

# THE SPATIAL AND TEMPORAL DISTRIBUTION OF BREEDING FEMALE MONTEZUMA OROPENDOLAS: EFFECTS ON MALE MATING STRATEGIES<sup>1</sup>

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**Abstract.** In a Costa Rican population of Montezuma Oropendolas (*Psarocolius montezuma*), females nested in the dry season (January through May) and males did not help build nests or behave parentally. The length of the nesting period, from nest initiation to fledging, was relatively long (ca. 2.5 months). Approximately one-third of all nests fledged young. Between 19 and 32% of nests fell out of colony trees before fledging, and most of these fell during periods of heavy rain. Females bred colonially, with up to 130 nests (median = 24) in a single tree. In addition, nests were clustered within colony trees: several nests were often built together on a single limb. This behavior appears to be costly, as the clustering of nests caused limbs to break, contributing to the high rate of nest loss. The degree of nesting synchrony was low among nest clusters within the colony, but relatively high within clusters. The overall degree of breeding synchrony within an oropendola colony (SD of nest-lining date = 13–25 days) was lower than reported for most monogamous colonial birds, but similar to that reported for other polygynous colonial species. Breeding synchrony within but not among nesting clusters appears to increase the ability of high-ranking male oropendolas to defend or court multiple females.

**Key words:** *Breeding synchrony; colonial nesting; female-defense polygyny; Montezuma Oropendola; Psarocolius montezuma.*

## INTRODUCTION

Male mating strategies in birds are generally thought to be determined, at least in part, by the spatial distribution of breeding females (Emlen and Oring 1977, Wittenberger 1980a, Davies 1991). When sexually receptive females are clumped in space, such that they are defensible by a single male, males are expected to actively compete for and defend female groups, leading to a polygynous mating system. For the American blackbirds (Icterinae), comparative studies have demonstrated an association between polygyny and the spatial dispersion of nesting females (Robinson 1986, Webster 1992), and intraspecific studies have documented competition among males of polygynous species for groups of females or prime nesting sites (e.g., Lenington 1980; Wittenberger 1980b; Robinson 1985a; Post 1992; Webster, in press).

Factors other than the spatial distribution of females must affect male mating strategies, however: many species of birds nest colonially (e.g., many seabirds, shorebirds, herons and swal-

lows), yet polygyny has evolved in very few (Lack 1968). There are at least two hypothesized reasons for why this might be. First, if male parental care is essential to the survival of nestlings in colonial birds, such paternal care will limit a male's ability to attract or defend multiple mates (Lack 1968, Emlen and Oring 1977, Davies 1991). Although this is likely to be an important factor in some colonial species, particularly colonial seabirds that feed on widely dispersed and unpredictable resources, some recent studies have suggested that the importance of male parental care is not the only factor determining male mating strategies in passerines (Webster 1991a, Dunn and Robertson 1992).

Alternatively, interspecific differences in male mating strategy might reflect differences in the opportunity to obtain or defend multiple mates (Emlen and Oring 1977, Westneat et al. 1990, Davies 1991, Webster 1991a). For example, if females are highly synchronous, and males require some time to court or guard each mate, then polygynous mating will not be possible even if females nest in dense aggregations and paternal care is unimportant. This hypothesis predicts that male mating behavior will be associated with patterns of female breeding synchrony within the colony, and that female breeding synchrony will be lower for colonial species in which males de-

<sup>1</sup> Received 20 October 1993. Accepted 7 March 1994.

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defend multiple mates than for those in which males pair with a single female.

The Montezuma Oropendola (*Psarocolius montezuma*) is a colonial-nesting, neotropical blackbird (Icterinae, Emberizidae). Males of this species compete for and defend groups of females at nesting colonies, and copulation success is strongly biased toward those few males most successful in this competition (Webster, in press). This male mating strategy is quite rare among birds (Oring 1982, Post 1992), and has apparently led to the evolution of alternative male mating strategies and an extreme level of sexual size dimorphism (Webster 1991b, 1992).

Although nests and colonies have been described for this (Skutch 1954, Fraga 1989) and other species of oropendola (Chapman 1929, Schäfer 1957, Tashian 1957, Drury 1962, Smith 1983), no published study has followed marked female oropendolas over the course of an entire breeding season. In this paper I describe the breeding biology of female Montezuma Oropendolas, including nesting phenology, estimates of nesting success, and movements of marked individuals between nesting attempts. In particular, I describe the spatial and temporal distribution of sexually receptive females and the factors likely to affect this distribution. I then compare the breeding synchrony of Montezuma Oropendolas to that of other colonial birds, and discuss the effects of coloniality and female breeding synchrony on the evolution of male mating strategies.

## MATERIALS AND METHODS

Montezuma Oropendolas inhabit lowland forests ranging from southern Mexico to the Canal Zone in Panama (Skutch 1954). This species is highly sexually dimorphic in body size, with adult males (mean = 521 g) weighing more than twice as much as females (246 g, Webster 1991b). There are no differences in plumage coloration between the sexes or between juveniles and adults.

I studied a population of Montezuma Oropendolas at the Estación Biología La Selva near Puerto Viejo de Siripiquí, Costa Rica (10°25'N, 84°01'W). La Selva is a lowland rainforest site, with annual rainfall averaging 3.8 m/year (McDade et al. 1993). A pronounced dry season occurs from early January into May, during which Montezuma oropendolas breed. My studies took

place each dry season from 1986 through 1990, for a total of 18 months.

Birds were captured using elevated mist nets (Mease and Mease 1980) placed near nesting colonies and at foraging sites baited with bananas. Captured birds were individually marked with leg bands made from colored PVC plastic. Sex was determined from body size, and male age class (adult vs. juvenile) was determined using the size of facial wattles (males with wattles less than 8 mm in depth were considered to be juveniles, Webster 1991b).

For the purposes of this study, I defined a colony as a group of nests built in the same tree or adjacent trees during a breeding season (Fraga 1989). In the majority of cases, trees containing nests were separated by one or more kilometers, making colony delineation unambiguous (see below).

Several assistants and I observed oropendolas at a focal nesting colony ("La Selva Colony") each season, for a total of more than 1,200 hr of observation. We conducted colony observations from around dawn until late morning (ca. 10:30), and from mid-afternoon (ca. 14:30) until dusk. Observations through the entire day indicated that very little activity occurs at the colonies during the hot midday hours (Webster 1994). During colony observations, we noted individual arrival and departure times, aggressive interactions and attempted copulations. During the 1987, 1988 and 1989 seasons, we also recorded the nest to which an arriving female went and, if possible, whether or not she carried anything in her bill (e.g., nesting material, leaves, arthropod prey). These data were used to determine female nesting stage and sexual receptivity in those three years (because of the relative inaccessibility of nests, it was impossible to examine nest contents directly). For most females, detailed records of nesting activity were not made during the early construction stages when the nest was difficult to discern. We monitored female nesting activity in 1986 as well, but did not keep detailed records of daily activity in that year. In addition to the focal observation colony, two other oropendola colonies in the La Selva area ("Crocodile Point" and "Colony B") also were observed, but on an irregular basis. All known colonies in the La Selva area were visited at the end of each breeding season to determine colony size (total number of nests built during the course of the season).

At the end of the 1989 field season, we at-

tempted to find all *Oropendola* colonies in an approximately 55 km<sup>2</sup> area around La Selva. Because of their large size, open aspect, and the loudness of male displays, colonies were relatively easy to locate, and we believe we found all colonies in the area. At each colony in the study area, plus a small number incidentally encountered outside of it, we counted the number of nests at or near completion. Because this survey was conducted relatively late in the breeding season, this count gives an approximation of the total number of nests that were built in each colony over the entire season (old nests fall out of the colony tree between breeding seasons). We also recorded the spatial distribution of nests within each colony by counting the number of nests built together in a single cluster. Most nests in clusters were built on the same branch and within a few centimeters of each other (see below), though some were a meter or more away. We arbitrarily defined two nests as being in the same cluster when they were estimated to be within 1.5 m of each other. Finally, we collected fallen nests from beneath colonies for nest descriptions. Unless otherwise indicated, all measures are given below as mean  $\pm$  standard deviation.

## RESULTS

### GENERAL BREEDING BIOLOGY

*Nests.* Female Montezuma *Oropendolas* built long, pouch-like nests with no assistance from males. The nests were woven from a variety of fibrous plant materials, including strips of palm frond and epiphytal roots. The bottom of nests were lined with a thick layer of dry shredded leaf material, possibly to cushion and insulate the eggs and nestlings. Fallen nests ( $n = 28$ ) averaged  $111.3 \pm 26.5$  cm in length and  $68.3 \pm 5.7$  cm in maximum circumference of the pouch. These nests weighed  $414.4 \pm 101.4$  g when dry, but were fully two times heavier ( $874.1 \pm 239.3$  g) after we soaked them in water.

*Nesting phenology and female receptivity.* As with nest-building, females incubated and fed the young alone with no assistance. The frequency of a female's arrivals and departures from her nest and the identity of items she carried varied across the nesting cycle (Fig. 1). I used these observations to determine each female's stage in the nesting cycle (see also Tashian 1957). Nest construction lasted 2–3 weeks, but the exact duration of this stage was difficult to determine

because nest initiation was not observed for most nests. Females brought dead leaves, which they used to line the inside of the nest, for an average of  $5.8 \pm 2.44$  days ( $n = 35$  nests). Incubation, defined as the period between last observations of leaf-lining and the first observed trips with food, lasted for  $15.5 \pm 1.9$  days ( $n = 14$  nests). It was difficult to determine the length of time that females fed nestlings, because females who stopped bringing food to the nest may have fledged or lost their young. Skutch (1954) reported that feeding lasts for 30 or more days. In this study, one female known to have fledged young brought food to her nest for 32 days, and six other females thought to have fledged young brought food for 29–42 days. I considered a female to have fledged young if she brought food to the nest for at least 29 days. A wide variety of food items were brought to the young, including large arthropods (mostly spiders and orthopterans), vertebrate prey (frogs and lizards), and some fruits.

Work with closely related species (Schäfer 1957, Robinson 1985a, Post 1992) suggests that a female is sexually receptive at the end of nest construction, when she is lining her nest with leaves. Of 30 copulations observed during this study that involved an identifiable female, 23 (77%) involved females in the nest-lining stage, and five (17%) involved females within two days of nest-lining. Therefore, a female was considered to be sexually-receptive during the period she was observed bringing leaves to her nest.

*Nesting success.* The clutch size for this species has been reported to be two eggs (Skutch 1954), and in this study four of five nests that fell during incubation and were recovered on the day they fell contained two eggs (the fifth contained a single egg). However, females rarely fledged more than a single young; of 22 nests that fell during the feeding stage or were accessed for blood samples (Webster 1991b), all contained a single nestling.

Of 45 nests started at the focal colony and not abandoned within a day or two (31 in 1987 and 14 in 1988), 20% never reached the nest-lining stage, 36% were lined but never had food brought (eggs apparently lost or never laid), and 16% apparently hatched but did not fledge any young (female brought food to the nest for fewer than 29 days). Only 29% of these 45 nests (or 36% of the nests were that were lined) were considered to have fledged any young (female brought food to the nest for at least 29 days).

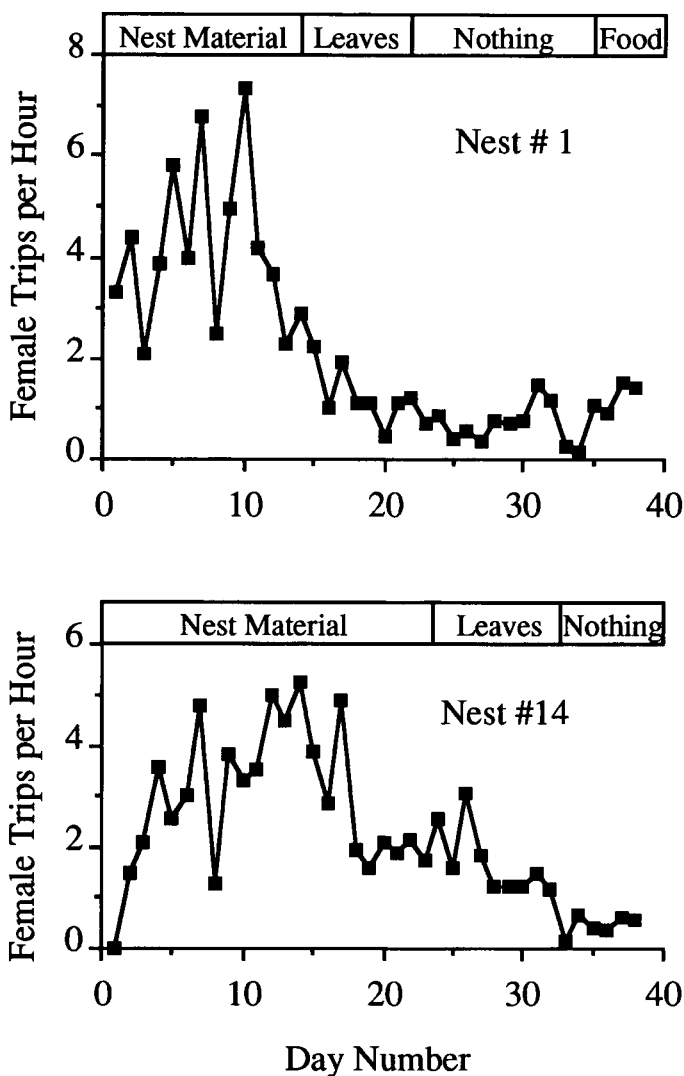


FIGURE 1. Female activity at two nests in the focal colony (1989). Bars at top show items the female was observed carrying in her bill on most visits during that period. Day 0 corresponds to January 15 for both nests.

Many oropendola nests fell out of colony trees during this study, and this appeared to be a major source of nestling mortality: seven of the 36 nests that were lined (19%) fell during incubation or the feeding of the nestlings. If data from the two additional colonies that were studied less intensively also are included, 22 of 68 nests (32%) were lost by falling. Some of these nests fell because the limb to which they were attached broke, while others tore free. Severe weather appeared to be the immediate cause of falling for 19 of these 22 nests, because they fell during or immediately after a rainstorm. For example, eight nests fell when, during a heavy rain, the limb

holding all eight snapped under their combined mass and fell. Similarly, six nests fell, one at a time, from a focal colony during 11 days of unseasonable rains in March 1990 (all but one of the other 16 females building nests at that colony abandoned their nests during this period of heavy rains).

#### COLONY DESCRIPTIONS AND THE SPATIAL DISTRIBUTION OF FEMALES

During the 1989 breeding season, 27 colonies containing a total of 795 nests were found in the 55 km<sup>2</sup> region around La Selva. As each female

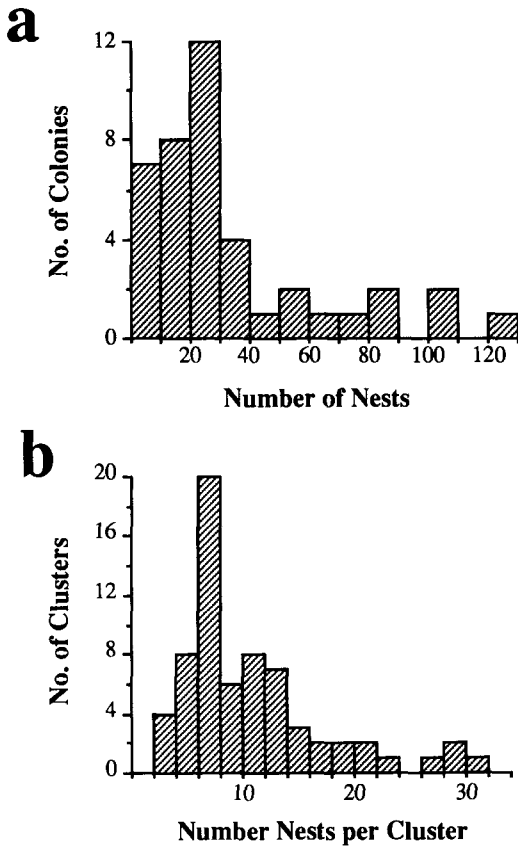


FIGURE 2. Number of nests in (a) colonies and (b) nest clusters (nests  $\leq 1.5$  m apart) within colonies. Based on 41 colonies surveyed during the 1989 breeding season. Only nests built in discrete clusters (694 nests in 67 clusters) are included in b.

builds her own nest, this gives a density of approximately 14.5 nesting females per  $\text{km}^2$ . We encountered three cases in which pairs of colonies were located within 100–400 m of each other. In these cases, marked individuals from each colony visited and interacted with individuals at the other. Therefore, nests occupying two trees a few hundred meters apart should probably be considered part of the same colony. Excluding these three cases and colonies near the edge of the study area, nearest neighbor distance between colonies was  $1.33 \pm 0.45$  km ( $n = 9$  colonies).

Most colonies (39 of 41) were located in single, isolated trees whose canopies did not touch that of any other. These colony trees were tall, contained few lower branches or epiphytes along the trunk, and had large, umbrella-shaped crowns.

All were located in cleared or abandoned agricultural land and were less than 200 m from a forest edge.

Median colony size was 24 nests ( $n = 41$  colonies), and ranged up to 130 completed or nearly completed nests (Fig. 2). The size of colonies varied somewhat across years (Fig. 3), and fluctuations in size were not consistent across colonies. One cause of fluctuations in colony size was the movement of individual females between colonies: marked females switched colonies on 43% of all breeding attempts ( $n = 28$  cases in which a marked female was seen during two consecutive nesting attempts).

Although oropendola colonies are typically thought to be built in traditional sites, the focal study colony (La Selva Colony) occupied five different trees within a 1.5  $\text{km}^2$  area from 1985 through 1990 (Fig. 4). Three colony site changes occurred when females abandoned active nests and moved to a new colony site. Human disturbance was responsible for one of these moves (in 1989 the birds were disturbed by our attempts to access nests for blood samples), and severe weather appeared to be the cause of colony abandonment in early 1987 (move from “Site A” to “Coop”) and in mid-1990 (abandonment of “LS Road” site; it is not known to where females moved). The other colony site changes occurred between breeding seasons and were due to unknown causes. Counting all colonies in the La Selva area, small colonies appeared to be less stable and more likely to switch location between years than large colonies (Fig. 3).

Nests were not randomly distributed within colony trees: of 597 nests in colonies where nest clustering data were collected, 530 (88.8%) were built in distinct clusters (Fig. 5), and only 67 (11.2%) were built in relative isolation ( $> 1.5$  m from nearest neighbor). Many of the “isolated” nests appeared to be grouped in loose, poorly defined clusters, but did not meet our criteria to be considered part of a nesting cluster. The size of nesting clusters ranged from two to 32 nests (Fig. 2), with a median of eight nests.

#### THE TEMPORAL DISTRIBUTION OF BREEDING FEMALES

Nesting began in early January of each year. The degree of breeding synchrony within a colony was low in this study, and sexually receptive females (those lining nests with leaves) could be found at the La Selva Colony throughout much

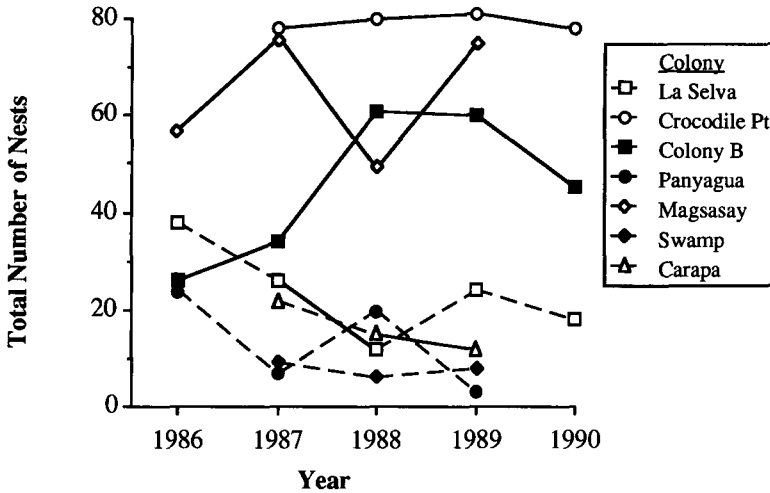


FIGURE 3. Colony size versus year of observation. Shown are the number of nests counted in each colony near the end of each breeding season. Only those colonies observed in three or more seasons are included. Dashed lines indicate that the colony changed locations between seasons. The focal observation colony is shown with unfilled squares.

of each breeding season (Fig. 6). The standard deviation of date of first nest-lining was 24.88 days in 1987 and 13.24 days in 1988. (The 1989 data were excluded from synchrony analyses be-

cause the colony was abandoned mid-way through the breeding season.)

In contrast to the over-all asynchrony of colonies, breeding synchrony within a nesting clus-

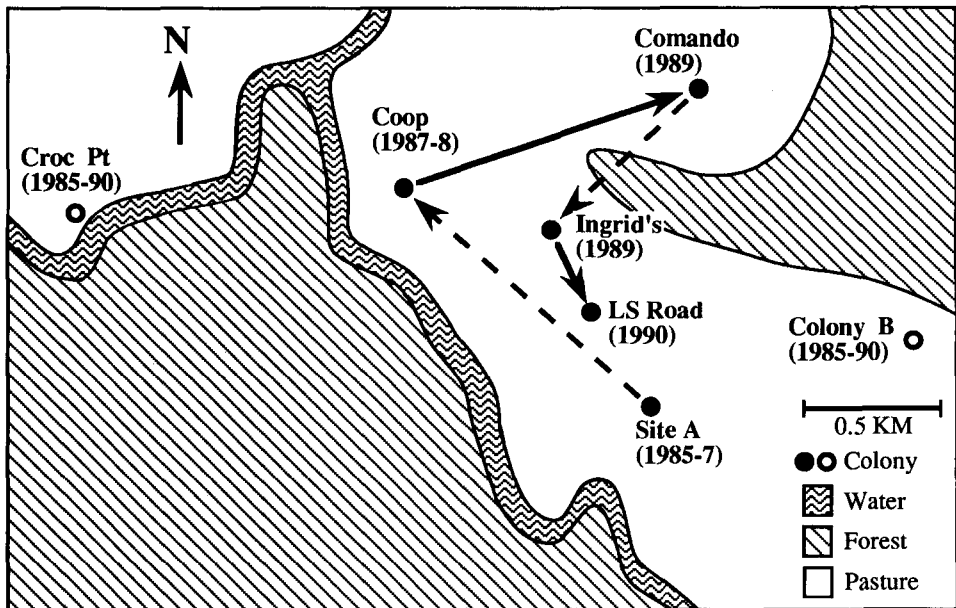


FIGURE 4. Location of Montezuma Oropendola colonies in La Selva area, 1985–1990. Colony B and Crocodile Point Colony were located in the same two trees throughout this period, whereas females nesting in the focal colony (La Selva Colony) changed locations frequently. The name and years of occupation are given for each colony site used by the focal colony. Solid arrows show changes in colony location between breeding seasons, and dashed arrows show changes that occurred within a season. Females nesting at the “LS Road” site abandoned that site in the middle of the 1990 season; it is not known where they nested subsequently.



FIGURE 5. A photo of La Selva Colony in 1986 showing distinct nesting clusters (right side of colony tree) and two relatively isolated nests (left lower side of colony tree).

ter was relatively high. Analyses of variance showed that mean date of first nest-lining differed significantly among clusters within a colony (1987:  $df = 2, 24, F = 26.51, P \leq 0.001$ ; 1988  $df = 1, 8, F = 5.63, P = 0.045$ ); variation among nesting clusters accounted for 41% (1988) and 69% (1987) of the total variance in mean nesting date (ratio of between group sum-of-squares to total sum-of-squares). To test further whether nests within a cluster were more synchronous than the colony as a whole, I randomly selected  $n$  nests from the colony and calculated the standard deviation of first nest-lining for these nests (where  $n$  = the mean number of nests in a cluster in each year). By repeating this 100 times, I could calculate the mean standard deviation of first-nest lining. In both 1987 and 1988, the mean standard deviation of nest lining date within a nesting cluster (14.3 and 10.3 days, respectively), was significantly lower than the standard deviation

for randomly selected nests (mean  $\pm$  standard error:  $23.3 \pm 0.7$  and  $12.0 \pm 0.3$  days, respectively).

## DISCUSSION

### COSTS AND BENEFITS OF CLUSTERING NESTS WITHIN COLONIES

One striking feature of Montezuma Oropendola nesting colonies is the degree to which females cluster their nests within the colony tree (Fig. 5, see also Fraga 1989). This behavior is likely to be costly, as nest clustering is likely to magnify the costs of coloniality. For example, ectoparasite transmission has been shown to increase with nest density in several species of colonial swallows (Hoogland and Sherman 1976, Brown and Brown 1986, Møller 1987). Oropendola nestlings are parasitized by avian lice and botflies, and nests in clusters might be more susceptible than

isolated nests to these parasites. In addition, female oropendolas nesting in the same cluster fought frequently and stole nesting material from each other (see also Skutch 1954, Robinson 1985a). Finally building several heavy oropendola nests on a single limb appeared to increase the risk of that limb breaking and falling, particularly during heavy rains. Skutch (1954) also reported finding broken limbs with nests on the ground below colonies, one of which contained 21 nests.

The reasons for aggregated nesting within Montezuma Oropendola colonies are unclear. It is unlikely that nest clustering is the result of females independently converging on certain "safe" limbs within the colony (Lightbody and Weatherhead 1987; Post, unpubl. ms.), because the packing of nests together was extreme (Fig. 5), many seemingly suitable limbs were unoccupied, and the limbs used for nesting sometimes changed from one year to the next (pers. observ.). Although the nests of social hymenoptera were located in a few colony trees, in no case did Montezuma Oropendolas cluster their nests near the insect nests (see also Fraga 1989) as has been reported for other species of oropendola and cacique (Smith 1968, 1983; Robinson 1985b). It is also unlikely that female oropendolas derive any foraging benefits (Horn 1968, Ward and Zahavi 1973, Emlen and Demong 1975, Brown 1986, Greene 1987) by clustering their nests within a colony, because it is easy to observe females carrying food from a distance and females could easily monitor the success of others without entailing the costs of clustered nesting.

Females might benefit from nesting in close proximity to each other through increased protection from predators (e.g., Hoogland and Sherman 1976, Picman et al. 1988) and/or brood parasites (Clark and Robertson 1979, Wiley and Wiley 1980). Nesting in synchronous clusters has been shown to reduce the risk of nest predation in the closely related yellow-rumped cacique (*Cacicus cela*, Robinson 1985b). Unfortunately, I have never observed a potential nest predator at or near an oropendola colony and this possibility remains untested. Some observations, though, suggest that nests in clusters are better protected than isolated nests from interspecific brood parasitism by giant cowbirds (*Scaphidura oryzivora*, Webster 1994). Finally, females might cluster their nests to allow high-ranking males to defend them more easily against harassment by

low-ranking males, as has been suggested for some polygynous mammals (Le Boeuf 1972, Trillmich and Trillmich 1984, Wrangham and Rubenstein 1986, Mesnick and Le Boeuf 1991). Although male courtship behaviors are vigorous and appear to be disruptive to females (Webster 1991b), the consequences of courtship to females and the frequency of courtship in the absence of nest clustering are unknown.

#### FACTORS AFFECTING FEMALE SYNCHRONY WITHIN COLONIES

Whether aggregated nesting reduces predation, brood parasitism, or both, the benefit of such a nesting dispersion is likely to be enhanced by breeding synchrony among females. For example, if females feeding nestlings are unlikely to chase cowbirds away from their nests, females near egg-laying would not benefit from nesting near feeding females. Similar arguments have been made for protection from nest predators (Hoogland and Sherman 1976, Robinson 1985b, Wittenberger and Hunt 1985).

Although selection should favor breeding synchrony among female oropendolas, synchrony was only evident within nest clusters, and nesting in each colony as a whole was relatively asynchronous (Fig. 6). Synchrony within but not among nesting clusters was most likely due to two proximate factors. First, because the rate of nest failure was high, many females who started nests early in the season lost those nests and had to renest later (at the same or different colony). Young females might also start nests later than females that have bred in previous seasons (e.g., Post, unpubl. ms.). Second, although females in established nesting clusters were extremely aggressive toward females not nesting in that cluster (see also Robinson 1985a), females in the very earliest stages of nest establishment were somewhat more tolerant of each other and would often perch together for long periods of time (pers. obs.). As a consequence, females starting nests at approximately the same time built nests near each other rather than near females in later stages of the nesting cycle, leading to local synchrony.

#### THE DISTRIBUTION OF FEMALES AND MALE MATING STRATEGIES

Although the ultimate factors underlying the highly clumped spatial distribution of female Montezuma Oropendolas are not entirely clear, this nesting distribution appears to have been an



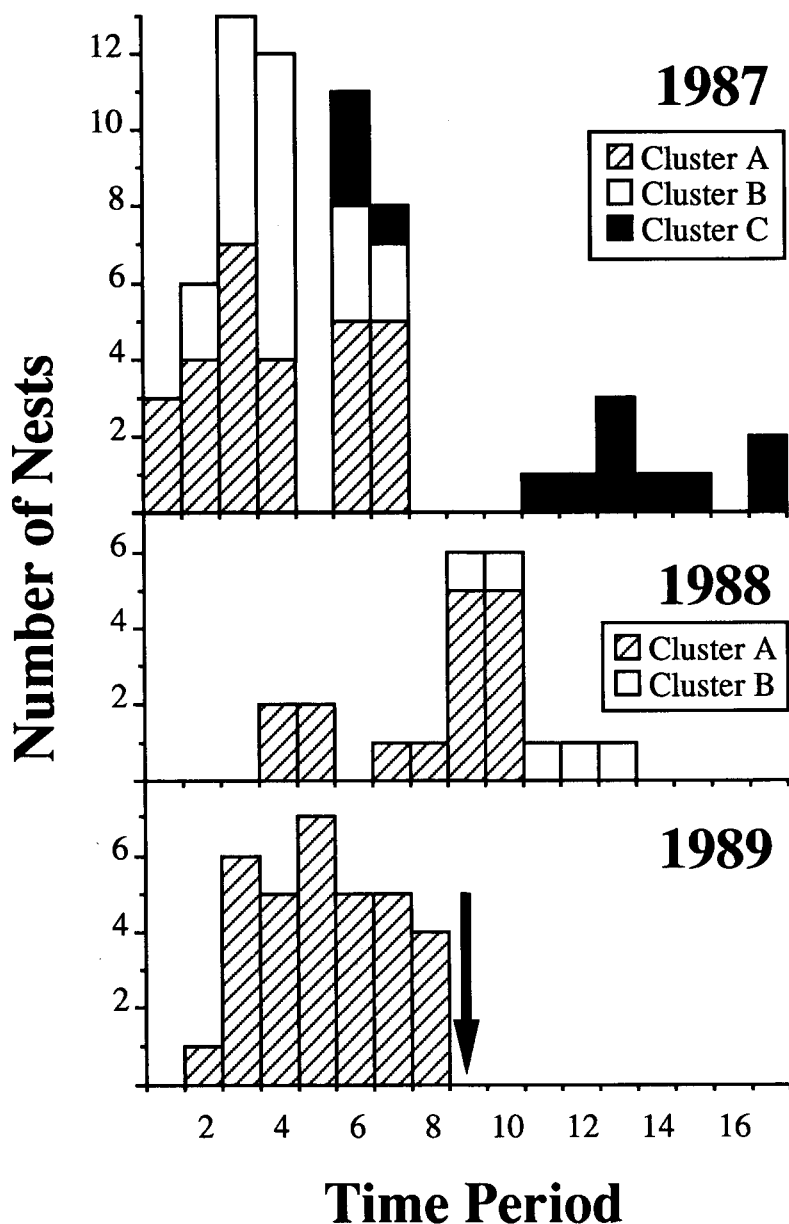


FIGURE 6. Nesting synchrony at the La Selva Colony in 1987, 1988, and 1989. Bars show the number of females lining nests during five-day time periods in each year. Individual nesting clusters are shown with different patterns. In 1989, nests at the focal colony were built in a single large, loosely organized group and could not be easily assigned to distinct clusters. This colony site was deserted on day 42 (arrow).

important factor leading to the female-defense mating strategy of males. If males defended territories, rather than converging on nesting colonies, the vast majority would obtain no mates at all. Furthermore, many colonies changed location frequently and unpredictably (Figs. 3, 4),

suggested that, before nest building begins, it might be difficult for males to determine which potential colony sites will be used. By waiting, on the other hand, a high-ranking male can go to where females begin nesting, defend those females, and thereby obtain a high number of cop-

TABLE 1. Mating system and degree of breeding synchrony in colonial birds.

Species	Mating system*	SD of nest date (no. days)†	Source
Montezuma Oropendola	Highly polygynous	13.3, 24.9	This study
Yellow-rumped Cacique	Highly polygynous	38.9	Robinson 1985b
Boat-tailed Grackle	Highly polygynous	7.0, 20.6‡	Post 1992, submitted
Black-headed Weaver	Polygynous	16.9	Hall 1970
Viellot's Black Weaver	Polygynous	18.1	Hall 1970
Brewer's Blackbird	Slightly polygynous	5.5	Horn 1970
Tricolored Blackbird	Slightly polygynous	1.4	Lack and Emlen 1939
Bank Swallow	Monogamous	6.3	Emlen and Demong 1975
Herring Gull	Monogamous	3.1–8.1	Gochfeld 1980
Black Skimmer	Monogamous	6.1–6.5	Gochfeld 1980

\* Degree of polygyny: "monogamous" = most or all males obtain a single mate; "slightly polygynous" = some males obtain more than one mate, but few obtain more than 2–3 mates; "highly polygynous" = most matings obtained by a small number of males at each colony; "polygynous" = some males obtain multiple mates, but exact level of polygyny unknown.

† Standard deviation of nest completion date or date of first egg in each nest, measured across entire colony. Figures obtained or calculated from data presented in indicated source.

‡ First figure, reported by Post (unpubl. ms), includes only first nesting attempts; second figure was calculated for one colony (unpubl. data) and includes all nesting attempts.

ulations (see Webster, in press). Interspecific comparisons support the hypothesis that the spatial distribution of females is an important correlate of polygynous mating systems in the American blackbird subfamily (Robinson 1986, Webster 1992).

Interspecific comparisons also suggest that the temporal distribution of sexually receptive females affects male mating strategies. Females of polygynous colonial species show relatively little breeding synchrony within a colony (Table 1), and sexually-receptive females are available throughout most of the breeding season (see Robinson 1985a, 1985b; Post 1992, submitted; this study). In contrast, females of most colonial species show a high degree of breeding synchrony within a colony (Gochfeld 1980) and are monogamous or only slightly polygynous (Table 1). A high number of females simultaneously receptive will likely reduce the opportunity for polygynous matings (Emlen and Oring 1977): if a male must spend some time courting and/or guarding a female during her receptive period, and females breed synchronously, few mating opportunities will remain after a male has mated with one female (see Grant and Kramer 1992). Under these conditions, a male should remain with his single mate and assist her in raising the brood. This hypothesis might also apply to non-colonial species. For example, breeding synchrony is lower among females of polygynous waterfowl than among females of monogamous species (McKinney 1985, Sorenson 1992).

Finally, the results of this study indicate that

male mating strategies are associated with the spatial and temporal distribution of female oropendolas *within* a colony. Females tend to breed in synchronous clusters within a colony (see above), and observations of color-marked individuals have shown that males (1) focus their defensive efforts on those clusters containing the greatest number of receptive females at any given time, and (2) shift the focus of their defensive efforts away from areas where females have laid eggs (Webster, in press). Observations of copulations (Webster 1991b, in press) suggest that asynchrony between clusters allows high-ranking males to more effectively guard females and monopolize matings at large colonies: although the top two ranking males obtained virtually all copulations at most colonies, a minimum of four different males obtained copulations at one large colony with three simultaneously active nesting clusters (La Selva Colony, 1986, 38 nests). However, this may not hold for smaller colonies: at the La Selva Colony in 1987 (26 nests), two clusters were simultaneously active (see Fig. 6), yet all observed copulations ( $n = 11$ ) were obtained by the alpha male. These results suggest that the ability of alpha male oropendolas to monopolize matings may be affected by both colony size and within-colony female synchrony.

In sum, female oropendolas and other polygynous colonial species show less breeding synchrony than females of monogamous colonial species, supporting the hypothesis that, in species where male parental care is not essential, a high level of female breeding synchrony might con-

strain the mating opportunities open to males. Moreover, the mating tactics of male oropendolas appear to be related to the spatial and temporal pattern of females within the colony; because females nest in synchronous clusters within the colony, high-ranking males are able to focus their defensive efforts and simultaneously defend those few females that are sexually receptive at any given time. Localized synchrony may not be necessary for polygyny to evolve in some species (e.g., Post, unpubl. ms.), and a moderate level of polygyny may be possible even when all females in a colony are highly synchronous (Table 1). Nevertheless, synchrony within a nesting cluster and relative asynchrony between clusters appears to facilitate the ability of a very small number of males to monopolize copulations at Montezuma Oropendola colonies.

#### ACKNOWLEDGMENTS

I thank S. T. Emlen, P. W. Sherman and L. K. Sterk for advice and encouragement, and I. Ayub, J. Guild, K. Merg, E. Phillips, and L. Sterk for unflagging assistance and friendship in the field. I thank W. Post for discussion and access to unpublished material. Valuable comments on an earlier draft were provided by C. Aquadro, S. Emlen, R. Hoy, H. Landel, F. Pough, S. Pruett-Jones, P. Sherman, L. Sorenson and two anonymous referees. The Organization of Tropical Studies and Jessie Smith Noyes Foundation provided critical financial and logistic support. Further generous support was provided by the following organizations: American Museum of Natural History (Frank M. Chapman Fund), Cornell University, National Institute of Mental Health, National Science Foundation (NSF Graduate Fellowship), Organization for American States, and Sigma Xi (Grant-in-Aid-of-Research). During preparation of the manuscript, I was supported by NSF grant IBN-9207609 to S. G. Pruett-Jones. Finally, I thank the La Selva staff and the many Costa Rican residents who allowed me to work on their land.

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