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## COLONY SIZES AND NEST TREES OF MONTEZUMA OROPENDOLAS IN COSTA RICA

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**Abstract.**—I examined 36 colonies of Montezuma Oropendolas (*Psarocolius montezuma*) to check whether colony size was related to characteristics of nest trees. Colonies were spread over 46 trees and contained a total of 1109 nests (range 3–172 nests per colony, median 21.5). Numbers of nests in multiple- and single-tree colonies were not significantly different. Thirteen species (11 dicots, 2 palms) were used as nesting trees, but 4 native species contained 82% of all nests. Above 500 m colonies in palms contained fewer nests per tree, but more trees per colony than colonies in dicot trees. At lower elevations the number of nests in palms was similar to the number in dicot trees. Six nesting trees (of 2 species) had *Synoeca* wasps. Trees of the same species with or without wasps had similar numbers of Oropendola nests.

### TAMAÑOS DE COLONIAS Y CARACTERÍSTICAS DE LOS ÁRBOLES EN DONDE ANIDA *PSAROCOLIUS MONTEZUMAE* EN COSTA RICA

**Resumen.**—Examiné 36 colonias de la oropéndola *Psarocolius montezumae* para relacionar el tamaño de las colonias con características de los árboles en donde anidaron. Las colonias utilizaron 46 árboles, y en estos construyeron 1109 nidos (rango 3–172 nidos por colonia, mediana 21.5). No hubo diferencias significativas en el número de nidos entre colonias que usaron uno o varios árboles. Trece especies de plantas (11 dicotiledóneas y 2 palmas) se utilizaron para anidar; 4 especies nativas contuvieron el 82% de los nidos. Las colonias en palmas contenían menos nidos por árbol, pero usualmente más árboles por colonia. Las especies de palmas o dicotiledóneas no difirieron en el número de nidos por árbol. En 6 árboles (de 2 especies) había avisperos de *Synoeca*. No hubo diferencias en el número de nidos entre árboles de la misma especie con y sin avispas.

Ecological factors influencing coloniality and colony size in oropendolas (*Psarocolius* and related genera) are not well known, with little quantitative information on colony size for most species. Colony size varies considerably among species and *P. angustifrons* may nest solitarily (Schafer 1957). Characteristics of nest trees may affect colony size. The idea is plausible, because some species of oropendolas and the related caciques (*Cacicus*) nest in different species of trees, at least locally (Drury 1962, Koepcke 1972, Oniki and Willis 1983, Schafer 1957). Presence of wasps

and bees in nest trees has been reported for several species of oropendolas and caciques (Feeke 1981, Koepcke 1972, Skutch 1954, Smith 1968). These insects deter predators and ectoparasites (Robinson 1985, Smith 1968). Nevertheless, there is no information on how the presence of wasps and bees influences colony size.

The literature suggests selectivity of tree species by nesting Montezuma Oropendolas *Psarocolius montezuma* (Alvarez del Toro 1980, Crandall 1914), and at least one source indicates regular associations with unidentified wasps (Richmond 1893). I report in this paper characteristics of Montezuma Oropendola colonies in Costa Rica (particularly numbers and species of nesting trees and presence of wasps) and examine whether these characteristics affected numbers of nests. Effects of geographical location and habitat on colony size were also investigated.

#### STUDY AREA AND METHODS

Montezuma Oropendola colonies were observed along 315 km of roads in eastern Costa Rica. I located colonies while driving slowly or by asking local residents. All colonies were within 300 m of a road. Roads (195 km) in which slow driving was difficult were scanned 6–11 times. Vocalizations of male oropendolas helped locate colonies. Colonies were examined with the help of 8 × 30 binoculars. Only four nest trees could not be reached on foot.

The study area extended from Río Frío (province of Heredia) south to Bribri (province of Limón) and west to Turrialba (province of Cartago), and up to an altitude of 800 m. I divided the study area into four areas: (1) Turrialba, which included all colonies located 500 m above sea level (all in the province of Cartago) (2) Cahuita, including all locations in the province of Limón south of the Río Estrella (3) Limón, all locations in that province between the Río Estrella and Río Reventazón and (4) Guápiles, with the locations west of the Río Reventazón, and including the easternmost part of the province of Heredia.

I located colonies at various dates between 26 May and 21 August 1987. The breeding season of the species extends from January to September (Skutch 1954). The first colonies were seen at Turrialba, where I resided for 10 d between 26 May and 12 June 1987.

Variables measured for each colony included the habitat, species of tree, number of nests and presence of wasp nests. Trees were identified from several sources (Allen 1977, Holdridge and Poveda 1975, Sánchez Vindas 1983), and from common names given by local residents.

As in the literature, colony size in this study was the number of nests in the tree. Nests found on fallen branches were not counted. Females with nests on broken branches will renest in the same tree (Schafer 1957, Skutch 1954). In three large colonies there were clusters of inactive nests that looked discolored and worn, by comparison with the remaining nests. These nests could have been built in past breeding seasons and were also excluded; they represented 11 to 17% of the total number of nests in the colonies. The low number of old nests was probably related to the fact

that I started my study 7 mo after the end of the previous season (see above).

#### RESULTS AND DISCUSSION

*Colony size, geographical location and habitat.*—I found 36 colonies, spread over 46 trees, containing 1109 nests. The mean linear density was one oropendola colony every 8.7 km. The highest density occurred at Cahuita, with six colonies (and 341 nests) in 19 km.

The mean number of nests per colony was 30.9 (SD = 35.2), the median number 21.5, and the range 3–172 nests. The largest difference in colony size occurred between Cahuita (median = 34 nests) and Turrialba (median = 13 nests), perhaps reflecting a gradient between coastal plain and mountains. However, there were no significant differences in colony size between the four subareas (Kruskal-Wallis statistic = 6.77,  $df = 3$ ,  $P = 0.08$ ). The range of colony sizes reported from Costa Rica was 9–88 nests (Crandall 1914, Skutch 1954). Four colonies in Colón, Panama, contained 10–41 nests (period 1964–1975), with a median of 23 nests (Neal Smith, pers. comm.).

Within Central America probably no oropendola surpasses *P. montezuma* in the size of its colonies. The maximum colony size for *P. wagleri* in Central Panama was 132 nests (Neal Smith, pers. comm.).

The commonest habitats for colonies were small plantations, mostly of cacao or bananas ( $n = 13$  colonies) or cattle pastures ( $n = 11$ ). I found no significant differences in colony size between these habits (Mann-Whitney,  $U = 56.5$ , 2-tailed,  $P > 0.10$ ). Other locations included large suburban gardens and lawns. I observed 3 colonies near rivers only in Guápiles.

Six of 36 colonies (16.7%) were spread over two or three trees (with a total of 16 trees). The average distance between the trees was 13.7 m (range 6.5–22 m). One might expect more nests in multiple-tree colonies. Single tree colonies had a median of 19.5 nests, multiple tree colonies 24.5 nests, but the difference was not significant (Mann-Whitney  $U$  test,  $z = 1.02$ , 1-tailed,  $P = 0.15$ ). Oropendolas nesting in palms often formed multiple tree colonies (see below). A multiple-tree colony of Montezuma Oropendolas was reported by Skutch (1954). This type of colony occurs in other oropendolas (e.g., *P. wagleri* in Panama and Costa Rica, pers. obs.). Multiple tree colonies spread over 100–200 m are particularly common in *P. angustifrons* in Venezuela; this loose coloniality probably affects the social organization of this oropendola (Schafer 1957).

My informants invariably stated that colony sites of Montezuma Oropendolas were traditional. One colony I found at Cahuita was photographed before 1983 (Sánchez Vindas 1983). Four colonies in Panama were in the same trees for at least 7–10 yr (Neal Smith, pers. comm.). This site constancy suggests selection of special characteristics of nest trees.

*Characteristics of nest trees.*—As reported in the literature (Crandall 1914, Skutch 1954) trees selected by Montezuma Oropendolas were usu-

TABLE 1. Tree species containing nests of Montezuma Oropendolas, and numbers of colonies and nests per species. Two trees were identified only with common names.

Tree species	Single tree colonies	Multiple tree colonies	Total nests
DICOTS			
<i>Bursera simaruba</i>	8	3	271
<i>Terminalia oblonga</i>	4	0	232
<i>Ficus werckleana</i>	4	2	229
<i>Cordia alliodora</i>	4	2	175
<i>Licania arborea</i>	1	0	75
<i>Andira inermis</i>	1	0	18
<i>Albizia caribaea</i>	2	0	13
<i>Rollinia microsepala</i>	1	0	8
<i>Cedrela mexicana</i>	0	1	2
"Pejibayito"	1	0	12
"Guatarrama"	1	0	8
PALMS			
<i>Bactris gassipaes</i>	2	3	41
<i>Roystonea regia</i>	1	5	23

ally isolated (I saw only two exceptions), had the shape of an umbrella, lacked lower limbs or branches, and mostly ranged 12–30 m high. I found little or no variation in these characteristics. The only spiny tree used was the pejibaye palm (*Bactris gassipaes*). Richmond (1893) mentions use of dead trees for nesting. I did not observe this, but five of six *Cordia* used for nesting were leafless or almost so in May–August.

I found Montezuma Oropendolas nesting in 13 species of trees (Table 1) 2 of which could only be identified by common names. Two species of palms were used, and both were cultivated. Otherwise no introduced trees were used. Most nests (82%) were found in only four species of trees (*Bursera*, *Terminalia*, *Ficus* and *Cordia*, Table 1). The data would suggest high selectivity by oropendolas, but a comparison with published censuses of tree species in eastern Costa Rican forests would be misleading. Oropendolas nest in man-modified environments, and the species of large trees remaining in pastures and plantations are probably not a random sample of those occurring in forests. Allen (1977) lists 31 species of large trees (canopy and subcanopy species in Hartshorn and Poveda 1983) as common in pastures in Costa Rica. Five species in the list were used by oropendolas (including *Cordia*, *Ficus*, and *Terminalia*, Table 1).

Some tree species were used for nesting only in restricted areas. Colonies in *Ficus werckleana* were seen only at Cahuita, although this fig is widespread in Costa Rica below 800 m (Sánchez Vindas 1983). Pejibaye palms are commonly planted throughout Costa Rica (Vandermeer 1983, pers. obs.) but I observed colonies in this plant only at Turrialba. Skutch (pers. comm.) found in 1941 a colony in this palm near Turrialba, suggesting persistence of local traditions.

Crandall (1914) mentions *Ceiba pentandra* as the main nest tree at Guápiles. I saw several isolated *Ceiba*, but only once was I told that oropendolas had used one of them. I could not verify the information, as no nests remained. *Bursera simaruba* and unidentified *Ficus* are often used by Montezuma Oropendolas in Chiapas, Mexico (Alvarez del Toro 1980) agreeing with my sample from Cahuita. Within the oropendolas there are specialists as regards nest trees (*Psarocolius latirostris* in *Cecropia*, Koepcke 1972) and generalists which freely use exotic trees (*P. angustifrons*, Schafer 1957). *P. montezuma* seems to occupy an intermediate position in this spectrum.

In Turrialba, palms had fewer nests per tree (median = 6,  $n = 11$ ) than dicot trees (median = 18,  $n = 5$ ) ( $U = 10$ , 2-tailed,  $P < 0.05$ ). Possibly as a result of this, palms were more frequently part of multiple tree colonies (8 of 11 cases) than dicot trees (8 of 35 cases,  $P = 0.004$ , Fisher exact test). The only multiple-tree colony reported in the literature (Skutch 1954 and pers. comm.) was built on seven pejobaye palms.

Within broad taxonomic categories (palms and dicot trees) I did not detect relationships between tree species and numbers of nests per tree. There were no significant differences in numbers of nests per tree between *Bursera*, *Ficus*, *Terminalia*, or *Cordia* (Kruskal-Wallis statistic = 1.51,  $df = 3$ ,  $P = 0.68$ ). The result applies even within subareas: I found no differences in numbers of nests between *Ficus* ( $n = 6$ ) and *Bursera* ( $n = 6$ ) in Cahuita ( $U = 10$ ,  $P = 0.20$ ). In Turrialba the palms *Bactris* ( $n = 5$ ) and *Roystonea* ( $n = 6$ ) contained comparable numbers of nests ( $U = 24$ ,  $P = 0.12$ ). Tree species was not a major determinant of colony size in this oropendola.

*Organization of colonies.*—Montezuma Oropendolas nesting in 11 dicot trees with wide crowns clustered their nests in 35 separate clumps, leaving most branches unoccupied (cf., Skutch 1954). Clump size ranged from 1 to 48 nests, with a mean of 10.9 nests. In palm trees there were usually 1–2 nests per frond and the nests were not clustered.

I have little information on the behavioral significance of nest clumps. Females that were building late nests in May–June within three colonies at Turrialba and Cahuita were segregated in discrete clumps (cf., Schafer 1957, Skutch 1954). Nest clumping blurred the differences between single and multiple-tree colonies, as clumps in the same tree could be as distant as those in different trees.

I obtained information on number of males per colony for four colonies at Turrialba. Two colonies with three and 14 nests had one male, two colonies with 26 and 47 nests two and three males respectively. I saw only one male singing in the nest tree at any time in the last colonies. The other males were sometimes singing in peripheral trees. In three sequences songs of central and peripheral males occurred at random ( $P > 0.05$ , runs test).

*Wasps in nest trees.*—Six nesting trees (the two *Albizzia* and four of the 11 *Bursera*) had large and active vespiaries built by the “guitarrón” wasp (*Synoecca septentrionalis*, Richards 1978). The samples are too small

for a significance test, but the presence of wasps in nest trees was apparently not independent of the species of tree. If the six *Synoeca* vespiaries were distributed at random in the 46 nest trees (with probability = 0.13) their expected occurrence in *Albizzia* and *Bursera* would have been 0.26 and 1.43, respectively.

Montezuma Oropendolas could still be selecting trees with wasps (e.g., selecting *Albizzia*, if *Synoeca* was present). The spatial arrangement of oropendola nests and vespiaries within the trees did not suggest a strong association. Only once (in *Albizzia*) was the vespiary within 3 m of the nearest nests. In one of the four *Bursera* the nests and the wasps were in opposite branches. In the other two *Bursera* only a minority of the nests (33 and 37%) were at the distal end of a branch with wasps (i.e., a climbing predator could have reached the remaining nests without meeting the wasps).

The hypothesis of protective association would predict higher numbers of nests in the presence of *Synoeca*. Within *Bursera*, nest trees with wasps had a median of 27 nests ( $n = 4$ ) and those without wasps a median of 18 nests ( $n = 7$ ). Nevertheless, the difference in numbers of nests between the samples is non-significant ( $U = 15$ , 1-tailed,  $P = 0.46$ ). The data of Crandall (1914) do not suggest a significant association between Montezuma Oropendolas and wasps, and Skutch (1954, and pers. comm.) did not observe wasps in his colonies. There is no evidence of a protective association between *Synoeca* wasps and Montezuma Oropendolas.

Colony size in Montezuma Oropendolas was largely independent of the characteristics of nest trees. Palms contained fewer nests per tree, but most colonies in palms were spread over many nest trees. In the related icterines *Cacicus cela* and *C. haemorrhous* colony size is probably related to food supply and predation pressure (Feekes 1981, Robinson 1985).

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## NOTES AND NEWS

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