

NEST PREDATION AND ITS RELATIONSHIP TO HABITAT AND NEST DENSITY IN DICKCISSELS

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ABSTRACT.—Analysis of the histories of over 500 Dickcissel (*Spiza americana*) nests found in eastern Kansas showed that those in old-field habitats suffered more predation than those in prairies. Predation rates on the prairie, were not correlated with the weeks of the nesting season, but those in old-fields varied significantly with time. Although both predation rates and nest densities increased concurrently to a peak during the middle of the nesting season in old-fields, an analysis of the relationship between nest densities per week and both daily predation rates and the percent of nests lost to predators each week indicated that predation was not density-dependent. Predation rates are higher in old-fields than in prairies, not because of greater nest densities, but perhaps because predators are more abundant in old-fields. Snakes are the most probable nest predator, and their method of hunting, by chance encounters rather than by directed search, is suited to the absence of a density-dependent effect of predation on Dickcissel nests.

Overall mortality rates in avian populations may be density-dependent (Ricklefs 1973), but "it is not a popular notion that [predation on nest contents] . . . operates in a density-dependent fashion to regulate population size" (Cody 1971:486). Indeed, von Haartman (1971) concluded that there was no evidence that nest loss due to predation was greater in dense populations. Since the publication of these reviews some data have accumulated that support the idea that nest predation is density-dependent in both cavity-nesting (Krebs 1971) and open-nesting species (Fretwell 1972, Goransson et al. 1975). An experiment specifically designed to test this hypothesis, however, did not support the density-dependent conclusion (Gottfried 1978). Although Fretwell and Shipley (1981) argued that Gottfried's failure to demonstrate density-dependence was an effect of sample size rather than a biological reality, both Gottfried (1978) and Best (1978) suggested that the kind of predator may be important in determining whether or not nest predation is density-dependent. In the studies showing density-dependence, the predators (*Mustela*, *Corvus*, *Larus*, *Cyanocitta*) hunted visually. For such animals the development of a search image (permitting goal-oriented foraging) probably depends upon the density of the prey items (Tinbergen 1960). In Gottfried's old-field, however, the major predators were snakes (Gottfried and Thompson 1978), which probably find nests randomly (Best 1978).

The density of Dickcissels (*Spiza americana*) varies according to habitat, being higher in old-fields and lower in prairies (Zimmerman 1971). Parasitism by the Brown-headed Cowbird (*Molothrus ater*) depresses the productiv-

ity of Dickcissels, and both the frequency and intensity of parasitism are inversely related to the density of available nests (Zimmerman 1983). Hence, Dickcissels nesting at low density in prairie habitat suffer high parasitism (Elliott 1978). Productivity per nest, however, is similar in prairies and old-fields (Zimmerman 1982). This suggests that predation rates in the high-density old-fields are greater, offsetting the lowered effect of cowbird parasitism, while in the low-density prairies, the high loss caused by cowbird parasitism is offset by low predation rates. I present this analysis of nesting success in the Dickcissel in order to test the hypothesis that nest predation is density-dependent, as these data suggest.

METHODS

I obtained nest history data from 1965 through 1979 from over 500 nests in populations on the Ft. Riley Military Reservation and the Konza Prairie Research Natural Area in Riley and Geary counties of Kansas. Most nests were found by watching the females. Except for a few populations where nests were visited every three or four days, most data were gathered by weekly visits to the nests. For nests expected to fledge young between visits, I determined the fate of the nests by the female's behavior. At successful nests the female remained nearby, feeding the young and displaying aggressively towards me. If a nest was lost since the last visit, the female was always gone. Nesting success data are presented as survival rates (Mayfield 1961, 1975) with the 95% confidence limits calculated by Johnson's (1979) method. For three old-field and two prairie populations, concurrent studies of territorial-

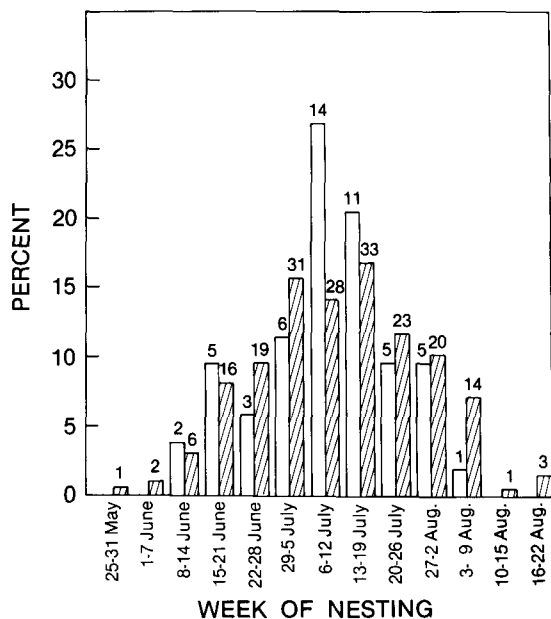


FIGURE 1. Percent frequency distribution of predation nest losses by week of loss in prairie (open bars) and old-field (cross-hatched bars) habitats. Number at top of each histogram is the number of nests lost.

ity and mating patterns in 1967, 1968 and 1979 provided an intensity of coverage that makes me confident that most nests were found. For these populations it was then possible to correlate nest densities, determined on a weekly basis, with predation.

RESULTS

PHENOLOGY OF NEST PREDATION

Nesting in Kansas old-field populations began in the third week of May and continued until mid-August. The cumulative frequency of nest losses due to predation surpassed 50% by the week of 6–12 July; the weekly proportion of predation losses reached a maximum the following week and then dropped to very low levels by August (Fig. 1). Nesting began a week later and ended two weeks earlier in the prairie (Fig. 2). The cumulative frequency of predation

exceeded 50% during the week of 13–19 July, although the maximum proportion of weekly nest loss occurred the previous week. The variances in the temporal distribution of the proportions of nests lost to predators in the two habitats, however, were not significantly different.

The daily mortality rates due to predation showed a similar peak in mid-July in the old-field, coming soon after the peak period when new nests were started (Fig. 2). The quadratic relationship between week of nesting and predation rate is significant ($F = 18.96$; $df = 2, 8$; $P < 0.01$). Best (1978) also showed a positive relationship between the number of active nests in an old-field and the intensity of predation. In the prairies, daily predation rates also peaked soon after the period of most frequent nest starts, but the daily predation rate showed no temporal pattern.

RELATIONSHIP OF PREDATION AND OTHER CAUSES OF LOSS TO THE NESTING CYCLE

In both old-fields and prairie, the daily mortality rate attributed to causes other than predation, principally cowbird parasitism, was greatest during the egg-laying period (Table 1). These rates exceeded predation rates during all phases in the nesting cycle. In the prairie this value was significantly different from non-predatory losses during incubation ($F = 5.28$; $df = 10, 10$; $P < 0.01$), while in the old-fields this value was significantly different from losses due to other causes during both incubation ($F = 28.4$; $df = 34, 31$; $P < 0.01$) and brooding ($F = 31.5$; $df = 42, 7$; $P < 0.01$). Comparing habitats, mortality rates due to other causes during the incubation and brooding phases were not significantly different.

The highest daily predation rate occurred in the old-field during incubation. This value was significantly different from the daily predation rate during incubation in the prairie ($F = 2.13$; $df = 24, 136$; $P < 0.01$) and during egg deposition in the old-field ($F = 3.36$; $df = 16, 136$; $P < 0.01$), but similar to all other predation

TABLE 1. Daily mortality rates \pm 95% C.L. due to predation and all other causes.*

	Egg-laying	Incubation	Brooding
Old-field			
Predation	0.039 \pm 0.006 ⁴	0.064 \pm 0.010 ¹	0.042 \pm 0.012 ^{1,5}
All other	0.084 \pm 0.028 ⁴	0.014 \pm 0.005 ⁶	0.006 \pm 0.005 ⁶
Prairie			
Predation	0.062 \pm 0.054 ¹⁻⁶	0.038 \pm 0.015 ²	0.043 \pm 0.017 ^{1,2,5}
All other	0.123 \pm 0.073 ^{1,4}	0.016 \pm 0.010 ^{3,6}	0.002 \pm 0.004 ¹⁻⁶

* Data are based on 3,624 days of exposure for 401 old-field nests and 1,244 days of exposure for 134 prairie nests. Values with the same superscript are not significantly different ($P > 0.05$) from each other.

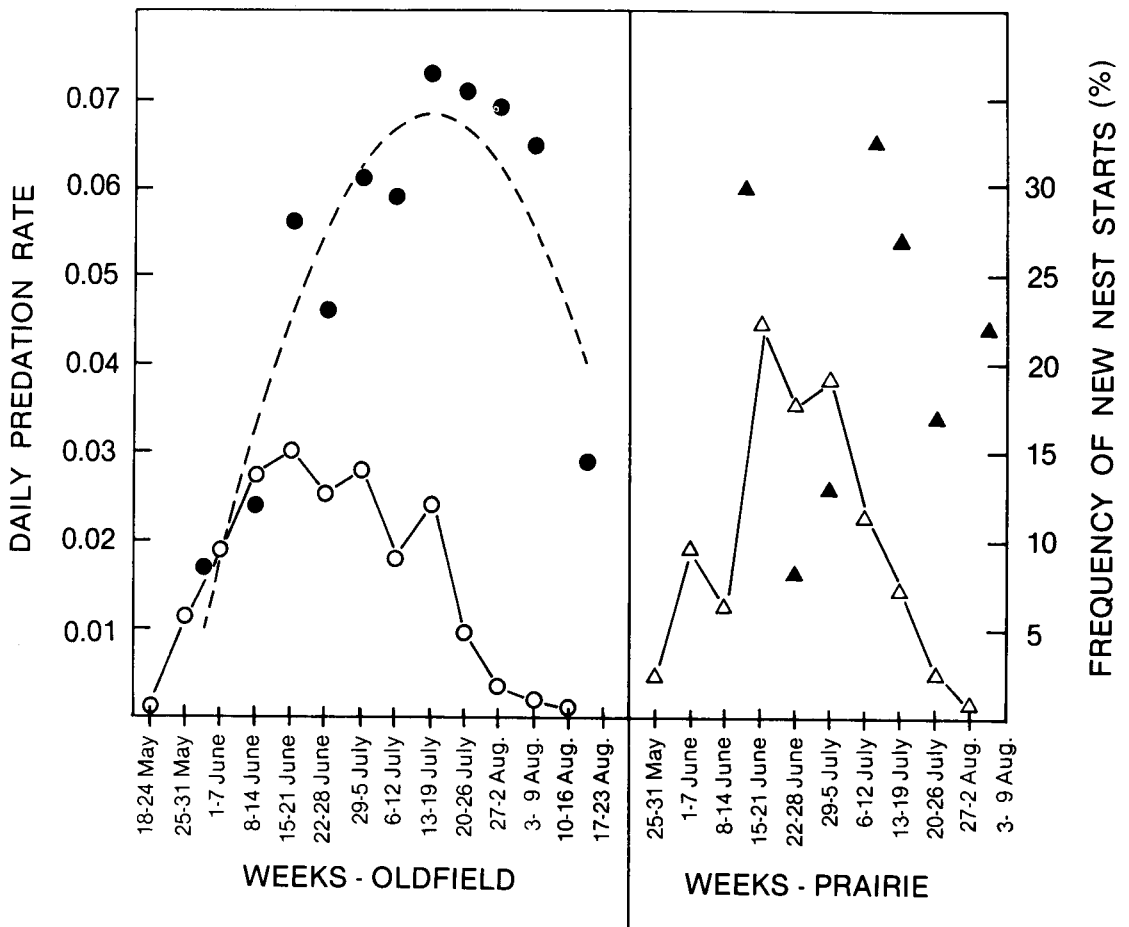


FIGURE 2. Daily predation rates in old-fields (solid circles and dashed curve) and prairies (solid triangles) and percent frequency distribution of new nest starts in old-fields (open circles) and prairies (open triangles) according to week of nesting season.

rates. Higher losses during the incubation phase have been recorded for the Dickcissel (Harmeson 1974) as well as for various other species (Best and Stauffer 1980). Daily predation rates of prairie nests, however, did not differ among the three phases in the nesting cycle.

Using the separate daily predation rates for nests in the egg-laying, incubation and brooding stages (Table 1) and the mean number of days for each of these stages (3, 12 and 9, respectively), I calculated the overall probability for a nest being taken by a predator during the entire 24-day period after nest completion. The result for these independent, daily probabilities was 104 times greater for old-field nests than for prairie nests. Owing to the significantly greater predation rate on old-field nests during the long incubation period, predation affected nesting success more severely in old-field than in prairie populations.

DENSITY AND PREDATION

The density-dependent hypothesis predicts that predation rates will be greater in denser than in sparser prey populations. To test this expectation, I used data from three old-field and two prairie populations in which the number of nests found was thought to be close to the actual number present. For the old-field populations the mean daily nest density per week was related to the daily predation rate as well as to the percentage of available nests lost to predators that week. I analyzed the prairie populations in a similar manner. I found no significant relationships between nest density and the percent of nests depredated in either prairies (Spearman $R = 0.010$, $n = 20$, $P > 0.05$) or old-fields (Spearman $R = 0.125$, $n = 34$, $P > 0.05$). Neither could I demonstrate a significant relationship between nest density

and daily predation rates in prairies (Spearman $R = 0.016$, $n = 20$, $P > 0.05$) or in the old-fields (Spearman $R = 0.269$, $n = 34$, $P > 0.05$). These results match those from my earlier analysis of a smaller sample of Dickcissel nests (Zimmerman 1971) as well as those of Best (1978) and Gottfried (1978).

DISCUSSION

In the old-fields studied, the density of nests increased 32-fold from May to July, and a significant relationship between predation rate and time of nesting was demonstrated. In the prairie, however, densities increased only two to six times during this period and predation rates followed no regular pattern. Although the prediction that predation was greater in old-fields than in prairies is correct and nest densities and predation rates in old-fields increased concurrently, I found no support for the hypothesis that there is a density-dependent response. No significant associations between nest densities and the percent of nests depredated or daily predation rates in either habitat were shown. By analyzing data from populations in which actual prey (nest) density was closely approximated, using a time period (one week) that was sensitive to changes in prey population densities, estimating predation by measuring two variables, and having a sufficiently-sized sample, I am convinced that predation of these Dickcissel nests was not density-dependent.

Fretwell (1977), on the other hand, contended that prey densities and predation rates were significantly related in Dickcissels. He plotted the density of females in different habitats against the percent of nests lost to predators in each of these habitats using some data of his own, some of mine (Zimmerman 1966, 1971) and some of Harmeson's (1974). Predation rates increase with an increase in female density, but I suggest that the correlation is spurious. The variation in predation rate is not dependent upon variation in female (nest) density in a way suggesting a negative feedback effect. My analysis shows that predation is two orders of magnitude greater in old-fields, a habitat in which female density and nest density are also greater, compared to predation in prairies, where female and nest densities are lower. These data would fit Fretwell's plot nicely, but I found that predation rates in Dickcissel populations are not density-dependent.

The data that Fretwell used and those reported here both show that predation is greater in habitats where female density is also higher, namely, in old-field habitats where there is more structural heterogeneity (Zimmerman

1971). An alternate hypothesis that explains these results is simply that predators are also more abundant in old-fields. The predation rate on Dickcissel nests depends upon the density of the predators, not the nests.

I agree with Best (1978) and Gottfried and Thompson (1978) that snakes are the most probable predator in old-field habitats and perhaps in the prairie as well. Indeed, the only observed predation on a Dickcissel nest was by a snake (Facemire and Fretwell 1980). I suspect that snakes are not primarily visual predators, but rather probably depend additionally upon olfaction. Furthermore, I doubt that hunting by snakes is facilitated by acquiring a search image, a behavioral development that depends upon the density of the prey (Tinbergen 1960). Snakes find nests by random close encounters (Best 1978), and the finding of one Dickcissel nest does not appear to increase the chance of finding another. Snake populations can be expected to be higher in habitats where prey are more plentiful; hence, I suggest that the increase in predation during the nesting season simply reflects a seasonal addition of young snakes in the resident population.

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RECENT PUBLICATIONS

The Foraging Behavior of Mountain Bluebirds/with emphasis on sexual foraging differences.—Harry W. Power. 1980. *Ornithological Monographs* No. 28, American Ornithologists' Union, Washington DC. 72 p. Paper cover. \$8.50 (\$7.50 to AOU members). Source: Assistant to the Treasurer of the AOU, Dr. Glen E. Woolfenden, Dept. of Biology, University of South Florida, Tampa, FL 33620. This monograph examines the possible evolutionary and ecological causes of sexual differences in foraging behavior of insectivorous passerines. Mountain Bluebirds (*Sialia currucoides*) were chosen for the study not because there is anything unique about their foraging, but because the author was already familiar with their habits and the species met his criteria for the investigation. Arising from observations during two breeding seasons, several experiments were run in order to test alternative hypotheses. Although samples were necessarily small, the rigorous design and careful analysis of the tests yielded some clear insights about the roles of vegetation, foraging tactics, and work load. The report deserves attention not only for its findings but also for its demonstration of the value of experiments in field studies. Illustrations, references.

Population Ecology of the Dipper (*Cinclus mexicanus*) in the Front Range of Colorado.—Frank E. Price and Carl E. Bock. 1983. *Studies in Avian Biology* No. 7, Cooper Ornithological Society [Los Angeles, CA]. 84 p. Paper cover. \$9.00. Source: Allen Press, P.O. Box 368, Lawrence, KS 66044. Owing to their relatively simple ecology, dippers appear to be ideal subjects for studies of animal population dynamics. Such a study is reported here, focussing on a particular population, its resources, social interactions, reproductive success, and the potential effects on it of certain abiotic factors. Three years of field work produced an abundance of data which, after statistical analysis, yielded seventeen major factors impinging on the population at different seasons. All of this is solid new information. The major conclusion that emerges, however, is a reinforcement of the view from other recent studies that populations are not regulated by only one or a few environmental factors. "Instead, there are many interacting variables that operate with differing intensities to influence the major population processes . . ." While not novel, this message is perhaps more widely important than the study's findings and methodology. Illustrations, references.