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ADAPTIVE SIGNIFICANCE OF THE VARIABLE DISPERSION PATTERN OF BREEDING NORTHERN ORIOLES

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Although birds of most species exhibit a single spacing pattern throughout their ranges, there may be circumstances in which a species varies from all-purpose territoriality to coloniality. This paper examines conditions which may be responsible for such variability. Spacing systems will be considered from an ecological rather than a behavioral point of view. The ecologically important aspect of Type A territoriality (Mayr 1935, Nice 1941) is the territory owner's exclusive access to all requisites for breeding (Pitelka 1959), regardless of the behavioral means by which the territory is established and maintained. Should the exclusive area be limited to nest site alone, the form of territory is Type B (Mayr 1935, Nice 1941). The latter territories may be grouped into colonies, resulting in high local population densities.

Territorial and colonial systems can be differentiated on the basis of patterns of habitat utilization. Foraging birds with Type A territory make relatively short trips radiating in all directions from their nests. Since territoriality is expected in situations of uniform food distribution (Brown 1964, Horn 1968) territory holders may uniformly use all parts of the territory (Stenger and Falls 1959). Colonial birds travel long distances to a food supply that may be unpredictable and patchy in distribution. Foraging trips need not radiate in all directions from the nest, but can be focused toward a concentrated food supply.

Although food resources usually are the primary factors influencing spacing system and territory size (Stenger 1958, Horn 1968, Cody and Cody 1972, Yeaton and Cody 1974), other resources, when limiting, will affect the spacing system. Limited nest sites may be largely responsible for coloniality in some species (Emlen 1971, Snapp 1976). The purpose of my study was to investigate the way in which food and nest resources might act together to determine a spacing system. When the abundance and distribution of one or both of these resources vary among populations of a single species, does the spacing system vary as a result?

Riparian habitats in the southwestern United States offer an opportunity to answer this question. A narrow band of trees and associated undergrowth may abruptly give way to grassland or scrub. Nest sites for tree-nesting species are patchily distributed over a large area and may be scarce. The more extensive surrounding habitat may provide abundant food but have no suitable nest sites. The riparian habitats provide both food and nest sites. I examined the spacing system of a common tree-nesting species in these habitats, the Northern Oriole (*Icterus galbula*). This species has been described as defending Type A territories (Bent 1958, Lowther 1975); however, Rising (1970) mentioned a tendency toward coloniality in Great Plains populations.

The Northern Oriole breeds throughout most of North America. It is a typical summer resident of cottonwoods (*Populus*) along streams in the Great Plains and of cottonwoods or sycamores (*Platanus*) in the southwest. These arid regions contain little habitat that is continuously forested with broad-leaved trees. Orioles nest almost exclusively in large trees and generally suspend their nests from branch tips (Bent 1958, Rising 1970); nest sites may be a limiting resource for such birds. I studied seven populations of *I. galbula* in California, Nevada, Utah, and Oklahoma during the springs of 1973–1975. Populations were examined with respect to their spacing and foraging patterns and the ecological factors which might be responsible for them.

STUDY SITES

One subspecies of Northern Oriole, formerly Bullock's Oriole (*I. galbula bullockii*) was studied at several locations which differ in type and density of vegetation.

Big Sycamore Canyon is a coastal canyon in Ventura Co., California. The riparian zone trees are sycamores (*Platanus racemosa*) and the steep canyonsides are covered with coastal sage vegetation. During 1973 all the vegetation was tall and dense as there had been no fires for at least twenty years. In addition to *I. galbula*, Hooded Orioles (*I. cucullatus*) nested in this canyon. They behaved in much the same way as the Northern Orioles with respect to nesting and foraging; for this reason, I obtained data on the foraging patterns of both species. This site was visited 26 times between 28 March and 3 June. In September 1973, a fire burned a large area of southern Ventura County, including Big Sycamore Canyon. During the spring of 1975 I returned to the canyon. All of the sage vegetation was regenerating and the sycamores had not been killed, but the height and density of riparian understory and sage components were greatly reduced. The study area for 1975 overlapped that for 1973. Between 2 April–13 June 1975, I made 17 visits to this site.

Rustic Canyon is located in the Santa Monica

TABLE 1. Characteristics of Northern Oriole study sites.

Study site	Size (hectares)	Number of pairs	Bird density (pairs/ha)	Mean nearest neighbor distance (m)	Nest site density (trees/ha)	Percent of foraging trips in nest habitat	Total nest habitat vegetation[a]	Nest habitat undergrowth vegetation[a]	Non-nest habitat vegetation[a]
Salt Plains, OK	1.0	17	16.8	12.7	116	16	–	1.9–2.8	–
Little Cottonwood Lake, NV	1.0	9	9.4	53.5	47	29	45.7	2.0	5.8
Juniper Grove, CA	2.4	8	3.2	29.8	5	60	52.7	11.8	81.1
Sycamore Flat, CA	0.8	3	4.0	40.6	27	81	64.0	18.3	6.7
Big Sycamore Canyon, CA 1973	2.5	8	3.2	34.4	25	57	–	–	–
Big Sycamore Canyon, CA 1975	1.0	10	10.0	16.4	19	20	71.8	9.3	8.3
Rustic Canyon, CA	0.8	4	4.9	34.4	17	50	138.8	all canopy	61.8
Green River, UT	2.4	7	3.0	40.6	50	54	182.8	31.9	17.8

[a] Vegetation measured as m^2 per 30.5 m transect (see Methods).

Mountains of Los Angeles Co., California. The surrounding hillsides are covered with mature chaparral. The canyon floor has scattered, large sycamores, oaks (*Quercus agrifolia*), and along the stream a continuous cover of tall willows (*Salix*). Little light penetrates the canopy, so there is essentially no understory. Seven visits were made to this site between 22 April and 14 June 1975.

Sycamore Flat is located near Valyermo, Los Angeles Co., California in the southern portion of the Antelope Valley. It lies within a broad valley at the base of the San Gabriel Mountains. The trees of the riparian habitat are predominantly large sycamores, with a broad band of willows and *Baccharis viminea* adjacent to the creek. On the desert hillsides there are low shrubs such as *Salvia* and *Eriogonum* as well as scattered *Yucca schidigera*. Between 21 May and 17 June 1975 six visits were made to this study area.

Juniper Grove is located in the Antelope Valley about 24 km W of Sycamore Flat near Littlerock, Los Angeles Co., California. The study area was on the shore of a lake formed by Littlerock Dam. The sandy beach is bordered by a broad band of widely scattered cottonwoods (*Populus fremontii*), junipers (*Juniperus californica*), and Chinese elm (*Ulmus parvifolia*). The dominant understory shrub is sagebrush (*Artemisia tridentata*). Along portions of the shoreline are dense stands of willows; most of these are some distance from the cottonwoods and associated trees in which the orioles were nesting. These willows were used by foraging orioles, while the relatively barren desert slopes were not. Twelve visits were made to Juniper Grove from 24 April–17 June 1975.

Little Cottonwood Lake is located on the Stillwater National Wildlife Refuge, near Fallon, Churchill Co., Nevada. It is a small lake bordered by a thin band of cottonwoods. Beneath the trees and extending beyond them is Great Basin Desert vegetation including such shrubs as *Sarcobatus* and *Atriplex* spp. The cottonwoods grow along 483 m of shoreline and most are at the very edge of the lake. The riparian zone is roughly defined as the area under the cottonwood canopy. Between 25 May and 26 June 1973, 15 visits were made to this site during two periods: 24–29 May and 11–26 June.

Green River is bordered by an almost continuous belt of cottonwoods. I chose a site 12.5 km N of U.S. Route 50 in Emory Co., Utah on the west bank of the river because here the usually narrow band of riparian vegetation broadens. Instead of an abrupt transition from trees to scrub or desert as in the previously described sites, here the trees become progressively smaller and sparser farther away from the river. In addition, the undergrowth becomes shorter and less complex in structure. Birds nesting in large trees near the river did not venture into the bordering barren desert, which rises abruptly into cliffs about 1.5 km from the river. All nests I found were within 150 m of the riverbank and I considered the trees (which were smaller) beyond that distance to be non-nest habitat. I spent 24–26 June 1975 at this site.

The Baltimore subspecies of Northern Oriole (*I. galbula galbula*) was also included in this study, only at the Salt Plains National Wildlife Refuge near Jet, Alfalfa Co., Oklahoma. My work was done at one end of and beyond a primitive camping area on the shore of a large saline lake. The campground has vegetation typical of the rest of the shoreline, but herbaceous vegetation is periodically mowed. The dominant tree species is cottonwood (*P. sargentii*), which is mixed with some willow and introduced Russian olive (*Elaeagnus angustifolia*). On one side the cottonwoods are bordered by sandy beach and tamarisks (*Tamarix gallica*) and on the other side by a dense thicket separating the lake and refuge from extensive cultivated land. The thicket is mulberry (*Morus*) in one section and locust (*Robinea pseudoacacia*) in another. I remained on the study area from 13–20 June 1974.

Maps of all study areas are given in Pleasants (1977). Table 1 lists sizes of all study areas and numbers of nesting pairs of Northern Orioles.

METHODS

Detailed maps of all study areas were made. Included on these maps were the locations of all trees and large shrubs, various landmarks, and oriole nests. Nearest-neighbor distances for nests and sizes of study areas were obtained either in the field or from these maps.

Accurate data on numbers of breeding pairs could be obtained during the study periods. At most sites, observations were conducted throughout all or most of the breeding season, from before or at the start of nest-building to the fledging of young. All of these populations were single-brooded. During this work it became obvious that nesting in these populations was highly synchronized. At Big Sycamore in 1973, the first nestlings hatched on 14 May. By 30 May, only one of the eight pairs which nested that season still had young in the nest. At the same site in 1975, all 10 clutches hatched between 28 May and 9 June. Even at study sites visited over a brief span of time I could correctly estimate the numbers of breeding pairs. At some time during the eight days spent at Salt Plains, 15 of the 17 nests contained young. Two other nests at which no activity was noted were assumed to have fledged young and were included in the count of active nests. Seven nests were located at Green River and all contained young. I neither saw any sign of nest building on the part of other pairs nor found inactive nests.

Foraging patterns were determined by observing each pair on several days during the period when it was feeding nestlings. For periods of 30–60 min I noted for each foraging trip: sex of the adult making the trip, time of departure from and next arrival at the nest, and destination where foraging began. The accuracy of destination information varied with position of observer and visibility at a particular site. Generally this information included direction of flight from nest, habitat in which foraging occurred, and, if possible, precise location (with a map used as reference). A total of 5922 min of such foraging data were obtained from all sites combined. For individual sites, the total foraging observation period ranged from 280–1223 min.

The relatively sessile foods taken by orioles—caterpillars and other insect larvae, occasional fruit and nectar, slow-moving insects (pers. observ.)—are difficult to sample directly. I estimated food data indirectly by measuring foliage density. Cody (in press a and b) has shown that the number of insects captured on boards coated with a sticky substance is related to the amount of foliage at the capture location. Since orioles are generalized foragers with respect to height and substrate (pers. observ.), vegetation at all heights was included in my transects.

To sample foliage density, I made transects in both nest and non-nest habitats at each site with the exception of Big Sycamore in 1973 and Salt Plains. Nest habitat undergrowth was estimated for Salt Plains from the map made of the study area. Transects were 30.5 m (100 ft) in length; several were made in each habitat at a site (6–20 for nest habitat, 3–5 for non-nest habitat, depending on size of study area). A 30.5-m tape was stretched along the ground and all vegetation at any height directly above the tape was included in the sampling. All distances under foliage and the vertical extent of the foliage at those points were recorded. From this information, the area of undergrowth vegetation intersected by a vertical plane 30.5 m wide was calculated by multiplying the total width of all understory plants along the transect by the mean height of those plants. To obtain total vegetation area the same sort of calculation was made for canopy and the two figures added together. An average transect for each habitat was obtained by averaging all transects within that habitat. The result was a representative area (m^2) of foliage intersected by a vertical plane 30.5 m wide (Table 1).

For each study area, the number of potential nest sites was assessed by counting trees of suitable species. Generally these were either sycamores or cottonwoods. In some cases elms were present and were included.

RESULTS AND DISCUSSION

PATTERNS OF ORIOLE SPACING

Both the density of nesting oriole pairs and the mean nearest neighbor distances (Table 1) indicate a great variability in the degree of spacing among the eight study sites. For all sites, the riparian woodland was fully utilized and for this reason nearest-neighbor distance declined as bird density rose. There were areas of exclusive use within the nest habitats. The foraging areas of neighboring pairs within the riparian zone did not overlap (Pleasants, unpubl. data). I found only two instances of more than one pair nesting in a single tree. One of these was in the largest tree at Little Cottonwood Lake; the distance between the two nests was somewhat more than 10 m. The second was at Big Sycamore Canyon in 1975; one pair placed its nest about 7 m above that of an already established pair. In both cases, the second pair to establish itself had a male in first-year, female-like plumage. The birds of these two study areas nested in high densities, using the nest habitat for only a small proportion of their foraging trips (Table 1).

FORAGING PATTERN

I divided foraging trips into two categories: those within the nest habitat and those to the surrounding, non-nest habitat. All populations used both habitats, although the relative importance of the two habitats varied among sites. Trips within the exclusive areas in the nest habitat were distributed in and around the nest trees. Because these areas provided only some of the food necessary for adults and young they were classified between Types A and B. Trips outside of the nest habitat generally favored certain directions. A pair might fly in the same direction onto a hillside for many trips and for several days in a row. Several pairs were often seen using the same broad areas of non-nest habitat, yet aggressive interactions were rare, occurring only when individuals approached within a few meters of one another. I could not assign feeding territories to particular pairs, or see any sign of social facilitation in foraging.

The proportion of the total number of foraging trips that was made within the nest habitat is listed for each study site in Table 1. This proportion is a population mean, calculated by dividing the number of trips made within the nest habitat (by all pairs) by the total number of trips made to both habitats. The use of nest habitat varied from 16% (Salt Plains) to 81% (Sycamore Flat). Populations

TABLE 2. Correlations between environmental parameters and bird density and foraging pattern.

	Bird density		Percent use of nest habitat for foraging	
Parameter	r	P	r	P
Tree density	.77	$< .05$	–.55	n.s.
Total nest habitat vegetation	–.46	n.s.	.11	n.s.
Nest habitat undergrowth vegetation	–.74	n.s.	.63	n.s.
Non-nest habitat vegetation	–.50	n.s.	.25	n.s.
$\frac{\text{Nest habitat undergrowth vegetation}}{\text{Non-nest habitat vegetation}}$	–.50	n.s.	.65	n.s.

separated by only a few miles (Juniper Grove and Sycamore Flat) or the same population under different environmental conditions (Big Sycamore before and after fire) differed substantially in proportion of trips made within the nest habitat. This suggests that the pattern of foraging is flexible within and between populations and is a facultative response to the environment; the degree of territoriality corresponds to the importance of the nest habitat as a foraging area. Few cases of such intraspecific variability in a social system are known in birds; for one example, see Walsberg (1977).

EFFECTS OF ENVIRONMENTAL PARAMETERS ON BEHAVIOR

If nest site limitation is important for orioles, the number of nest sites in an area should be related to the number of nesting birds. There was a significant positive correlation ($r = .77$, $P < .05$) between the abundance of nest sites (trees/ha) and that of birds (pairs/ha). Correlations between bird density and other environmental parameters were not significant (Table 2), although nest habitat undergrowth approaches the critical value and the correlation coefficient is nearly as high as that for tree density. Values for all parameters are listed in Table 1.

Although nest site and bird density were significantly correlated, a substantial amount of unexplained variance remains. Some scatter may be resolved by considering an additional factor. The nearly significant relationship between bird density and nest habitat undergrowth (Table 2) is of the form predicted on the basis of defendability (Brown 1964), if undergrowth is a good index of food availability. As food becomes more plentiful, defense of a territory should become more advantageous. I assumed the volume of vegetation in the subcanopy layers to be proportional to abundance of insects; orioles foraged in the canopy as well, but measures of foliage which include canopy also include nest site abundance. In order to deal solely with food as a variable, undergrowth seems the only choice. It should be noted that undergrowth and tree density are independent variables ($r = -.3$, $P > .05$). Stenger and Falls (1959) found that territory size in Ovenbirds (*Seiurus aurocapillus*) increased as brush and ground vegetation decreased in density, leading to my suggestion that undergrowth is a good indicator of food abundance.

A regression line can be fitted to the data on bird density and tree (nest site) density and the residuals calculated. The degree of positive or negative deviation from the predicted relationship may be explained by additional variables such as the abundance of food. Plotting the residuals for bird density against nest habitat undergrowth, I found a significant negative correlation ($r = -.81$, $P < .05$). No other variable was significantly correlated with these residuals. There were fewer birds than predicted by nest site density if food was abundant and more birds than predicted if food was scarce.

Surprisingly, food quality of the surrounding habitat (non-nest habitat vegetation) was a poor predictor of oriole spacing and foraging behavior (Table 2) although that habitat was used to some extent by all populations. When considered in relation to the riparian habitat, as the ratio nest habitat undergrowth/non-nest habitat vegetation, its importance is more apparent. The positive correlation of .65 between this ratio and percent use of nest habitat is suggestive, but not significant (Table 2). It suggests that the better the nest habitat in comparison to the surrounding one as a source of food, the more foraging will be done in the former. Although the major determinants of the spacing system can be found by considering only nest habitat, the quality of the surrounding habitat also is influential.

To be certain that Northern Orioles are tending toward colonial behavior their foraging patterns must be examined. I expect that as birds fill nest sites in a circumscribed breeding habitat, distances between nests will decrease and the amount of foraging each pair can do within the nest habitat will decline.

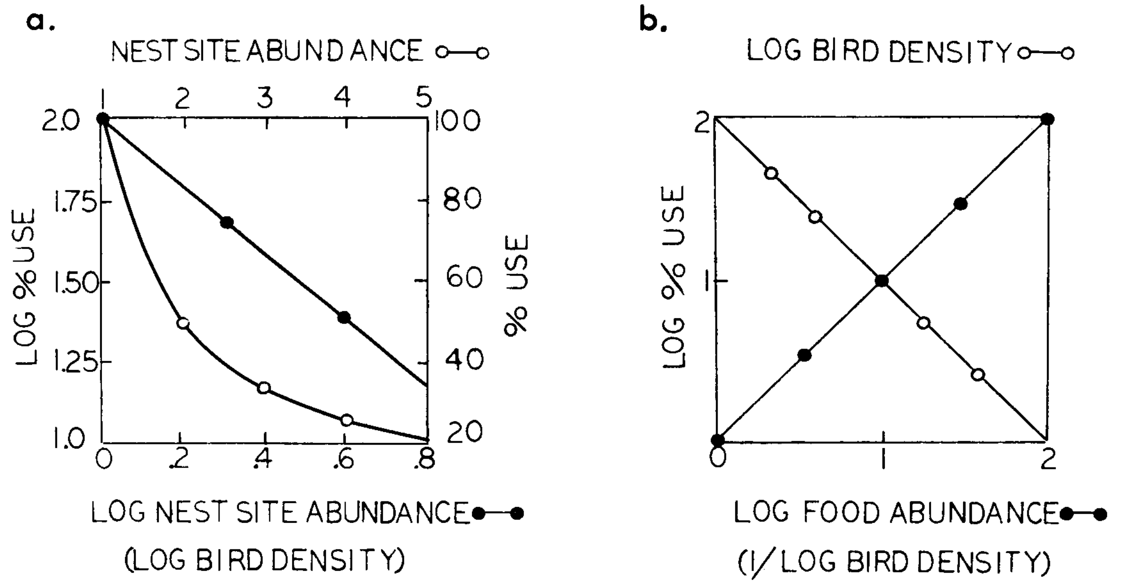

FIGURE 1. Theoretical predictions of foraging pattern. (a) Predicted relationship between nest site abundance and percent use of nest habitat with food abundance held constant. In this case bird density is directly proportional to nest site abundance. (b) Predicted relationship between food abundance and percent use of nest habitat with number of nest sites held constant (solid circles). Relationship between bird density and percent use of nest habitat (open circles) based upon negative correlation between food abundance and bird density.

As foraging within the nest habitat decreases, birds must search elsewhere for food and use of the surrounding habitat must increase. I have shown that two important factors (density of nest sites and of food) act upon bird density. How should these affect foraging?

I first examine a hypothetical situation where food density is constant over a variety of sites which differ only in nest site abundance. In this case nest site availability will be the only variable influencing bird abundance. At one site there is nesting space for only one pair of birds and just enough food for the adults and their young. At a second location there are two nest sites and two pairs of breeding birds. But each pair can obtain only 50% of its food needs within the nest habitat and the remaining 50% must be obtained elsewhere. If the number of nest sites (and of birds) is doubled to 4, only 25% of the food is obtainable in the nest habitat and so on. The result is shown in Figure 1a. The relationship is hyperbolic and can be plotted on a log-log scale as a straight line of slope = -1.0.

A similar analysis can be made for the expected effects of food abundance if nest site abundance is held constant. The initial condition is that of several pairs all doing 100% of their foraging within exclusive territories which each contain 100 arbitrary units of food. If food abundance is halved and all pairs remain, now only 50% of their food needs can be satisfied within the nest habitat. If food is halved again, only 25% of their foraging could be supported by the nest habitat and 75% must be done outside. In this situation the relationship between food abundance and percent use of nest habitat (percent use) is linear with positive slope; Figure 1b plots this on a log-log scale, solid circles.

Given that the abundance of nest sites and food both influence bird density, and given the theoretical relationships between these two variables and percent use, what is the relationship between bird density and percent use? The expected nature of the relationship can be seen in Figures 1a and 1b. In the development of Figure 1a, bird density was considered to be directly proportional to nest site abundance. Thus, log (logarithm) bird density is negatively related to log percent use. In the case of Figure 1b, the relationship between food abundance and bird density must be determined before a prediction can be made. Bird density and nest habitat undergrowth (food) were not significantly correlated (Table 2). However, if these two variables are transformed to logs, there is a significant negative correlation between them ($r = -.83$, $P < .05$). This means that there is a negative linear relationship between log food abun-

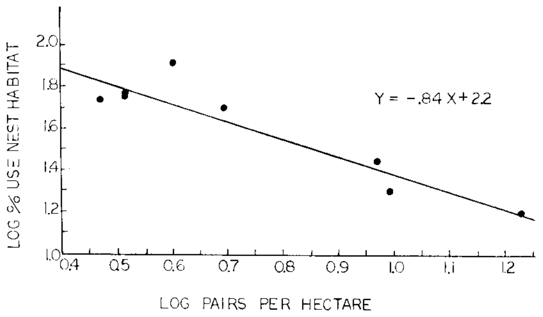

FIGURE 2. Proportion of foraging trips made within the nest habitat as a function of number of nesting pairs per hectare; r = –.93, $P < .01$.

dance and log bird density and thus a negative relationship between log bird density and log percent use (Figure 1b, open circles).

A theoretical consideration of either nest site or food abundance leads to the conclusion that log bird density and log percent use of nest habitat should be related in a negative, linear fashion. When the actual data for *I. galbula* are plotted, a highly significant negative correlation between log pairs per hectare and log percent use of nest habitat is obtained (Fig. 2, r = –.93, $P < .01$). The relationship is linear and the slope is negative (–.84) as predicted. The two environmental parameters have opposing effects on how the nest habitat is filled, so both must be considered in order to predict bird density. Bird density in turn is an excellent predictor of foraging pattern. Birds process the important information about their nest habitat and translate this into a site-specific nesting density. This in turn dictates the amount of foraging possible in that habitat. The availability and, to a lesser extent, the productivity of the surrounding habitat allow the system to operate.

CONCLUSIONS AND SUMMARY

Figure 3 summarizes the aspects I consider to be important in understanding spacing patterns in the Northern Oriole. Any riparian site can be represented by a point on the plane whose axes are nest site density and nest habitat food density. The plane is contoured with respect to the expected degree of territoriality for populations in each section. I assume that for all cases an alternative foraging habitat surrounds the riparian one. For any given nest site density, as food increases, populations can be arranged along a continuum from Type B (nesting) territoriality, through semi- (nesting and part of feeding) territoriality, to Type A (all-purpose) territoriality. This is due to the increase in defendability of their food supply. For any given level of food availability, as nest sites increase so will nesting bird density, so that the Type B territories of the bottom section become colonies. Most importantly, as nest site density increases, the threshold for any increase in defense of territory lies at a greater level of food density because of increased pressure from birds trying to use those nest sites. For any nest site density, there comes a point where Type A territoriality is the predicted behavior because of high food density and perhaps large extent of the riparian habitat.

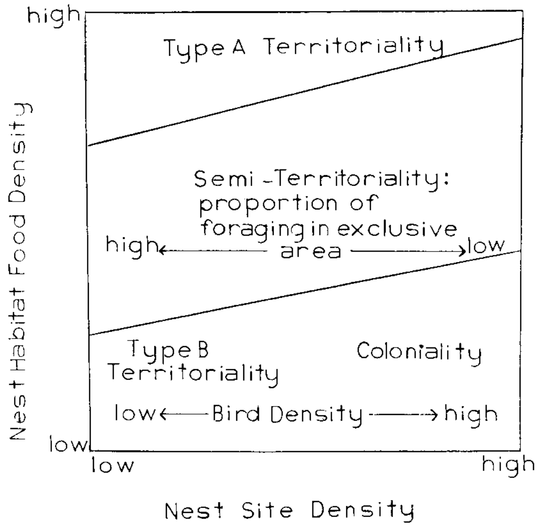

FIGURE 3. Predicted spacing systems for riparian birds in a variety of environmental conditions. See text.

This pattern should be found in other typically riparian birds of a body size large enough to permit utilization of both habitats. Hespenheide (1964) studied several species of kingbirds (*Tyrannus*) in Arizona and found that while they nested in riparian situations, they foraged in the surrounding habitats. The Western Kingbirds (*T. verticalis*) at Little Cottonwood Lake behaved in a similar manner. Carothers et al. (1974), in a discussion of foliage height diversity and bird species diversity among riparian birds in Arizona, commented on the apparent lack of Type A territoriality in many of the species. They suggested that productivity of the adjacent habitats and lack of territoriality account for the high population densities they found. They further proposed that the lack of territoriality was due to a lack of competition for food. The arguments I have presented in this paper may provide a more satisfactory explanation for their observations. In their study, the homogeneous cottonwood habitats with very little undergrowth (shrub) complexity were the ones with less territorial behavior (36% of species, 22% of pairs with Type A territory) than the more complex mixed woodlands (60% of species, 57% of pairs territorial). This indicates that quality of nest habitat—its defendability—is important in their systems.

My study has shown that the abundance of nest sites and of food act in opposition to one another in their effects on the spacing pattern of Northern Orioles in riparian woodland. The surrounding treeless habitat offers a food supply and serves as a buffer allowing territoriality to be reduced in accordance with the demand for nest sites and with the worth of the nest habitat. In its extreme, such a system becomes a colonial one, although not for the usually cited reasons of highly clumped or unpredictable food supply.

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LITERATURE CITED

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers and allies. U.S. Natl. Mus. Bull. 211:1–549.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

Carothers, S. W., R. R. Johnson, and S. W. Aitchison. 1974. Population structure and social organization of southwestern riparian birds. Am. Zool. 14:97–108.

Cody, M. L. In press, a. Habitat selection and interspecific interactions among the sylviid warblers of northern Europe. Ecol. Monogr.

Cody, M. L. In press, b. Species packing in insectivorous bird communities: density, diversity, and productivity. Proc. XVII Int. Ornithol. Congr. (1978).

Cody, M. L., and C. B. Cody. 1972. Territory size, clutch size, and food in populations of wrens. Condor 74:473–477.

Emlen, S. T. 1971. Adaptive aspects of coloniality in the Bank Swallow. Abstr. Am. Zool. 11:628.

Hespenheide, H. A. 1964. Competition and the genus *Tyrannus*. Wilson Bull. 76:265–281.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird. Ecology 49:682–694.

Lowther, P. E. 1975. Geographic and ecological variation in the family Icteridae. Wilson Bull. 87:481–495.

Mayr, E. 1935. Bernard Altum and the territory theory. Proc. Linn. Soc. N. Y. 45–46:1–15.

Nice, M. M. 1941. The role of territory in bird life. Am. Midl. Nat. 26:441–487.

Pitelka, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233–264.

Pleasants, B. Y. 1977. Ecological factors affecting the breeding dispersion patterns of some North American orioles (*Icterus*). Ph.D. diss. University of California, Los Angeles.

Rising, J. D. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19:315–351.

Snapp, B. D. 1976. Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. Condor 78:471–480.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75:335–346.

Stenger, J., and J. B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125–140.

Walsberg, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilogonatidae). Univ. Calif. Publ. Zool. 108:1–63.

Yeaton, R. I., and M. L. Cody. 1974. Competitive release in island Song Sparrow populations. Theor. Popul. Biol. 5:42–58.

Department of Biology, University of Missouri-St. Louis, St. Louis, MO 63121. Accepted for publication 24 July 1978.