THE TIME AND ENERGY BUDGET OF THE MALE DICKCISSEL (*SPIZA AMERICANA*)

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The ecological niche has been variously described. To Grinnell (1924) it was spatially defined in terms of a species' habitat. To Elton (1927:64), it was more a functional concept that portrayed a species' role in its environment. Although a simple synonymy between habitat and niche is still often made, a current synthesis of concepts about the niche expresses the complete relationship of a species to both the biotic and abiotic environment in terms of its morphology, physiology, and behavior (Kendeigh 1961:245). It is the sum of these interactions between the organism and its species-specific environment that is the niche of the species (Bock and von Wahlert 1965).

The description of a species' niche requirements, therefore, necessitates not just an enumeration of particular environmental factors, but also the elaboration of the involvement of the species with these factors. One approach to this problem is the quantification of the various activities in which birds are engaged (see Collias and Collias 1967; Gibb 1954, 1956, 1960; Kale 1965; Kluyver 1950; Lees 1948; Orians 1961; Verbeek 1964; Verner 1965). Birds spend time performing a variety of activities, and each activity, depending on its duration and intensity, requires an expenditure of energy above the resting metabolic level. The environment influences the amount of time and energy necessary to perform various activities and, consequently, the survival and reproductive success of the bird.

In this study, data were collected to quantify the distribution of time among the various breeding activities of the male Dickcissel (*Spiza americana*) in order to describe its behavioral regimen. These data are also prerequisite to determining the energy budget of the species. In eastern Kansas the Dickcissel is the dominant avian consumer in the early stages of the oldfield sere, and thus such an analysis, coupled with knowledge of its habitat utilization (Zimmerman, MS), can lead to a better understanding of the functioning of the ecosystem in its community.

STUDY AREA

A tract of 65 acres in sec. 31, T. 8 S., R. 6 E., Riley County, Kansas, was used in this study. Of this area, 27 per cent was in wheat until harvested on 17 July 1967, when lambsquarters (*Chenopodium album*) became dominant. Extensive stands of kochia (*Kochia scoparia*), ragweed (*Ambrosia trifida*), sunflowers (*Helianthus* sp.), sweetclover (*Melilotus alba* and *M. officinalis*), horseweed (*Conyza canadensis*) and a variety of other annual forbs with patches of brome (*Bromis inermis*) constituted 20 per cent of the cover, mainly along a waterway extending the length of the study area. Mixed grasses (*B. inermis, B. tectorum, Bouteloua curtipendula, Sporobolus clandestinus, Andropogon scoparius*) covered 23 per cent of the area, while the remaining 30 per cent was dense brome (*B. inermis*).

METHODS

Dickcissels were captured with mist nets, and combinations of colored leg bands were used to mark individual birds. Only one male was unbanded and recognition was made on the basis of song and color pattern.

The Dickcissel population was measured from census data collected over weekly periods. Territorial boundaries were defined by the locations of singing males and recorded on scale maps of the study area, and calculations of territory size were made by tracing their outlines with a compensating polar planimeter. A constant record of the number of mates present on the territories was kept. Nearly all of the nests of females that had established pair bonds with males selected for this study were found and their contents and locations recorded.

In 1967 and 1968 a thermograph housed in a standard weather shelter provided a continuous record of temperature. Weather data for 1966 were obtained from Manhattan station No. 2 at Kansas State University located 20 mi. E of the study area.

Samples of arthropod populations were taken on the three patches of vegetation on the study area (grasses, forbs, and wheat) on eight days between 26 June and 17 July 1967. Forty-eight sweeps with an insect net were considered a sample of one square meter (Shelford 1951), and provided an estimate of the numbers and kinds of insects and other arthropods and their distribution in the three vegetation types.

Randomly selected male Dickcissels (10 in 1966, 13 in 1967, and 7 in 1968) were observed with bin-

oculars and telescope. Their activities were timed with a stop watch and recorded in sequence on 17 days 27 June–18 July 1966, on 60 days 2 June–17 August 1967, and on 18 days 14 May–9 June 1968. Total observation time in this study was 326.1 hr: 52.3 in 1966, 212.9 in 1967 and 60.9 in 1968. Observations were conducted over a period of 6–9 hr, either in the morning beginning at 05:00 or in the afternoon ending at approximately 19:45. All references to time are in CST. Observations of each bird began on the hour and lasted 45 min. This allowed time for moving to a new location before beginning observations on the next bird. In this paper, time budgets are expressed as percentages of the observation period, but statistical treatments were performed on values expressed as minutes per hour. Only those data in 1967 (i.e., weeks 8, 9 and 10 of the reproductive cycle) which span the same time period as the 1966 data were used in comparisons made between these two years. The categorized activities of the males are discussed below.

ACTIVITIES OF MALES

Foraging. This includes all the time spent acquiring food. Dickcissels flit through the lower vegetation in search of insects or seeds, and it was necessary to assume males were foraging when they could not be seen. This was considered reasonable since other activities are usually performed in conspicuous places and often involve vocalizations. Furthermore, when foraging in the wheat field, they could be seen at times feeding on the grain and occasionally in other habitats a bird was seen with an insect in its beak or wiping its bill after returning from a trip to the vegetation. Time spent resting or preening may have been included in this category but was considered negligible since birds were rarely static and usually emerged from the vegetation some distance from their original point of entry.

Resting. This includes time spent resting or preening. A bird was recorded resting if it was inactive or preened for more than 30 sec.

Singing. Short intervals between songs as well as the time spent in vocalization are included in this activity.

Territory defense. This includes time spent in aggressive activities other than song, such as aggressive display, chasing, and fighting. Boundary disputes usually began with a lateral confrontation of two males and a display of black throat patches. Occasionally this terminated in a sudden vertical flight and actual fighting, but ordinarily one of the males retreated before fighting ensued. Vigorous pursuit of an overflying intruder by the territorial male was the most common expression of aggressive behavior.

Courtship. The time from the female's first arrival on the territory to nest completion spanned almost a week. During this period sexual chases and copulations were frequent and the male spent much time with the female, flying from perch to perch each time the female moved. Although attending the female, the male often sang from perches near the female, and it was also common for the male and female to forage together. In these instances males were recorded singing or feeding although they were attending a female.

Maintenance of the female. This category includes time spent attending the female after the nest was constructed on the territory. The male continued his attentiveness during egg laying and incubation, exchanging "chipping" notes with the female or following her when she was off the nest.

Distant flight. Male Dickcissels sometimes left their territories, usually flying out of sight but occasionally landing 150–275 m from the territory.

Interspecific aggression. Interspecific contests were infrequent and lasted only a few seconds. Nearly all encounters were with the Redwinged Blackbird (*Agelaius phoeniceus*), the only other nesting species sharing this habitat with the Dickcissel.

RESULTS

TIME BUDGET DURING REPRODUCTIVE CYCLE

The weekly averages of the per cent time spent in eight activities are shown in figure 1. The reproductive cycle in this latitude begins with the arrival of males in the first week of May. Females arrive in the next week and the peak of nesting occurs in the seventh week (mid-June). Portions of the yearly reproductive periods were nearly synchronous for 1966, 1967, and 1968, since the arrival of the males, the arrival of the females and first nest construction occurred within 3, 7, and 10-day intervals, respectively, for all three years. Table 1 gives the average per cent of time spent in each activity for each year.

Foraging. Foraging varied less than any other activity, averaging 17–21 per cent of the time budget throughout the breeding season.

Resting. Except for a sharp increase in the first week of July in 1966, resting was relatively stable at a level of 8–10 per cent. Associated with the increase in resting in 1966 there was a reduction in the time budget for all other activities except distant flight, which increased, and foraging, which remained unchanged.
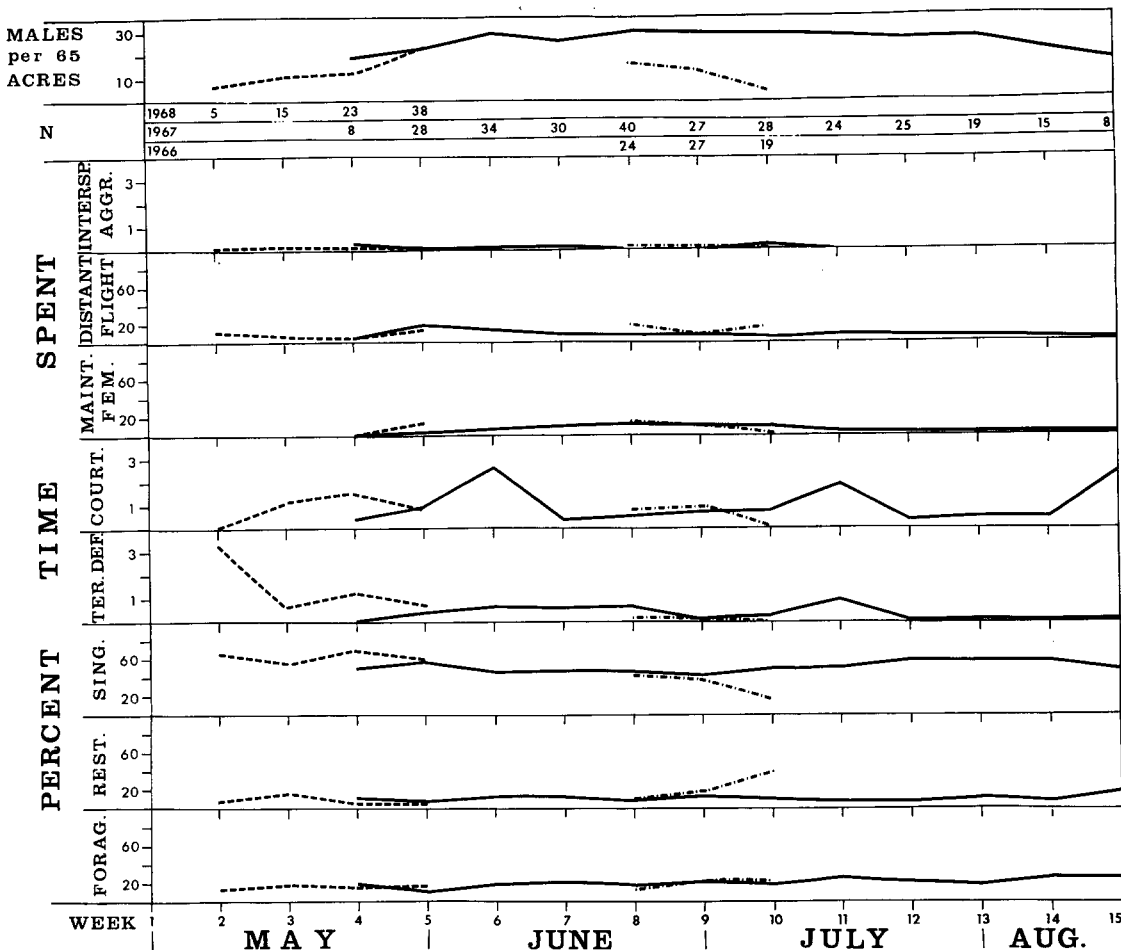
FIGURE 1. Density and weekly average of the per cent of time spent by male Dickcissels in eight activities (sample size = no. of 45-min observation periods; density = maximum weekly density; 1966, dot-dash line; 1967, solid line; 1968, dashed line).

Singing. Peaks in singing occurred in 1968 at the time of territory establishment (64.6 per cent in week 2) and during the major influx of females (70.5 per cent in week 4), but still usually comprised 50–60 per cent of the daily time budget in the other weeks of the breeding season. There was no correlation between the amount of time spent in singing by a male and the size of his territory (see below). Song rates (songs per minute) taken during routine observations averaged 9.4 (SE = 0.23, $n = 81$) in 1966, 10.1 (SE = 0.08, $n = 538$) in 1967, and 8.9 (SE = 0.12, $n = 238$) in 1968.

Territory defense. During territory establishment in the second week, territory defense averaged 3.5 per cent, decreasing to approximately 1 per cent the third week and to nearly zero in the last four weeks. As in other species studied (Collias and Collias 1967; Verner 1965), defense behavior demands only a small fraction of the males' time.

Courtship. Gradually increasing with the arrival of females, courtship in 1967 peaked in the sixth week prior to the height of nesting in the seventh week. Two smaller peaks in the eleventh and fifteenth weeks are difficult

TABLE 1. Average time budget of male Dickcissels expressed as per cent of time.

Activity	1966[a]	1967[b]	1968[c]
Foraging	20.09	19.80	17.00
Resting	21.48	10.40	8.18
Singing	33.66	50.78	62.82
Territory Defense	0.04	0.43	0.93
Courtship	0.64	0.97	0.86
Maintain Female	9.75	7.85	0.27
Distant Flight	14.28	9.75	9.82
Intersp. Aggression	0.06	0.02	0.12
Sample Size[d]	70	286	81

[a] Weeks 8–10.
[b] Weeks 4–15.
[c] Weeks 2–5.
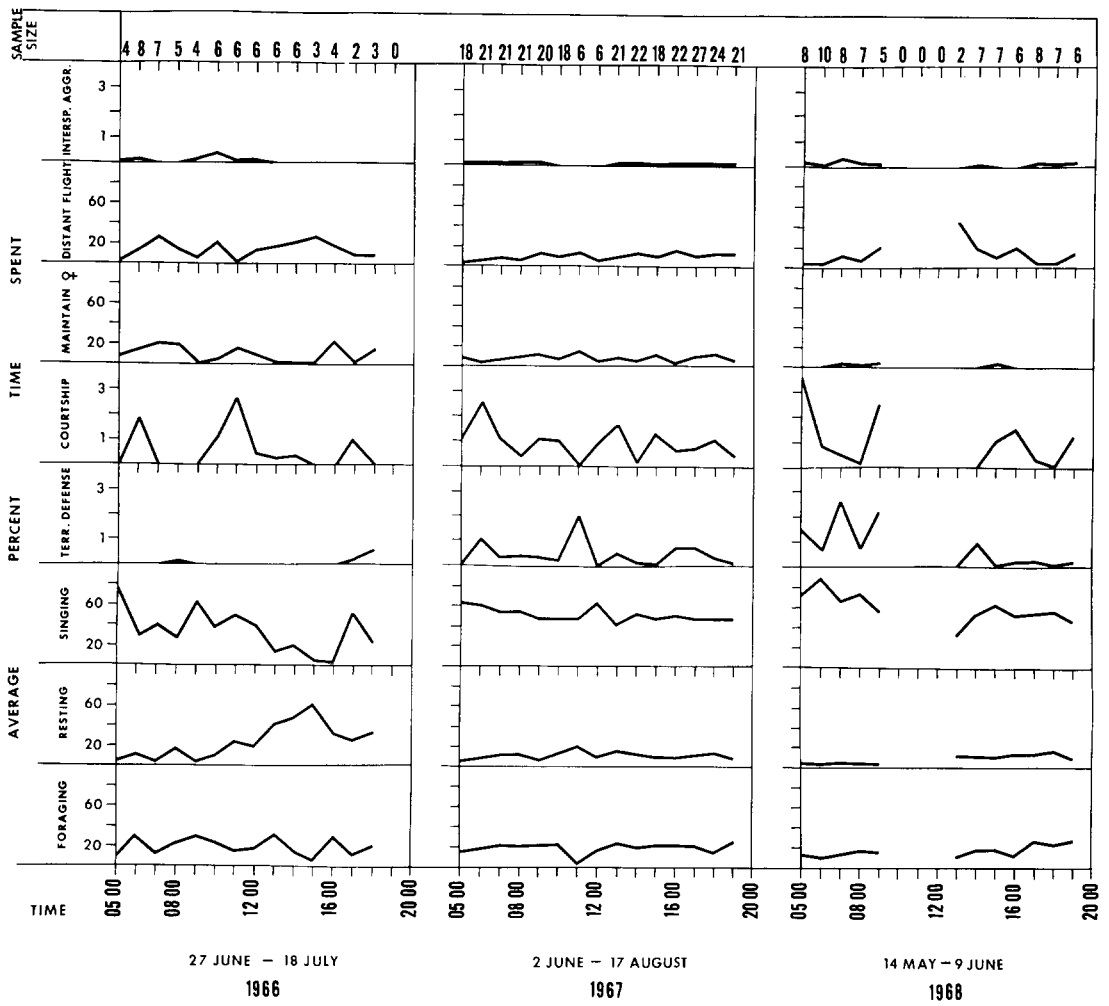[d] No. of 45-min observation periods.

FIGURE 2.   Diurnal activity patterns of male Dickcissels for portions of the breeding season in 1966, 1967, and 1968.

to assess. They appear to be associated with the third and fourth cuttings of hay in adjacent agricultural land and might have been due to an influx of females resulting from nest failures caused by mowing. Initial nest failures on the study area may also have contributed to an increase in the number of courting females in the eleventh week. Courtship in week 15 led to copulations but nesting attempts were unsuccessful.

Maintenance of the female. Time spent maintaining females began in the fourth week and reached a maximum the eighth week as the number of incubating and brooding females increased. A decline in nesting activities beginning the eleventh week was paralleled by a decrease in maintenance of females.

Distant flight. Distant flight was highest early in the breeding cycle, steadily decreasing after a maximum of 20 per cent in the fifth week.

Interspecific aggression. This activity accounts for a minor portion of the time budget and was not observed after the tenth week in this study.

The maximum density of territorial males in 1966 was 18 (27 males/100 acres) compared to 30 (46.2 males/100 acres) in 1967. For the first five weeks densities of males in 1968 were similar to 1967 densities.

DIURNAL ACTIVITY PATTERNS

Diurnal activity patterns (fig. 2) were obtained by averaging percentages of time spent by all males in each activity for hourly intervals. The maximum variation in photoperiod was 19 min in 1966, 83 min in 1967 and 36 min in 1968. Disparity in 1966 and 1968 was not considered large enough to alter the results. Anticipating that changes in day length might affect the results of the 1967 data, percentages were averaged for two week intervals as well

as the total 12 weeks. There were no major differences in the diurnal activity patterns for the six biweekly intervals and diurnal patterns were as effectively demonstrated by averaging hourly observations for the total 12 weeks. The reduced variation in the 1967 graphs compared with the 1966 and 1968 graphs is due largely to greater sample size.

Foraging. Birds commonly have bimodal daily feeding frequencies even at moderate temperatures (Baldwin and Kendeigh 1938), although Verner (1965) described a single peak in early or mid-afternoon in the Long-billed Marsh Wren (*Telmatodytes palustris*). During the breeding season, the male Dickcissel lacks either pattern, as evidenced by the absence of diurnal changes in the feeding activity.

Resting. Resting was below average in the mornings of 1968 and more than doubled in the afternoons when singing, territory defense and courtship became less intense. Resting was nearly constant in 1967, but a substantial increase in the afternoons of 1966 corresponded inversely with reduced time spent singing.

Singing. For all three years singing was linearly dependent on time of day. The co-efficients of dependence (slopes) of calculated regression lines were negative and significant (for 1966, $b = -1.72$, $t_b = -2.58$, $df = 13$, $P < 0.025$; for 1967, $b = -0.50$, $t_b = -2.72$, $df = 14$, $P < 0.01$; for 1968, $b = -1.24$, $t_b = -3.35$, $df = 11$, $P < 0.005$). Although the male marsh wren (Verner 1965) showed a burst of singing just at the end of the day, early morning values were usually highest and decreased to low levels by afternoon as in the Dickcissel. The highest averages for any activity were obtained for singing in 1968 at the initiation of the breeding cycle. The average of eight observations at 05:00 was 74.4 per cent and for 10 observations at 06:00 was 88.9 per cent. On one occasion at 07:00 on 25 May 1968, a male sang constantly from the same perch for 45 min. Although decreasing with time, singing never did drop to a low level throughout the day, a phenomenon which might be related to the polygynous mating pattern of the species (Zimmerman 1966).

Territory defense. No diurnal pattern in territory defense was conspicuous in 1967 but in 1968 the greatest activity was in the mornings, decreasing appreciably in the afternoons. Territory defense in 1966 was rarely observed.

Courtship. Courtship was also sporadic, lacking a diurnal pattern except in 1968 when there was an early morning peak. Less time was spent courting during the three-week period in 1966 than in the other two years.

Maintenance of the female. This activity was relatively stable at a level of 7–10 per cent. Variation in 1966 was partly due to small sample size. Low or zero averages in 1968 were consistent with the paucity of nesting females that early in the season.

Distant flight. Averages for distant flight in 1966 were higher than in 1967 but no differences in the distribution of time spent were detected. Time spent in distant flight for 1967 and 1968 increased slightly with time of day.

Interspecific aggression. Aggressive encounters, mainly with Red-winged Blackbirds, were interspersed throughout the day. Male redwings contested Dickcissels for perch sites and female redwings sometimes chased male Dickcissels from the area around their nests. In 1966, no interspecies contests were observed in the afternoons.

TERRITORY AND ACTIVITY

The average weekly territory size for the 10 males observed in 1966 was 1.76 acres (SE = 0.07, $n = 56$) while the weekly measured territory for the 13 males in 1967 averaged 1.25 acres (SE = 0.02, $n = 124$). Differences in territory sizes between males were not significantly attributable to differences in time spent by individuals in any activity. Although it has been shown that mated Dickcissels have larger territories than bachelor males (Zimmerman 1966), there was no correlation between size of territory and the mean number of mates of individual males. Territory size in the Dickcissel is a function of male density, which in turn is a reflection of the structure of the vegetation (Zimmerman, MS).

FORAGING IN RELATION TO ARTHROPOD POPULATIONS

The average density of all arthropods sampled by the sweep method in forbs was 117.9 individuals/m^2. Of this total the largest percentage was grasshoppers (24.6 per cent) followed by 24.3 per cent homopterans, and 21.2 per cent dipterans. In grass the average density was 73.0 individuals/m^2 of which 45.5 per cent were grasshoppers, 20.7 per cent were homopterans, and 16.0 per cent were dipterans. The lowest density (55.0 individuals/m^2) was found in wheat, in which 30.9 per cent were hemipterans, 20.0 per cent were psocopternas, and only 10.9 per cent were grasshoppers.

Percentages of foraging time spent in forbs, grass, and wheat, the number of trips and the

TABLE 2. Per cent of foraging time, number of trips, and average per cent time per trip spent in each of three patches.

Habitat, year	% foraging time	No. trips	$\bar{x}$ % time/trip
Forbs			
1966	73.09	108	0.676
1967	67.88	728	0.093
1968	48.39	149	0.324
Grass			
1966	24.85	53	0.467
1967	17.74	176	0.101
1968	41.71	115	0.363
Wheat			
1966	2.15	5	0.430
1967	14.38	170	0.846
1968	9.99	19	0.525

average per cent time per trip are included in table 2. Male Dickcissels spent the most time feeding in forbs where insects are most abundant. Lesser amounts of feeding in the grass corresponded with 38 per cent fewer insects found there than in the forbs, while the least time spent foraging was in the wheat, where insects were 53 per cent fewer than in the forbs. The size of the grasshopper renders it a very efficient food item, and males fed extensively on grasshoppers which were present in large numbers in the forbs and grasses. Foraging time in the wheat was spent feeding on the grain rather than on insects, and trips to the wheat were longer since it takes more time to extract and eat the grain than it does to catch an insect. Dickcissels prefer the succulent, immature seed rather than the hardened mature seed. Because the grain was nearly mature in 1966, records of foraging in wheat were scant, while in 1968 observations were too early in the season. The 1967 study, however, included the period when the seeds were immature, hence a substantially larger proportion of foraging time was spent in the wheat that year.

DISCUSSION

FORAGING

Except for more intense activity early in the breeding season at the time initial matings take place, there is no peak of work. Territorial advertisement continues at a high level, regardless of the number of mates a male has acquired, i.e., there is no significant correlation between a male's average number of mates and the average time spent in singing. Because of a constant turnover of females resulting from a high incidence of nest failure (only 16 per cent of the nests in 1967 fledged

any Dickcissels while success in 1966 was nil), reproductive activity is similarly continuous. Foraging does not change since energy demands paralleled the sustained level of activity characteristic of polygynous behavior. Unlike other species (Gibb 1954; Verner 1965) there is no increase in foraging behavior when nestlings are present, since the male Dickcissel does not participate in the feeding of the young. Even in situations where there are compensating decreases in some activities as other activities increase, foraging seldom varies. For instance, in 1966 decreased singing, courtship and maintenance of the female compensated for a sharp increase in resting while foraging changed little. A slightly lower foraging level early in the season may have been augmented by foraging in distant flight (see below).

The amount of time spent in foraging does reflect the effect of temperature on the energy demands for thermoregulation (Verbeek 1964). In the Dickcissel, chemical regulation in homeothermy becomes more important than physical regulation at temperatures below 60°F (Zimmerman 1965a). Since in our study temperatures were rarely lower than this during June, July, and August, the need for energy for this use remained low and relatively constant throughout the reproductive cycle. Only in 1968, when minimum temperatures averaged less than 50°F, was there an increase in foraging in the evenings. Male Dickcissels apparently store more than enough energy to survive the night, since singing and courtship are greater in the morning, while foraging shows no change throughout the day. Natural selection should favor males that are able to spend more time singing early in the day because involvement of females in courtship activities was observed more often at that time. Lack (1946) also found that pair formation in the European Robin (Erithacus rubecula) usually takes place in the morning, and Verner (1965) observed instances of mate-seeking behavior by female Long-billed Marsh Wrens only in the morning. Long periods of time devoted to foraging in the early morning could mean the loss of a potential mate. Males also forage with the females, particularly during the courtship period, thereby meeting their own energetic demands while at the same time maintaining the pair bond. This behavior is also prevalent among females that have established nests. Males accompanied females on 412 of 1074 feeding trips in 1967 (48.6 per cent), and this is probably an underestimate, since the female is secretive and easily missed.
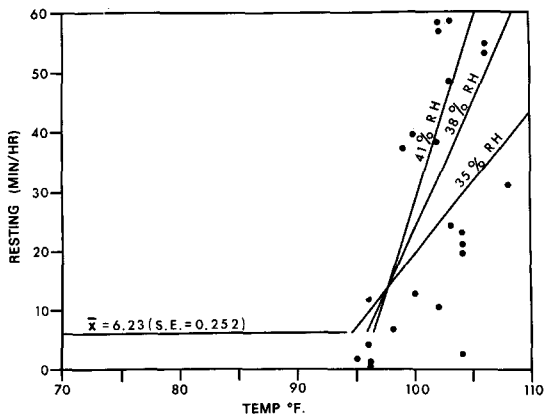
FIGURE 3. The effects of environmental temperature and relative humidity on resting in male Dickcissels. The three multiple regression lines are plotted for the mean relative humidity (38 per cent) and for ± 2 sp (35 and 41 per cent). Data points are given only for temperatures greater than 94°F; horizontal line represents mean resting time for temperatures below 95°F.

TABLE 3. Comparison between 1966 and 1967 of means of activities during weeks 8, 9, and 10 of the breeding season. .

Activity[a]	Min/hr ± se[b]		t[c]
	1966	1967	
Resting	12.89 ± 2.061	6.27 ± 0.686	3.411**
Foraging	12.06 ± 1.397	11.79 ± 0.849	0.170
Courtship	0.39 ± 0.193	0.37 ± 0.087	0.094
Maintenance of female	5.85 ± 1.471	8.38 ± 1.481	1.184
Singing	20.20 ± 2.132	27.91 ± 1.513	3.036**
Territory defense	0.02 ± 0.017	0.24 ± 0.069	2.698**
Distant flight	8.57 ± 1.811	5.12 ± 0.896	1.840*
Song rate[d]	9.40 ± 0.234	9.86 ± 0.139	1.780*
Perch changes[d]	13.20 ± 1.083	22.86 ± 1.120	6.200**

[a] Since interspecific aggression was minimal, it is not included.
[b] For all means except song rate, n for 1966 equals 70 and n for 1967 equals 95. For song rate, the sample size in 1966 is 91 and 148 in 1967.
[c] **, P < 0.01; *, P < 0.05.
[d] These measures are, for song, songs/min, and for perches, changes/hr.

RESTING AND ENVIRONMENTAL TEMPERATURE

While the linear correlation coefficient relating time of day to the average time spent resting in 1966 was positive and significant ($r = 0.76$, $df = 13$, $P < 0.01$), such a relationship was not detected in the 1967 data. Inspection of these data suggested that the diurnal pattern in 1966 resulted from higher ambient temperatures that summer. Temperatures in 1967 never exceeded 94°F during any of the observations, while in 1966 temperatures exceeded 94°F during 23 observation periods and during 16 of these, temperatures were above 100°F. The mean time spent resting in 1967 was 6.2 min/hr ($se = 0.22$, $n = 286$) and for temperatures less than 95°F in 1966, resting averaged 6.1 min/hr ($se = 2.02$, $n = 47$). Combining these data for both years, resting averaged 6.2 min/hr ($se = 0.25$, $n = 333$) for temperatures less than 95°F.

Resting data obtained during observations when the temperature was greater than 94°F were analyzed separately yielding a multiple regression:

$$y = 1820.02 + (-18.49)T + (-58.42)H + (0.60)T\,H,$$

where y = resting (min/hr), T = temperature (°F), H = relative humidity, and $T\,H$ = the interaction of temperature and relative humidity. This analysis was necessary in order to account for the independent effects of temperature and humidity as well as their combined effect, since heat loss by evaporative cooling of the breathing tract through panting becomes less effective at higher humidities due to a decrease in the vapor pressure gradient. The multiple correlation coefficient was significant ($R = 0.70$, $df = 22$, $P < 0.01$).

The results of this analysis (see fig. 3) show that, for temperatures greater than 94°F, resting increases, and increases at a greater rate as the relative humidity increases. At temperatures below 95°F, the effect of relative humidity is probably very slight within the range of 35 and 41 per cent. Zimmerman (1965a) determined a single thermal neutral point at 97°F. At environmental temperatures below this value, existence energy increases with the increasing need for thermogenesis, while at temperatures above this point existence energy increases due to metabolic demands of increased ventilation rates. It is quite evident from figure 3 that there is a compensating increase in resting when the bird is under physiological heat stress.

The increase in resting as a mechanism to minimize the heat load on a bird at high environmental temperatures means that some other portion of its time budget must suffer a decrease. Table 3 compares the mean time spent in the various activities in 1966 with comparable means calculated from the 1967 data. Not only was resting significantly higher in 1966 but males changed perches significantly less often. There were no significant differences between the two years, however, for time spent in foraging, courtship, or the

maintenance of females to which males were already mated. Singing, song rates, and territory defense were, on the other hand, significantly lower in 1966. We suggest that the early termination of reproductive activity of the males in mid-July of 1966 is a direct result of the increase in resting as a behavioral response to high ambient temperatures and the compensatory shift in the time budget leading to a decrease in singing and territorial defense. This decrease in territorial activity was soon followed by a decrease in courtship and maintenance of the female (fig. 1). This response is also apparent in the mean number of mates attracted by males in these two years. Over a comparable time period, males averaged 0.84 females (SE = 0.08, n = 70) in 1966, while in 1967 they averaged 1.37 females (SE = 0.12, n = 95). These means are significantly different ($P < 0.01$).

Studies on the bioenergetics of birds have hypothesized a decrease in productive energy at environmental temperatures at and above thermal neutrality (see Kendeigh 1969 for a recent review). These field data for the male Dickcissel support this hypothesis, and furthermore illustrate that this decrease in productive energy results in a reduction in reproductive activity as opposed to a decrease in maintenance activity (e.g., foraging).

DISTANT FLIGHT

Not all the birds banded on the study area were there as territorial males. During 1967, 28 males were color-banded, while only a maximum of 15 (54 per cent) were ever territorial. Although a few were territorial in adjacent areas, most were never seen again. (Some of these might have still been migrating northward when captured.) It was also observed that male Dickcissels, even though they had established territories on the study area, periodically left their territories (distant flight). Non-local Dickcissels flying low over a resident male's territory were regularly intercepted and chased by the territorial bird. It was not uncommon to see chases involving several males in tandem when such a non-local crossed through the study area. As one chasing male would turn away and return to his territory, other males would rise to follow the intruder in a rapid, twisting, turning flight. We have assumed that these non-locals were birds on distant flight from other areas, and that the intensity of their encounters with the resident population during this overflight could provide information to them on the density of that particular population.

Kluyver and Tinbergen (1953) suggested in their work with titmice that territorial behavior of resident birds is used as a density cue by unsettled birds so that they can avoid highly populated habitats. Similarly, Wynne-Edwards (1962) argued that singing is an epidictic display in territorial birds. We hypothesize that distant flight in the Dickcissel allows males to assess the population density and also habitat suitability in other locations. Habitat suitability in the Dickcissel is in terms of a sufficiently dense and tall vegetative structure (Zimmerman, MS) and could, perhaps, be assessed visually during the overflight of an area. According to this hypothesis, a male would reestablish a territory in a new location, providing the desirability of the new location exceeded that of his original area. Males with more suitable habitats would not be expected to spend as much time in distant flight as males with poorer habitats because of the lower probability of finding a better area. Since the Dickcissel is polygynous, females are free to choose males with more suitable habitat. Thus there is a selective advantage in distant flight behavior if it leads the male into a more suitable habitat for territory establishment and attraction of mates. Of 67 territories established in another population during the breeding season of 1967, 15 males were unmated (unpubl. data). These bachelors maintained their territories for an average of only 1.8 weeks. Although distant flight behavior data are not available for these males, it is obvious that they eventually left to go elsewhere and this relocation could have been facilitated by previous experience through distant flight over other areas. One of these bachelors did move to a territory within that particular study area, where within a week he became polygynously mated.

Zimmerman (1966) found that the vegetation in territories of bachelor males was restricted both in height and per cent coverage compared to vegetation in the territories of mated males. Additionally, he has shown that males with more mates have territories with higher habitat suitabilities (i.e., greater volume of vegetation) than males with fewer mates (Zimmerman, MS). The number of mates, therefore, can serve as an index to the suitability of the habitat a male occupies and in turn can be related to the occurrence of distant flight in order to test this hypothesis.

Based on data collected during 286 routine observations in 1967, the relationship of the proportion of time spent in distant flight to
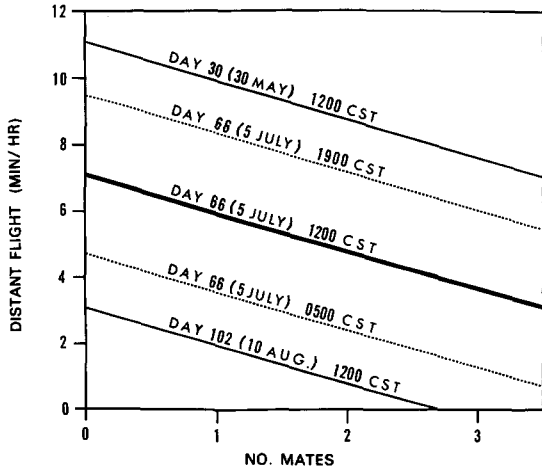
FIGURE 4. Time spent by male Dickcissels in distant flight as a function of the number of mates, time of day, and day of the nesting season (center or heavy line represents mean day and hour; dashed lines represent mean day at varying hours; lighter solid lines represent mean hour on ± 2 SD days).

the number of mates, the time of day, and the day of the reproductive cycle was tested, using y = distant flight in min/hr, x_1 = the number of mates (i.e., nesting and/or courting), x_2 = day of the reproductive cycle, with day 1 beginning on 1 May 1967, and x_3 = hour of the day beginning with 05:00 and ending with 19:00. In the results of the analysis, the number of mates showed a significant negative relation to the time spent in distant flight (b_1 = -1.16, t_{b_1} = -3.15, df = 282, P < 0.01), the day of the breeding cycle showed a significant negative relation to distant flight (b_2 = -0.11, t_{b_2} = -4.44, df = 282, P < 0.01) while the time of day showed a significant positive relation to distant flight (b_3 = 0.34, t_{b_3} = 3.18, df = 282, P < 0.01). The multiple correlation coefficient was significant (R = 0.33, df = 285, P < 0.01).

Figure 4, which plots multiple regression lines using the coefficients of proportionality calculated from these data, indicates that during an average day, distant flight increased by nearly 5 min in the 14 hr between 05:00 and 19:00, and that distant flight, on the average, decreased 8 min in 72 days between 30 May and 10 August. And, most importantly, for any given day and time, distant flight decreased with an increase in the number of mates (i.e., the suitability of his present territory).

The relationship between distant flight and number of mates and also the fact that this behavior is more prevalent early in the nesting season supports the hypothesis that distant flight is used to locate more suitable areas. Orians (1961) suggested that colonies of Tricolored Blackbirds (*Aqelaius tricolor*) assess the food supply of the surrounding environment by means of mass feeding flights. In our study a significant inverse relationship between the mean time foraging by the male Dickcissel and the mean time spent in distant flight was determined in 1967 (r = -0.88, df = 10, P < 0.01). This suggests that males may feed during distant flight and is consistent with our hypothesis as to the function of these flights, since the desirability of a habitat may be assessed by foraging as well as by the intensity of interaction with the resident birds and visual measurement of the vegetative structure. The time involved in distant flight plus the ready availability of food suggests to us that the function of distant flight is not solely that of an axillary foraging pattern.

There is no evidence to support the hypothesis that distant flight gives selective advantage to males by giving them the opportunity for stolen copulation in other areas. No stolen copulations by non-local males have ever been observed by us. Since copulations occur in the context of the companionate behavior that takes place during courtship and involves the female's moving to an exposed perch and giving a distinctive invitational call note, the probability seems very low that a male on a distant flight would be at the right place at the right time, uncontested by the territorial male.

ENERGY BUDGET

We know the existence energy requirements of the Dickcissel (Zimmerman 1965a). Using the equation for males at 15-hr photoperiod and the mean daily temperature of the study area in 1967 (21.8°C), the existence energy for the males was calculated at 17.262 kcal/bird × day. Since the data in table 1 are based on the per cent of observation time (daytime) they must be corrected for the 9 hr of nighttime not included by multiplying each percentage by 62.5 per cent (that portion of the 24-hr day that is daytime with a 15-hr photoperiod). In order to convert the percentage distribution of the time budget presented in table 1 into an energy budget for all males, a number of assumptions must be made. It was assumed that nighttime activity (37.5 per cent) had the same energy cost as daytime resting and that both were equal to the calculated existence energy. Using Orians' (1961) estimate of singing as 10 per cent above the resting level and his estimate of displays

TABLE 4. Energy budget of the male Dickcissel.

Activity	%/day	Unit cost (kcal/bird × day)	Total cost (kcal/bird × day)
Nighttime	37.50	17.2624	6.4734
Resting	6.50	17.2624	1.1220
Foraging	12.37	22.4411	2.7760
Singing	31.74	18.9886	6.0270
Courtship	0.61	29.3461	0.1790
Maintenance of female	4.91	29.3461	1.4409
Territory defense	0.27	34.5248	0.0932
Interspecific aggression	0.01	34.5248	0.0034
Distant flight	6.09	103.5744	6.3077
Total	100.00		24.4226

as double the resting level, the energy costs of singing, territorial defense, and interspecific aggression were estimated. Kale (1965) estimated that foraging demanded a 30 per cent increase above existence levels. Since courtship and maintenance of the female involved not only display but foraging behavior, an intermediate factor (1.7) was utilized for these activities. Tucker (1966) calculated that flight requirements were 6.25 times greater than those of resting, while LeFebvre (1964) determined a factor of eight. It appears that not all of the time attributed to distant flight was actually spent in flying, since the data suggest that males on distant flight also foraged (see above). Accordingly, an estimate of six times the existence level was used as the unit cost of distant flight. The energy budget of the male Dickcissel is presented in table 4.

Kendeigh (1949) assumed that the maximum metabolized energy attained by a bird under cold stress could be reached at higher environmental temperatures when existence energy levels are less so that more productive energy could be obtained. Kontogiannis (1968) has provided experimental evidence in support of this assumption. In the wild state this increased availability of productive energy could be channeled into reproductive activities and hence contribute to an individual's success in his deme. For the male Dickcissel this maximum potential energy at a 15-hr photoperiod is 29.569 kcal/bird × day. The energy budget for the Dickcissel in the summer in Kansas totals 24.423 kcal/bird × day. Since summer Dickcissels store little energy (Zimmerman 1965b), the discrepancy between these two values cannot be accounted for on this basis. It is attributed, rather, to the lack of precision in the assumptions made.

Although purely speculative on our part, the 24 kcal value may be the actual maximum attainable from the environment once the bird integrates all environmental factors in addition to the directly energetic ones in the optimization process that should be involved in habitat selection. The discrepancy in this case is what must be scarificed in order to inhabit, for example, a properly structured vegetation that is desirable to females but which may be not as good a trophic resource.

Assuming then that the male Dickcissel requires at least 24.423 kcal/bird × day, and knowing that the efficiency of assimilation of food ingested by males at a 15-hr photoperiod at 22°C is 68.5 per cent (Zimmerman 1965a), it was calculated that the male must ingest 35.653 kcal/bird × day. Since it is estimated that the male uses only 2.776 kcal/bird × day in obtaining this food, there is a return of 12.8 kcal for every kilocalorie expended.

The caloric value of grasshoppers of the size upon which Dickcissels feed is 5.1517 kcal/g dry wt. (sample of three Melanopus femurrubrum, C. Connell, unpubl. data). Five females and five males of this species averaged 0.099 g dry wt./individual. Thus one grasshopper provides the male Dickcissel with 0.510 kcal. Assuming the same level of efficiency of assimilation, it therefore requires 70 grasshoppers/day to provide the 35.653 kcal needed by the male for his existence and productive energy requirements. From table 1, and using the 1967 data, the male forages about 3 hr every day. Thus he must obtain about 23 grasshoppers/hr, a rate much lower than that estimated for tits on small insects (Gibb 1960) or for the Rock Pipit (Anthus spinoletta) on small snails (Gibb 1956). Grasshopper density in forbs is 29/m² and in grass is 33/m². Such a feeding rate derived through these calculations thus does not appear too unrealistic in relationship to the food supply and suggests that the assumptions made in computing the male's energy budget are fairly close to reality.

SUMMARY

The categorized activities of color-banded male Dickcissels were timed and recorded during 326 hr of field observation in Kansas during the nesting seasons of 1966, 1967, and 1968. From these data an average time budget was constructed on a diurnal basis as well as on a daily basis over the months of the breeding season.

Foraging varied less than any other activity, changing little from day to day and lacking

any diurnal pattern. We feel that this was due to the fact that energy demands paralleled the sustained level of activity throughout the nesting season that characterizes polygynous behavior, and that energy demands for thermoregulation were relatively constant. The integration of feeding with courtship and maintenance of the female as well as the preemption of feeding by singing in the early morning hours led to a sustained feeding level throughout the day. Most of the foraging time was spent in forbs where their insect food was most abundant.

Early in the breeding season resting increased slightly in the afternoons when reproductive activities were less intense. For temperatures greater than 94°F in 1966, resting increased, and increased at a greater rate with increased relative humidity. It was apparent that the significantly higher level of resting due to physiological heat stress resulted in a compensatory shift in the time budget through a decrease in singing, territorial defense, and eventually courtship and maintenance of the female, leading to an early cessation of breeding activities. Temperatures in 1967 did not exceed 94°F and resting did not change, nor was breeding activity curtailed.

Singing was highest early in the breeding season at the time of territory establishment and in the mornings when courtship activities were more frequent. Male Dickcissels sing, however, throughout the day and singing normally averaged at least 50 per cent of the time budget.

Territory defense was highest at the time of territory establishment. In 1966 territory defense was rarely observed; in 1967 no diurnal pattern was evident; but in 1968 a peak in territory defense occurred in the mornings.

Courtship gradually increased with the arrival of females, and a peak occurred in the week prior to the height of nesting. Initial nest failures on the study area and nest failures due to cuttings of hay may have been the cause for additional courtship peaks in week 11 and 15. Although copulations were observed as late as August 1967, nest attempts at that time were unsuccessful.

Maintenance of the female during the reproductive season corresponded with the nesting activity and no diurnal patterns was evident.

The Redwinged Blackbird is the only nesting species that shares the habitat with the Dickcissel; aggressive encounters between them were seldom observed.

It is hypothesized that distant flight functions to assess the population density and habitat suitability in other locations. Using the number of mates as an index of the suitability of the habitat occupied by a male, it is shown that for males with fewer mates (a lower habitat suitability), the amount of distant flight increases. This analysis also illustrates that more time was spent in distant flight earlier in the season, the time of peak territorial establishment, and that this behavior increased with time of day. A significant inverse correlation between the mean time spent foraging and the mean time spent in distant flight is consistent with the hypothesis, since foraging behavior may also be used to assess the desirability of a habitat.

Differences in territory sizes were not attributable to time spent in any activity.

An energy budget is presented, the daily total expenditure of which approximates the maximum potential energy expected from bioenergetic studies on this species. From these calculations it is suggested that there is a return of 12.8 kcal/bird for every kilocalorie expended in foraging, and that the caloric equivalent of 70 small to medium grasshoppers will satisfy the male Dickcissel's daily energy demands during the breeding season.

ACKNOWLEDGMENTS

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