do have larger wings and bills, suggesting a larger size. Zimmerman's physiological studies on the Dickcissel (1963) imply a cold sensitivity that might well be alleviated by large size. South Dakota has many near freezing mornings in May when the males arrive, yet Dickcissels normally can barely tolerate such temperatures.

Larger seed-eating birds typically eat larger seeds. My analysis of Tom Quay's data in North Carolina (Fretwell 1972b) provides an intraspecific proof of this point in Savannah Sparrows. The idea is also well established between species (see Newton 1967). Thus the larger and, coincidentally, more northern Dickcissels were the ones to take advantage of the crops. And only the males of this population were large enough to be successful in the exploitation of crops. Fretwell and Shane (1975) provide further evidence for this relationship.

WE DO NOT KNOW whether the northern females followed them on the food flights for crops or whether they stayed behind—probably some of each; but, in either case, it does not matter. The females did not survive as well, and thus the sex ratio was distorted and the breeding failures followed. Smaller males, normally the more southern breeders, avoided these food wanderings, and they probably survived even less well than the females. As a result, surviving small males found many mates available in Texas, enabling this population to breed successfully.

The stability of this system in time therefore, depends upon how genetically fixed are the migration patterns of different segments of the populations. What would happen if large, northern males stopped in Texas to breed? If they were able to do so, they would increase the male/female ratios with unfortunate results. Clearly any large male that stops in Texas (and many do—the range of measured male wing lengths in Texas is 77 to 85 mm, the average of eight males in South Dakota was 85.1 mm) should be a successful breeder. Being bigger, he should get a better territory in these southern regions, should have more females because there are fewer males to compete

Dickcissels, male above,
from a painting by J. McAleavey

with, and, until the dilution effect predominates, his mates should have more young. Enough generations of this sort of "accident" and large Dickcissels will become common in Texas. Then the Texas population will be taken over by the crop-type population and will suffer breeding loss accordingly. Perhaps (Table 3) these trends are already underway, and revealed in data published by Robbins and Van Velzen (1969).

Summary

I SUBMIT THAT THE DICKCISSEL be regarded as a threatened species (Blue List). Although my interpretation of the population regulation of this species is still largely tentative and theoretical there does seem to be a real and tangible possibility that Dickcissels have a low-density limit. When the females of the species fall much below this limit over most of the range, then we may expect the species to fade into extinction. Already, the females frequently fall below this limit, and apparently the factors that have caused this decrease are recent and increasing.

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Table 3. Changes in the distribution of Dickcissel males, 1967 and 1968.

Northern Tier States				*Southern States*	
Illinois	*Iowa*	*Nebraska*		*Oklahoma*	*Texas*
64*	99	54	*1967*	33	6
44	86	37	*1968*	41	21

* Birds per survey route.

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