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Predation in Relation to Spacing of Kingbird Nests

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Western Kingbirds (*Tyrannus verticalis*) and Cassin's Kingbirds (*T. vociferans*) usually breed in different habitats, but both species nest together in open habitats with tall trees (Hespenheide 1964, Ohlendorf 1974, Blancher and Robertson 1984). We noted previously that breeding success of Cassin's Kingbirds was higher in habitats where they nested alone than in habitats where Western Kingbirds also nested (Blancher and Robertson 1984). Here we test the hypothesis that a negative relation between predation rate and the spacing of kingbird nests is responsible for lower breeding success where both species nest together (i.e. predation rate is higher because nests are close together).

Several studies have shown a positive correlation between density and predation rate on birds' nests (e.g. Krebs 1970, 1971; Fretwell 1972; Goransson et al. 1975; Dunn 1977; Weatherhead and Robertson

TABLE 1.   Percent loss of eggs and young by kingbirds in the three years of study (includes only those nests where initial clutch size was known).

	Western Kingbird			Cassin's Kingbird		
	1978	1979	1980	1978	1979	1980
Number of eggs	88	358	214	55	102	52
Percentages of losses to:						
Predation	26.1	45.3	29.4	32.7	54.9	28.8
Weather	0	33.5	8.9	0	14.7	0
Desertion	0	0.8	0.5	23.6	3.9	26.9
Did not hatch	11.4	5.3	10.7	1.8	5.9	9.6
Starvation	0	0	3.3	1.8	0	0
Did not fledge	10.2	2.0	13.1	3.6	1.0	1.9
Misc. causes	4.5	7.0	1.9	0	3.9	0
Total % loss	52.3	93.9	67.7	63.5	84.3	67.2

1977; Knapton 1979; Page et al. 1983), although this relation may not hold when the principal predator does not find nests visually (Best 1978, Gottfried 1978, Zimmerman 1984). Furthermore, Snow (1970) suggested that density-dependent predation could select for a diversity of nests and nest sites within bird communities. Western and Cassin's kingbirds are of interest because their nests are very similar in appearance, they are placed in similar sites when in the same habitat, and interspecific spacing of nests is minimal (Blancher and Robertson 1984). Therefore, one might expect visually hunting predators to find kingbird nest sites more quickly in habitats where both species nest, because nest density probably will be higher than where each species nests singly.

The study was conducted from 1978 through 1980 along the eastern edge of the Chiricahua Mountains in southeastern Arizona. The study area is described in Blancher and Robertson (1984). Briefly, we chose 11 study sites to cover the transition from desert through open riparian habitat to dense riparian for-

est. Desert habitat was occupied almost exclusively by Western Kingbirds, riparian forest habitat exclusively by Cassin's Kingbirds, and both species nested together in open riparian areas.

Nests of both species were found as they were being constructed. Nearest-neighbor distances (NNDs) were measured between nests (of either species) active at the same time of the season. We checked nests every third day for the presence of eggs or nestlings. Accessible nests were checked by hand, nests up to 14 m were checked with a nest mirror, and higher nests were observed with binoculars. We noted any potential predators near nests and delayed nest checks until these predators had left the area. Predators generally were detected as a result of aggressive behavior of kingbirds. We used the proportion of nest checks during which kingbirds attacked or called at predators as an indication of the abundance of predators at a site.

Predation was assumed to have taken place when there was no other obvious cause for loss of nest contents. Time of predation was assumed to be midway between nest checks. Rate of predation was cal-

TABLE 2.   Mean nearest-neighbor distances (NND) for kingbirds in relation to habitat. Distances were calculated between nests of both species, and between nests of each species separately (intraspecific).

	Num- ber of nests	NND (m)[a]	
		Intra- specific	Both species
Western Kingbird			
Desert	163	256	241
Open riparian	47	283 ns	106***
Cassin's Kingbird			
Open riparian	91	230	111
Riparian forest	71	202 ns	202***

[a] ns = $P > 0.05$ (t-test); *** = $P < 0.001$.

TABLE 3.   Rate of nest predation for each species vs. habitat.

	Nest-days	Nests lost per 100 nest-days[a]
Western Kingbird		
Desert	2,984.0	1.94
Open riparian	823.5	2.79 ns
Cassin's Kingbird		
Open riparian	1,318.5	3.11
Riparian forest	1,543.5	1.62**

[a] ns = $P > 0.05$ (χ^2 test on the number of nests preyed upon vs. the number expected if predation rate were equal in each habitat); ** = $P < 0.01$.

TABLE 4. Comparison of mean nearest-neighbor distances (NND) for successful nests and nests that were preyed upon (includes only those nests found before the start of incubation). Nests of both species were included in all calculations of NND. None of the differences was statistically significant (*t*-tests). Sample sizes are in parentheses.

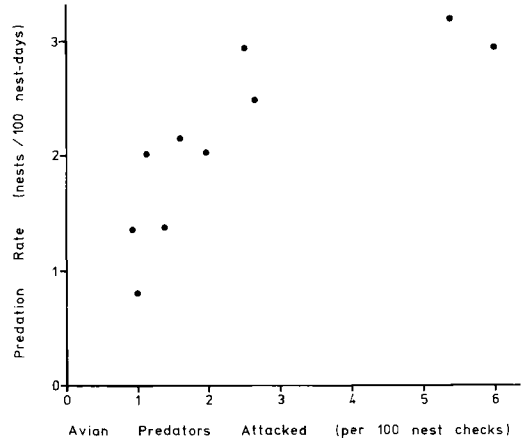|	NND (m)	
	Successful	Preyed upon
Western Kingbird		
1978	177 (9)	260 (6)
1979	209 (12)	199 (31)
1980	203 (31)	185 (18)
All years	200 (52)	201 (55)
Cassin's Kingbird		
1978	178 (10)	138 (18)
1979	133 (7)	193 (19)
1980	160 (23)	167 (17)
All years	160 (40)	166 (54)

Fig. 1. Predation rate on kingbird nests vs. the frequency with which potential avian predators were seen being attacked by kingbirds. Each dot represents one study site.

culated by dividing the number of nests preyed upon by the total number of days that nests were active (nest-days).

Predation on nest contents accounted for the loss of 26–55% of the eggs laid by both species in all three years, or about half of all losses (Table 1). This was far more than any other cause of nest loss, although losses to wind and rain were high in 1979, and nest desertion by Cassin's Kingbirds was frequent in 1978 and 1980, apparently caused by our climbing of nest trees (fewer trees were climbed in 1979).

Kingbirds rarely nested less than 50 m from another nest of the same species (see Blancher and Robertson 1984), although interspecific spacing was much less than this, with nests as close as 3 m in one instance. For this reason nearest-neighbor distances were only half as large in open riparian habitat where both species were present as in the other habitats (Table 2).

Rate of nest predation tended to be higher in open riparian habitat than in the desert for Western Kingbirds (χ^2 = 2.19, df = 1, P > 0.05), and was significantly higher in open riparian habitat than in riparian forest for Cassin's Kingbirds (χ^2 = 6.85, df = 1, P < 0.01; Table 3). If this higher predation rate in open riparian habitat was causally linked to the closer spacing (lower NNDs) of kingbirds in that habitat, then we should expect successful nests of each species to have a larger NND on average than those nests that were preyed upon. In fact, we found no significant difference between the NNDs of successful nests and nests that were preyed upon for either species, in any single year or in all years combined (Table 4). Nor did we find any significant differences in predation rate between nests grouped by NNDs (1–50 m, 51–100 m, etc.).

Most nest defense by kingbirds was directed at predatory birds, particularly Cooper's Hawks (*Accipiter cooperii*) and Chihuahuan Ravens (*Corvus cryptoleucus*). A Cooper's Hawk was observed taking a nestling from a Cassin's Kingbird nest. We found a positive correlation between predation rate in each study site and the frequency of kingbird attacks on avian predators in that study site (r = 0.80, df = 8, P < 0.01; Fig. 1). This result could have occurred if we led avian predators to the nest during nest checks. However, this did not appear to be happening because only 4 of 77 instances of nest predation on either species occurred within 3 days of sighting a predator. In addition, there was no difference in predation rate between nests that had been checked by hand and those that were watched only with binoculars.

Kingbird attacks on avian predators (accipiters, falcons, ravens, owls) were observed more frequently in open riparian habitat than in desert areas (χ^2 = 9.04, df = 1, P < 0.01) or riparian forest (χ^2 = 3.70, df = 1, 0.10 > P > 0.05; Table 5). Cooper's Hawks accounted for more than 50% of the attacks in open

TABLE 5. Frequency of attacks by either species of kingbird on potential avian predators (i.e. accipiters, falcons, ravens, owls) in each habitat.

	Nest-checks	Attacks per 100 nest-checks
Desert	1,891	1.75
Open riparian	982	3.56
Riparian forest	552	1.81

riparian habitat and were known to nest in sycamore trees in this habitat.

At first glance, it appears that nest predation may be causally linked to kingbird nest spacing since the highest rate of predation occurred in open riparian habitat where kingbird nests were most closely spaced. In addition, avian predators, which rely primarily on vision to find prey, appeared to be responsible for much of the predation. However, on closer examination, the rate of nest predation was not related directly to spacing of kingbird nests.

There are two plausible reasons for a lack of increased predation on closely spaced kingbird nests. First, kingbirds engage in aggressive defense of their nests against potential predators, and this appears to reduce the probability of nest predation (Blancher and Robertson 1982). Nesting close to other aggressive birds could be advantageous in reducing predation (e.g. Goransson et al. 1975, Andersson and Wiklund 1978, Clark and Robertson 1979, Wiklund 1979, Dyrcz et al. 1981, Burger 1984, Gotmark and Anderson 1984). Certainly, hawks and ravens appeared to be repelled by large numbers of attacking kingbirds in our study area; we observed as many as 10 kingbirds simultaneously attacking predators where nesting density was high. Nevertheless, we did not see any evidence for a reduction in nest predation when nests were closely spaced, as one would expect if aggressive mobbing were truly effective.

A second possible explanation stems from the fact that kingbird nestlings and eggs are not likely to be a primary diet item of the predators involved. For example, 50% of the diet of Cooper's Hawks in the Chiricahua Mountains is composed of small mammals and lizards, and much of their avian prey consists of adult or fledged birds (Snyder and Snyder 1974). The presence of these predators, and hence the rate of predation on kingbird nests, is more likely related to the abundance of these primary diet items than to the spacing of kingbird nests. The net result is that kingbird nests are subject to greater predation where there are more predators, independent of their own nesting density. Zimmerman (1984) reached this same conclusion for Dickcissel (*Spiza americana*) nests in old-field habitat. Thus, the high rate of predation on kingbird nests in open riparian habitat does not appear to result from the presence of both species in this habitat. Nevertheless, the high predation rate in open riparian habitat selects against birds nesting there, and thus tends to maintain the habitat separation shown by these two kingbird species.

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Ten-year Periodicity in Whooping Crane Census

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Although the Whooping Crane (*Grus americana*) has received more public interest than perhaps any other endangered species in North America, amazingly little is known of the factors influencing its demography and population dynamics. A reasonably accurate census of the endangered Whooping Crane population overwintering at Aransas National Wildlife Refuge, Texas has been recorded since 1938, affording a 46-yr time series (Miller et al. 1974, Binkley and Miller 1983). Here we report the discovery of a previously unreported 10-yr periodicity in this time series.

In April, cranes migrate north to nesting grounds in Wood Buffalo National Park, N.W.T., Canada. Complete nesting surveys are available only since 1970, although counts of juvenile-plumaged birds are available from Aransas for all years (Binkley and Miller 1983). Mortality rates have been estimated by Binkley and Miller (1980, 1983). The population experienced a per capita growth rate of 0.02 for the period 1938–1956, and 0.04 since 1957 (Binkley and Miller 1983).

Taking square roots of population sizes to homogenize variance (cf. Anderson 1977—a necessary step overlooked by Miller et al. 1974), the time series was detrended separately for the two growth periods defined by Binkley and Miller (1983) by calculating residuals from least-squares linear regression (similar results may be obtained by second-order differencing). The resulting stationary time series was examined for periodicity by plotting the sample autocorrelation function (Box and Jenkins 1970) illustrated in Fig. 1 and by calculating a periodogram (Fig. 2) using fast Fourier transform procedures outlined by Bloomfield (1976). Both approaches indicated a strong periodic pattern with period length of approximately 10 yr. Although statistical inference procedures for

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autocorrelation and periodogram peaks are only approximate (Shimshoni 1971, Bloomfield 1976), in both cases the significance probabilities for 10-yr periodicity were quite small ($P < 0.001$).

The periodic pattern is particularly apparent after removing high-frequency "flutter" by calculating a 3-yr moving average (although a moving average is not necessary to demonstrate the patterns we describe). In Fig. 3 we illustrate a least-squares regression fit to the periodic model:

$$X(t) = 0.0013 + 0.826 \cos \omega t - 0.291 \sin \omega t + \epsilon,$$

where $X(t)$ is the moving average of the detrended square root of population size, ω is $2\pi/(\text{period length} = 10)$, and ϵ is an error term. Nearly ⅔ of the variance in the detrended time series is attributable to this 10-yr harmonic ($R^2 = 64.7\%$, df = 41, $P < 0.001$).

Although Binkley and Miller (1983) ascribe periodic fluctuations in the Whooping Crane population to variation in recruitment, our results are inconsistent and suggest that variation in mortality also must be important. Recruitment of juvenile-plumage cranes into the Aransas Refuge counts varied considerably among years but did not possess significant periodicity. Furthermore, we found no significant correlation between rate of recruitment and the detrended square root of Whooping Crane census ($R^2 = 0.059$, df = 44, $P > 0.1$). We further note that recruitment of young into the Aransas census is confounded by mortality of chicks on nesting grounds because chicks are not counted until they reach the Aransas area in late autumn.

Recruitment is thought to vary as a function of water levels on nesting grounds (Kuyt et al. 1981), which also may influence vulnerability of cranes to predation because terrestrial predators can better penetrate nesting areas in years of low water levels. Also, during drought conditions, crane families presumably range farther to find suitable wetland feed-