GEOGRAPHIC VARIATION IN THE PLACEMENT AND STRUCTURE OF ORIOLE NESTS

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The placement and structure of bird nests are often believed to be adaptive in minimizing adverse climatic effects or reducing predation (Collias 1964). The nests of certain species are placed to be inaccessible to predators (Kendeigh 1942), to maintain an amenable microclimate (Calder 1973, Corley Smith 1969, Dorst 1962, Pearson 1953), and to reduce wind stress (Chapman 1928, Collias and Collias 1964). The structure has been said in some cases to conserve warmth (Schaefer 1953), to discourage snakes from entering the nesting chamber (Chapman 1928, Collias and Collias 1964, Crook 1960), and to protect young from intense sunlight (Collias and Collias 1964).

Adaptive variation among species in bird nests has been discussed, i.e., different species coping with radically different biological and climatic conditions (Holcomb and Twiest 1968). However, similar variation would be anticipated (in the absence of physiological and behaviorial mitigating factors) intraspecifically since species with a wide geographic range also are confronted with a wide variety of nesting conditions.

This study relates intraspecific variation in the placement and structure of the nests of Northern Orioles (*Icterus galbula*; both Baltimore and Bullock's subspecies groups) and Orchard Orioles (*I. spurius*) to local climatic and biotic conditions. These orioles are amenable to such a study since their nests persist into the early winter months when the leaves have fallen from the trees; it was imperative to this study that all nests in a given area be found, in order to preclude a sampling bias. The Baltimore-Bullock's oriole "hybrid zone," an area where heat stress may well affect the distribution of these birds (Rising 1969, 1970), is considered carefully. Any adaptations in nesting would be expected to be especially evident within this zone as interlocal contrasts in nesting strategies may be correlated with the previously demonstrated interlocal variation in morphology and physiology (Rising 1969, 1970, Sibley and Short 1964, Sutton 1968).

METHODS

Twenty areas were sampled—two in southern Ontario (2.0 km NE of Campbellville, Halton Co., and 3.2 km NE of Pickering, Ontario Co.), one in southern Quebec (Chomedey, ville de Laval), and the remainder in the Great Plains region of the United States (forming a cross section through the Baltimore-Bullock's oriole hybrid zone). The latter region includes samples along the Platte, Smoky Hill, and Cimarron rivers, as well as some in the Texas Panhandle; these localities are shown in figure 1. At all plains localities except Guthrie, trees grew in approximately linear stands along streams and geographic variation in vegetation was minimal. During November and December of 1972 and 1973 I attempted to find all oriole nests within these areas. Only nests from the previous nesting season were examined to preclude the bias of the different capacities of nests to persist on trees after a winter.

In the Great Plains, Northern Oriole nests were characterized according to the index values of the birds for the localities given in Rising (1970:328); a value greater than 24.5 was arbitrarily taken to be Bullock's Oriole, less than 4.7, Baltimore Oriole, and between 4.8 and 24.4, hybrids. The 0.05 level of significance was accepted as standard. Only localities with five or more nests were included in the analyses. Samples for the Orchard Oriole were not large enough for geographic comparison. Data for the two years of the study were pooled since there were few annual differences.

I measured the following aspects of nest placement from the middle of each nest *in situ*: height from the ground, distance from the top of the tree, distance from the tree perimeter (the distance to the edge of the branch on which the nest was attached or to the tip of the longest branch on the tree covering the nest), distance from the trunk, diameter of the largest branch within 30 cm, and compass direction on tree (detailed character descriptions are in Schaefer 1974). Values for the first two characters were obtained with a SUUNTO model PM-5/3600 clinometer. Other values were measured whenever possible.

Tree heights and the radius of the crown at the level of the nest were also examined to determine the effects of vegetation on nest placement. Correlations were tested between the height of the nest from the ground and the distance from the nest to the top of the tree and tree height, and the distance of the nest from the tree perimeter with its trunk distance and the radius of the crown at the level of the nest.

An analysis of variance (ANOVA) was used to test for interlocal taxonomic (localities grouped by taxon: Baltimore Orioles, hybrid zone, and Bullock's Orioles), and regional (localities grouped by the three river systems, Texas Panhandle, and Ontario-Quebec) differences. Geographic variation was also analyzed using a principal component analysis (Sneath and Sokal 1973), where character loadings are computed from a correlation matrix. The data were standardized.

The frequency distributions of the compass directions of nest placement were tested against random and equiprobable expected distributions using a G-test. Nonsignificance for both was taken as an indication of some preference.

The characters of nest structure considered were:

The Condor 78:443–448, 1976

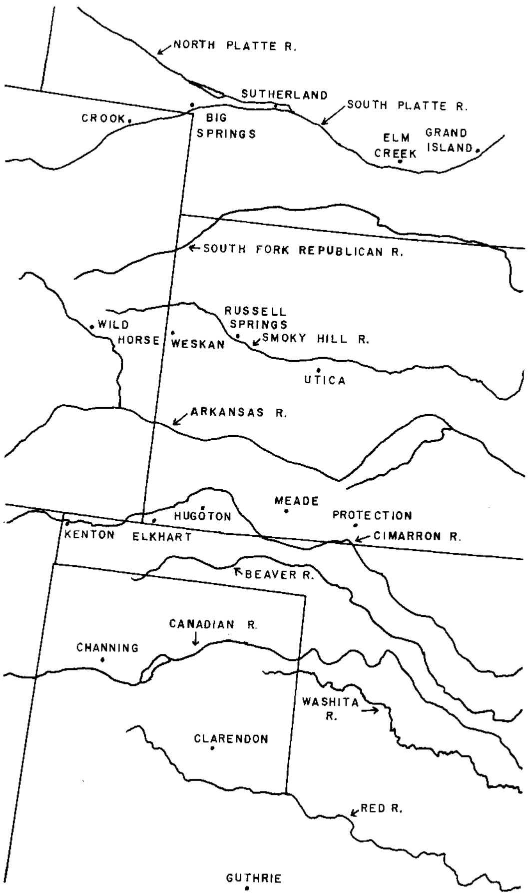

FIGURE 1. Map of the Great Plains region of the United States. The study areas were: 1) 12.0 km S of Grand Island, Hall Co., Neb.; 2) 3.2 km S of Elm Creek, Buffalo Co., Neb.; 3) 1.5 km S of Sutherland, Lincoln Co., Neb.; 4) Big Springs, Deuel Co., Neb.; 5) 2.4 km S of Crook, Logan Co., Colo.; 6) 1.0 km S of Wild Horse, Cheyenne Co., Colo.; 7) 4.8 km N of Weskan, Wallace Co., Ks.; 8) 12.0 km ESE of Russell Springs, Logan Co., Ks.; 9) 15.2 km NNW of Utica *in* Gove Co., Ks.; 10) 24.8 km S of Protection, Commanche Co., Ks.; 11) 32.8 km S of Meade, Ks., *in* Beaver Co., Okla.; 12) 28.8 km N of Hugoton *in* Grant Co., Ks.; 13) 12.8 km N of Elkhart, Morton Co., Ks.; 14) 5.6 km NE of Kenton, Cimarron Co., Okla.; 15) 19.2 km N of Guthrie *in* Cottle Co., Tex.; 16) 35.2 km S of Clarendon *in* Hall Co., Tex.; and 17) 18.4 km S of Channing *in* Oldham Co., Tex.

depth of the nest, diameter of the opening and cup, number of attachments, length of the longest attachment, and the diameters of the thinnest and thickest supports. Measurements were made by passing a thin metal rod through the nest and crossing a second rod at right angles at the point of measurement; the length from the edge of the rod to the intercept was read against a ruler. The diameter of the nest cup and the depth of the nest included the thickness of the nest wall and bottom, respectively. Statistical treatment was the same as for the placement characters. The number of attachments was examined only qualitatively.

TABLE 1. Means of the nest placement characters for the Northern Oriole given by locality.[a]

Locality	Height	Distance to top	Perimeter	Trunk	Branch diameter
Grand Island, Neb.	8.3	5.7	2.3	2.7	2.6
Elm Creek, Neb.	9.2	4.5	1.7	3.0	2.5
Sutherland, Neb.	8.7	5.2	2.4	3.5	2.1
Big Springs, Neb.	10.2	3.9	1.4	2.1	2.5
Crook, Colo.	7.2	8.5	2.6	5.0	1.2
Wild Horse, Colo.	10.2	3.2	1.2	2.1	2.3
Weskan, Ks.	6.7	5.1	1.5	2.5	3.0
Russell Springs, Ks.	8.7	6.1	1.2	2.6	2.8
Utica, Ks.	6.7	6.5	1.1	3.6	2.3
Protection, Ks.	6.9	4.2	1.8	1.9	3.5
Meade, Ks.	7.4	3.6	1.2	1.3	2.9
Hugoton, Ks.	9.7	4.1	1.2	1.7	3.9
Elkhart, Ks.	8.4	3.9	1.3	2.3	3.0
Kenton, Okla.	7.3	3.4	1.0	1.5	3.2
Guthrie, Tex.	4.9	2.7	0.9	2.2	1.4
Clarendon, Tex.	3.7	0.9	0.5	0.7	1.6
Channing, Tex.	7.7	5.1	1.1	2.2	2.3
Campbellville, Ont.	8.9	3.0	0.6	2.2	1.6
Pickering, Ont.	9.6	2.6	0.4	0.7	1.7
Laval, Que.	11.1	2.1	3.7	1.3	1.5

[a] Measurements in meters, except for branch diameter which is in centimeters.

RESULTS

NORTHERN ORIOLE

I obtained placement data for 516 Northern Oriole nests. Character means are given by locality in table 1. A log transformation $(Y + 1)$ of the data was used for the ANOVA. All characters showed significant local and regional differences, but there were no significant taxonomic differences.

The correlations between nest placement and the vegetational parameters were significant for most localities, and all those for the localities combined were significant. Correlations among placement variables themselves were also significant.

The results of the principal component analysis for the Northern Oriole nest placement are shown in figure 2. Component I has high correlations with the distance of the nest from the top of the tree and trunk distance, II with the distance of the nest from the tree perimeter and the diameter of the largest branch within 30 cm of the nest, and III with the height of the nest from the ground. All these correlations were positive; there were some negative correlations on the lower scores.

Only one locality, Crook (CR), is separated along the first component. For the second

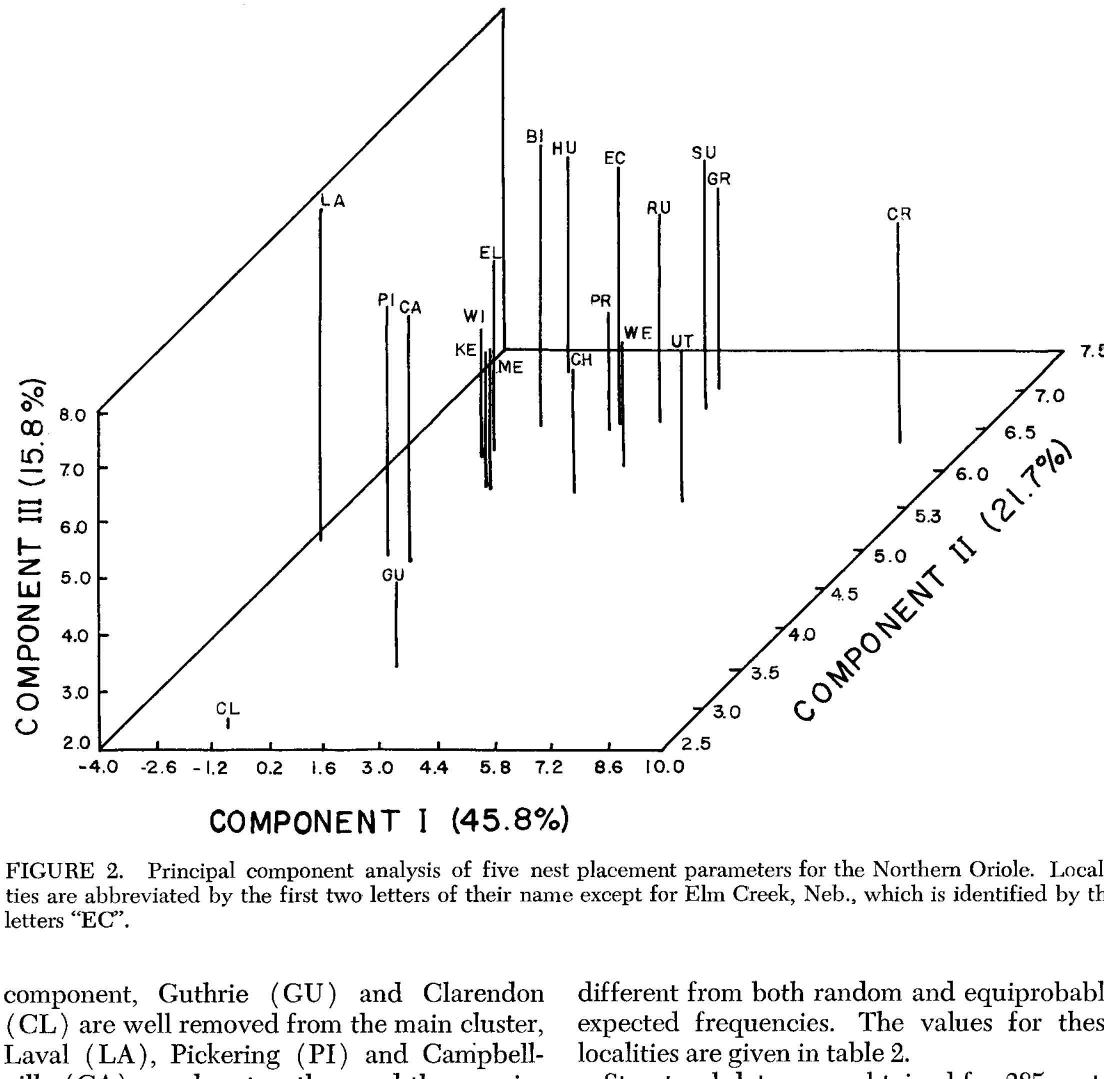

FIGURE 2. Principal component analysis of five nest placement parameters for the Northern Oriole. Localities are abbreviated by the first two letters of their name except for Elm Creek, Neb., which is identified by the letters "EC".

component, Guthrie (GU) and Clarendon (CL) are well removed from the main cluster, Laval (LA), Pickering (PI) and Campbellville (CA) are close together, and the remainder of the Great Plains localities form a large central group. For the third component the Texas Panhandle (GU, CL, CH), Cimarron (PR, ME, HU, EL, KE), and Smoky Hill (WE, RU, UT, WI) localities have low scores, and the Ontario-Quebec (CA, PI, LA) and Platte (GR, EC, SU, BI, CR) localities high scores.

For the frequencies of the compass directions of nest placement, only six of the localities had distributions that were significantly different from both random and equiprobable expected frequencies. The values for these localities are given in table 2.

Structural data were obtained for 285 nests. The means for the characters considered are presented by locality in table 3. The ANOVA showed significant geographic differences for the diameters of the nest opening, the nest cup, and the thickest support. All characters except the diameter of the thinnest support were significant for both taxonomic and regional groupings. The principal components analysis of nest structure revealed no geographic trends.

Nest attachments most commonly numbered

TABLE 2. Compass direction of nest placement for the six Northern Oriole localities where there appears to be some preference. Values indicate the number of nests facing in each direction.

Locality	N	NE	E	SE	S	SW	W	NW
Elm Creek, Neb.	3	6	0	3	11	2	0	3
Utica, Ks.	6	0	0	0	2	2	0	2
Weskan, Ks.	0	1	0	0	6	1	1	0
Elkhart, Ks.	18	5	2	1	5	2	3	4
Wild Horse, Colo.	2	2	0	6	1	0	1	1
Campbellville, Ont.	4	6	0	3	3	2	0	1

TABLE 3. Means of nest structure characters (in cm) for the Northern Oriole, given by locality.

Locality	Depth	Opening	Cup	Longest attachment	Thinnest support	Thickest support
Elm Creek	8.7	6.6	8.2	6.7	0.3	0.6
Sutherland	9.4	6.2	8.3	6.9	0.3	0.8
Big Springs	9.6	6.6	8.9	5.1	0.3	0.7
Crook	9.6	8.2	9.3	5.8	0.2	0.8
Wild Horse	9.8	7.5	8.7	5.4	0.3	0.9
Weskan	10.5	6.7	8.5	5.2	0.3	0.8
Russell Springs	8.7	8.0	8.7	5.4	0.3	0.8
Utica	8.4	7.1	8.4	5.7	0.3	0.6
Protection	8.8	6.7	8.4	5.3	0.2	0.6
Meade	10.3	6.6	8.5	5.3	0.3	0.7
Hugoton	9.9	6.6	9.1	4.4	0.2	0.7
Elkhart	9.9	6.9	8.1	6.3	0.3	0.7
Kenton	9.8	8.7	9.5	6.5	0.3	0.9
Guthrie	10.6	7.6	8.9	5.9	0.3	0.8
Clarendon	10.5	7.9	8.9	6.2	0.2	0.9
Channing	10.7	7.7	9.5	5.1	0.2	0.9
Campbellville	10.4	6.5	8.7	6.8	0.3	0.6
Pickering	10.2	6.8	8.9	6.1	0.2	0.6
Laval	8.5	7.8	9.3	7.3	—	—

3–5, the Texas Panhandle localities having somewhat more.

ORCHARD ORIOLE

I examined the placement of 138 Orchard Oriole nests. Samples were too small to permit geographic comparisons. When the localities were grouped by zones (corresponding to the Baltimore Oriole, hybrid zone, and Bullock's Oriole ranges), variations in the height of the nest from the ground and the diameter of the largest branch within 30 cm of the nest were found to be significant. Regional (grouped by the three rivers and the Texas Panhandle) differences occurred for the tree perimeter and trunk distances. Correlations between nest placement and vegetational parameters, and between the placement variables themselves, were all significant. In only one locality was the frequency distribution for compass direction of placement significantly different from both random and equiprobable expected frequencies.

Structural data were available for 33 nests. Only the diameter of the opening of the nest in the groupings by zones varied significantly.

DISCUSSION

Although the nest placement of the Northern Oriole varies geographically, this can be explained mostly by differences in vegetation. Only the differences between Ontario-Quebec and the Great Plains localities, and the compass direction of placement for six localities, seem to be independent of this influence. Nests at Ontario-Quebec were placed higher in the tree and closer to the tree perimeter. The decrease in the diameter of the largest branch within 30 cm of the nest in Ontario-Quebec may be related to this change. Alternatively, orioles in the Great Plains could be nesting on thicker, more stable branches due to greater wind stress. Nests in the Great Plains are more securely attached to the tree than in Ontario-Quebec, which seems to indicate that wind stress is an important factor. There is an increase in the diameter of the thickest support, and a slight increase in the number of nest attachments (notably in the Texas Panhandle).

Predation by squirrels may also be a contributing factor. Orioles may build on the tips of branches high in trees to make their nests inaccessible to squirrels where such are abundant, at the risk of having their nests blown out by strong winds (Rising 1970).

The importance of compass direction of nest placement was mentioned by Chapman (1928) for the Wagler's Oropendola (*Zarhynchus wagleri*), and by Collias and Collias (1964) for the White-browed Sparrow Weaver (*Plocepasser mahali*). In each case nests were placed on the leeward sides of trees. The investigators speculated that this reduces the risk that the nest would be blown out during storms. Also, the nest would be more stable, preventing possible damage to the eggs and young. Leeward placement may facilitate access to and from the nest (Diamond 1973).

A predominant direction of nest placement for orioles is not evident at most localities. However, there is a tendency for placement on the leeward sides of trees where it is significant.

The other significant differences obtained for nest placement appear to be consequences of vegetation structure as Root (1967) suggested for the Blue-gray Gnatcatcher (*Polioptila caerulea*). At Crook and a few other places, there were mainly mature spreading cottonwoods (*Populus* spp.) with a poorly developed understory. Northern Orioles usually place their nests at least a meter above the understory and towards the periphery of the tree crown. Therefore, the distance from the top of the tree tended to be greater at Crook than at Clarendon, where the crown of the mesquite (*Prosopis* sp.) trees grew close to the understory. Again, because of the understory effect, trunk distance was greater at Crook than at Pickering and Clarendon, where the aspens (*Populus tremuloides*), young maples (*Acer* sp.), and mesquite had a smaller crown radius. The significant differences in the height of the nest from the ground between some localities was not reflected in the differences in tree heights, but again may be determined by the height of the understory.

As further evidence for the importance of vegetation structure, nest placement at Guthrie and Clarendon, the only two Great Plains localities where nests were commonly placed in mesquite, differed from the others in the principal component analysis. Also, the Ontario-Quebec localities where nests were commonly placed in aspens and maples, were similar in placement.

The nest placement of the Orchard Oriole does not reflect trends seen in the Northern Oriole. The differences in the height of the nest from the ground between the intermediate (Baltimore-Bullock's hybrid zone) and east (Baltimore Oriole range) zones may be due to differences in understory growth. Russell Springs, an intermediate locality, was the only Orchard Oriole locality with a significant compass direction of nest placement on the tree, possibly because nests there were built on thinner branches. Orchard Oriole nests are small and generally placed in the fork of a branch making them more secure than Northern Oriole nests—wind may not be so important a factor.

My analysis of nest structure indicates that the nest of the Bullock's Oriole is deeper and wider than that of the Baltimore Oriole. Bullock's Oriole is the larger morph in the Great Plains (Rising 1970); the difference in nests may reflect a difference in the size of the birds. However, the diameter of the opening to the nest is smaller for Bullock's Orioles, perhaps conferring some benefits through shading.

Southern nests tended to be larger than northern ones (the difference between the Texas Panhandle localities and the Ontario-Quebec and Platte regions is significant). This may again reflect size differences in the birds, or it may be due to geographic variation in clutch size; the Texas Panhandle nest may be larger, on the average, to accommodate the slightly larger clutches in the southwestern Great Plains (Rising 1970).

Among Orchard Oriole nests, only the diameter of the nest opening showed any geographic variation, the western nests having the larger opening. This may facilitate heat dissipation.

SUMMARY

The placement and structure of the nests of the Northern Oriole vary geographically, mainly because of differences in vegetation, but also in response to variation in environmental conditions such as wind and the abundance of predators. Nests in the northeast are built on thinner branches, presumably to make them less accessible to squirrels. Nests in the southwest (Oklahoma Panhandle, southwest Kansas) are better protected from the rays of the sun; they have a smaller opening and are more spacious (although the latter may reflect size differences in the birds themselves, or geographic variation in clutch size) than those in the northeast. Texas Panhandle nests are an exception, possibly because the mesquite trees provide more shade and the larger openings of these nests may be more amenable to heat dissipation. The southwest nests are also placed more securely in the trees. At certain localities the compass direction of placement may be significant with respect to wind stress.

The nests of the Orchard Oriole do not, in general, reflect the same trends found for the Northern Oriole. The Orchard Oriole may, however, build a nest with a wider opening, or place it beyond the insulating effects of the surrounding vegetation, in places where the heat stress is likely to occur.

ACKNOWLEDGEMENTS

I am especially grateful to J. D. Rising who supervised the study and advised on the preparation of the manuscript. P. A. Westall and M. Rosen helped find and collect nests. M. Gates provided statistical advice, and J. C. Rice and F. W. Schueler commented on the manuscript. This study was supported by a grant (#A5999) to J. D. Rising from the National Research Council of Canada.

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