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EFFECTS OF FEMALE CHOICE AND COPULATIONS AWAY FROM COLONY ON FERTILIZATION SUCCESS OF MALE MONTEZUMA OROPENDOLAS (*PSAROCOLIUS MONTEZUMA*)

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ABSTRACT.—In a Costa Rican population of Montezuma Oropendolas (*Psarocolius montezuma*), high-ranking males defended groups of females at nesting colonies and prevented other males from copulating there. Observed male mating success was strongly biased toward high-ranking males; the top-ranking (alpha) male obtained 90 to 100% of all observed copulations at a focal colony in three of four breeding seasons. The probability of success per copulation attempt was significantly higher for the alpha male than for the beta male, suggesting that females prefer mating with high-ranking males at nesting colonies. However, low-ranking males unable to copulate at the colony followed females and courted them away from the protection of the alpha male. I used multilocus DNA fingerprinting to determine the relative fertilization success of alpha and lower-ranking males. Using M13 and Jeffreys 33.15 probes, I determined the paternity of 21 sampled nestlings from four colony sites. Seven of these nestlings matched with the alpha male at their colony, 4 matched with the beta male, and the remaining 10 did not match up with any sampled male. The fertilization success of alpha males was significantly lower than expected from the observed copulation success at nesting colonies. Paternity assignments and levels of band sharing among nestlings indicate that most nestlings not attributable to the alpha were sired by several low-ranking males copulating away from the colony. These results indicate that alpha males sire more progeny than other males, but that lower-ranking males are able to achieve some reproductive success by copulating with females away from the colony. The combined effect of fertilizations by low-ranking males was to reduce significantly the alpha male's monopolization of fertilizations below that suggested by observed copulation success. *Received 25 May 1994, accepted 27 January 1995.*

FEMALE-DEFENSE or "harem" polygynous mating systems are characterized by high levels of intrasexual competition among males for mates. In such mating systems, males physically compete for access to female aggregations, and those males most successful in this competition have extremely high copulation success (Le Boeuf 1974, Clutton-Brock et al. 1982). Consequently, male size and competitive ability are important determinants of lifetime reproductive success (Clutton-Brock et al. 1988, Le Boeuf and Reiter 1988).

Although physical control of female groups is closely associated with observed male mating success in female-defense systems, other processes might act to reduce the fertilization success of those males defending females. First, intrasexual competition among males does not necessarily preclude female choice of mates (Bradbury and Davies 1987). Some authors have argued that male success in intrasexual competition should be an indicator of overall male phenotypic and genetic quality, and that females should mate preferentially with those males who most successfully compete for mates (Cox and Le Boeuf 1977, Borgia 1979, Kodric-Brown and Brown 1984, Borgia 1985). Others have criticized such "good-genes" models (Kirkpatrick 1987) and have argued that mate choice frequently will not coincide with the outcome of intrasexual competition for mates or resources (Weatherhead and Robertson 1979, Bradbury and Davies 1987). At present, it is unclear whether the forces of intrasexual competition and intersexual mate choice act in opposition, or whether they complement each other in favoring the same male phenotypes.

Second, alternative male tactics have been re-

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ported for many female-defense mating systems. In these systems, males who are physically excluded from the vicinity of females attempt to obtain fertilizations by: (1) attempting to copulate with females near the edge of harems (Le Boeuf 1974, Trillmich and Trillmich 1984, Wilkinson 1985); (2) physically separating females from the male defending them (Clutton-Brock et al. 1982, Rubenstein 1986), sometimes by forming coalitions with other males (Packer 1979, Campagna et al. 1988); and (3) copulating with females when they leave the harem (Gwynne 1980, Le Boeuf and Mesnick 1990). The success of males employing such tactics is thought to be quite low because successful copulations by males without harems are rarely observed (Le Boeuf 1974, McCracken and Bradbury 1981, Wilkinson 1985), and females often appear to avoid mating with such males (Cox and Le Boeuf 1977, Trillmich and Trillmich 1984, Mesnick and Le Boeuf 1991).

Although harem-holding males are thought to obtain the majority of fertilizations, few studies have directly measured the fertilization success of males employing different mating tactics in female-defense systems. Instead, most studies have relied on observations of matings. Observed mating success may not be a good predictor of realized mating success (i.e. number of young sired), as matings by nonharem males are usually secretive, rapid, and often occur away from the harem. Furthermore, genetic analyses of paternity in polygynous birds and mammals have shown that, though rarely observed in the field, females often mate with males other than their social mate and/or mate with multiple males (Hanken and Sherman 1981, McCracken and Bradbury 1981, Wilkinson 1985, Gibbs et al. 1990, Bollinger and Gavin 1991, Gelter and Tegelström 1992, Westneat 1993). Thus, estimates of fertilization success in female-defense systems are necessary to understand the evolution of behavioral and morphological traits associated with male mating success.

The Montezuma Oropendola (*Psarocolius montezuma*) is a Neotropical blackbird (Icterinae, Emberizidae) with a female-defense mating system characterized by high levels of physical competition between males for access to groups of sexually-receptive females (Webster 1994a). As a consequence of this competition, observed male mating success at nesting colonies is strongly biased toward a small number of males who are able to prevent other males from approaching females. However, low-ranking males that are excluded from females at nesting colonies frequently are observed courting females away from the colony (Webster 1991). In this paper, I examine whether males unable to defend groups of females are able to sire young, and whether observed male mating success is an accurate predictor of fertilization success. I use a combination of behavioral observations and DNA profiles (DNA fingerprints) to examine the effects of female mate choice and copulations away from the colony on male fertilization success.

METHODS

Study species.—Montezuma Oropendolas inhabit lowland rain forests ranging from southern Mexico to central Panama (Skutch 1954). This species is large (adult male body mass $>$ 500 g) and highly sexually dimorphic in body size (male body mass is more than two times greater than that of females; Webster 1991). Females nest colonially in trees separated from the surrounding forest canopy. The median number of nests in a colony is 20 to 25, but colonies can range up to over 100 nests in a single tree (Fraga 1989, Webster 1994b). Female oropendolas construct nests and care for their young with no assistance from the males (Skutch 1954).

Patterns of competition among male Montezuma Oropendolas for access to sexually-receptive females at nesting colonies are described in detail elsewhere (Webster 1994a). A highly linear dominance hierarchy exists among males. The top male in this hierarchy, the alpha male, spends most of each day at the colony and physically prevents other males from approaching females there. During periods when the alpha is absent, a lower-ranking male (usually the beta) takes his place in the colony and continues to exclude all lower-ranking males. Males focus their defensive efforts on those areas of the colony containing the highest number of sexually-receptive females, and the number of males competing at the colony increases with the number of such females.

Field methods.—I studied a population of Montezuma Oropendolas at the Estación Biológia La Selva in Sarapiquí, Costa Rica (see McDade et al. 1993) during each breeding season (January-May in Costa Rica) from 1986 to 1990. Birds were captured with mist nets placed near nesting colonies and at foraging sites baited with bananas. At the time of capture, I used a wing rule to measure flattened wing length to the nearest millimeter, and dial calipers to measure culmen length and tarsus length to the nearest 0.1 mm. I also used a Pesola scale to weigh each individual to the nearest gram, and marked each individual with a unique combination of leg bands made from colored PVC plastic. Body size was used to determine the sex of each bird

TABLE 1. Summary of colony sites monitored and blood samples collected for paternity analyses in 1989.

	Colony site				
	Comando[a]	Ingrid's[a]	Milagro[b]	Colony B	Total
No. nests	22	14	10	61	107
Hours observed	270	80	20	15	385
Sampled (identity if known)					
Alpha	Yes (RRR)	Yes (RRR)	Yes (GOG)	Yes (SH5)	4
Beta	Yes (OMO)	Yes (OMO)	No	No	2
Other males	2	0	1	4	7
Nest females[c]	1	2	4	0	7
Other females[c]	3	4	3	4	14
Nestlings	4	5	5	7	21

[a] The Comando and Ingrid's sites were part of the La Selva Colony in 1989.

[b] Colony unusually close (ca. 300 m) to much larger colony of 35 nests.

[c] Nest females were those associated with nest from which nestling sample was also collected (i.e. presumed mothers of those nestlings), and other females were those associated with nests from which no nestling sample collected.

(Webster 1991). I marked 61 males and 58 females during this study. Many unmarked individuals of both sexes were present in the study area.

Most behavioral data were collected at a focal-observation colony (La Selva Colony) during each season. Depending on the year, most or all adult males and a few females were color banded and individually recognizable at this colony. Although the location of the focal colony changed each year of this study, most of the males competing there were the same from one year to the next (Webster 1994a, b). Colony observations were conducted from around dawn until late morning (ca. 1130 EST), and from midafternoon (ca. 1430) until dusk. Scan samples, in which I and several field assistants noted the location and activities of all individuals visible in the colony area, were conducted every 20 min. In addition, we recorded courtship displays, attempted and successful copulations, and aggressive interactions among males (chases and fights). Males were ordered in a dominance hierarchy based on the outcome of aggressive interactions (Webster 1994a); the alpha male was the one aggressively able to displace all other males at the colony, and the beta was that male able to displace all males except the alpha, and so forth.

Males courted females by performing a series of deep-bowing displays with rapid pecking on the female's tail between each bowing display (for full description of displays, see Webster 1991). Courtship was loud and vigorous and could be heard easily from a distance of more than 150 m. Courtship displays were relatively infrequent, were directed primarily at females near egg laying (see below), and usually proceeded to attempted mounting unless the female left the colony area. Therefore, I defined an attempted copulation as any occasion when a male initiated courtship displays in close proximity (<1 m) to a female, and the copulation was considered successful if he mounted and made cloacal contact. A female was defined as being sexually receptive during the period if she was observed regularly bringing leaves to her nest (the last stage of nest construction), as 28 of 30 observed copulations involved females at or within two days of this stage in the nesting cycle (Webster 1994b).

During the 1989 breeding season, four separate colony sites were monitored for paternity analyses (Table 1). Two of these, the Comando site and Ingrid's site, were sites of the focal-observation colony (La Selva Colony) that year. Females nested at the Comando site early in the 1989 season. Midway through the season, though, these females were disturbed by our efforts to access nests (see below) and moved to Ingrid's site, which was located approximately 0.5 km from the Comando site (see Webster 1994a). Therefore, many of the adults active at the Comando site also were active at Ingrid's, including the alpha and beta males (Table 1). The third site, Colony B, was the nearest neighboring colony site to Comando and Ingrid's (1.5 km away), and the fourth site, Milagro Colony, was about 6.5 km from the other three sites. The Milagro Colony was located very near (≤300 m) a much larger colony (Chilamate Colony, 35 active nests).

Blood samples (ca. 0.3 ml) were collected from as many adults active at these four colony sites as possible (Table 1). Five adults were killed (AOU guidelines were followed; Oring et al. 1988), but samples from most adults were collected at the time of capture and had no visible effect on their subsequent behavior. Many unsampled adult males were present in the vicinity of each colony site and may have sired offspring. Blood samples were collected from nestlings by using mountain-climbing ropes and equipment to access nests (after Perry 1978). Because the process of accessing nests was highly disruptive to the colony, we were only able to sample a handful of nests at each site (Table 1), for a total of 21 sampled nestlings from 20 different nests. Seven of the adult females sampled were associated with nests from which a nestling sample also was collected.

DNA-profile analyses.—All molecular analyses were performed in the laboratory of C. F. Aquadro at Cornell University, following methods detailed in Westneat (1990) and using the restriction enzyme *Hae III.* Each resulting blot was probed twice—once with replicative form M13 DNA (Vassart et al. 1987) and once with Jeffreys 33.15 (Jeffreys et al. 1985a, b). These DNA fragments are multilocus probes that label several hypervariable minisatellite regions to produce complex banding patterns (Jeffreys et al. 1985b, Georges et al. 1988). I used the degree of band sharing between two individuals as a measure of the degree of genetic similarity between them (Burke and Bruford 1987, Wetton et al. 1987).

DNA samples from all nestlings and adults associated with a colony site were run on the same gel. Most comparisons were made between individuals separated by fewer than six lanes, and no comparisons were made between lanes on different gels. Bands in two lanes were considered to be identical if they were within 0.5 mm (vertical migration distance) of each other and of similar intensity. Bands visible in a lane were not scored if the presence or absence of that band in the second lane could not be judged. Band sharing between two individuals (S) was calculated as

$$S = 2n/T, \tag{1}$$

where n is the number of bands shared, and T is the total number of bands scored in both lanes (Wetton et al. 1987, Westneat 1990).

Assignment of paternity proceeded in three steps. First, I calculated the proportion of bands shared between adult birds. Given the number of comparisons made, the small clutch size in this species, and the wide-ranging habits of adults, it is likely that many of these adults were unrelated to each other. Therefore, I used the distribution of band-sharing scores for adults as an expected distribution for band sharing between unrelated individuals. Note, however, that this distribution may be biased upward if some adults were related to each other. Second, this distribution was compared to that of band sharing between offspring and adult females. Each nestling was compared to all females sampled at its colony site including, when possible, the nestling's putative mother (dam), as well as females associated with other nests (nondams). Finally, the distribution of band sharing between nestlings and adult males was compared to the above two distributions. A nestling was considered to be the offspring of a particular male if the band-sharing score for those two individuals fell above the distribution of band sharing between adults and within the distribution of band sharing between nestlings and their mothers. Unfortunately, analyses based on the number of "novel fragments" present in the nestling's lane but not in either of the parents (e.g. Westneat 1990) could not be performed because I obtained samples from both parents for only a single nestling (see below).

For band-sharing scores, calculation of standard deviations and standard errors for statistical comparisons are complicated by the fact that each individual is compared to several others, such that pairwise band-sharing scores are not independent of each other (Lynch 1988, 1990). To avoid problems of nonindependence, I used equations 7 to 9 in Lynch (1990) to calculate unbiased estimates of the standard deviation and standard error of mean band-sharing scores (unless otherwise indicated).

Band-sharing scores also were used to estimate average coefficients of relatedness (i.e. the average proportion of genes in two individuals that are identical by descent) among nestlings at a colony site. Although it is difficult to use band sharing to determine the genetic relatedness of any given pair of individuals (Lynch 1988), the average level of band sharing for a group of individuals often does correlate with average relatedness among individuals within that group (Jones et al. 1991, Haig et al. 1993). Therefore, average band sharing can be used to estimate average relatedness within a group (Reeve et al. 1992). Following Reeve et al. (1992), if w is the mean band sharing within a group and b is the mean band sharing between groups (equal to mean degree of band sharing between unrelated individuals), then average relatedness among individuals in the group (r) can be estimated by

$$r = (w - b)/(1 - b). \tag{2}$$

For this study, I used average band sharing among adults as an estimate of band sharing among unrelated individuals (see above). Because some adults may have been related to each other, I may have overestimated b and consequently underestimated r. To judge the magnitude of any such error, I used the method of Reeve et al. (1992) to estimate r for groups of known relatedness. Nevertheless, estimates of r given below should be considered approximate, and they should be used for comparisons among groups in this study and not for comparison to estimates derived in other studies.

RESULTS

Observed copulation success.—The alpha male obtained 90 to 100% of the copulations observed at the La Selva Colony in all but one season (Table 2). The one exception to this pattern occurred in the latter half of 1988, when a new male (EJ) appeared at the Coop site midway through the breeding season. This new male assumed the alpha position, effectively disrupting the normal pattern of copulations. Af-

TABLE 2. Observed copulation success at La Selva Colony by year (with site in parentheses).

Male	Rank	Percent scans in colony	Copulations				
			No. successful	Percent all copulations	No. attempted	No. interrupted	Percent acceptance[a]
			1987 (Coop)				
RRR	Alpha[b]	57.7	11	100.0	53	7	23.9
OMO	Beta	16.6	0	0.0	14	0	0.0
RBR	Gamma	4.3	0	0.0	2	0	0.0
BBW	Delta	2.0	0	0.0	0	0	0.0
			1988[c] (Coop, early)				
RRR	Alpha	58.0	8	87.5	33	0	24.2
OMO	Beta	13.5	2	12.5	13	0	15.4
			1988[c] (Coop, late)				
EJ	Alpha	52.6	2	13.3	14	0	14.3
RRR	Beta	17.4	12	80.0	18	1	70.6
OMO	Gamma	14.1	1	6.6	6	2	25.0
			1989 (Comando)				
RRR	Alpha	50.1	34	89.5	91	8	41.0
OMO	Beta	14.9	4	10.5	29	1	14.3
			1989 (Ingrid's)				
RRR	Alpha	—	4	—	—	—	—
OMO	Beta	—	0	—	—	—	—
			1990 (LS Road)				
RRR	Alpha	78.4	9	90.0	—	—	—
OWO	Beta	16.2	1	10.0	—	—	—
GRG	Gamma	0.0	0	0.0	—	—	—
			Total (all years)				
—	Alpha	—	68	77.3	—	—	—
—	Beta	—	19	21.6	—	—	—
—	Gamma	—	1	1.1	—	—	—

[a] Calculated as $100n_s/(n^a - n_i)$, where n_s is number of successful copulations, n_a is number of attempts, and n_i is number interrupted.

[b] Male RRR not marked until midseason, after most copulation attempts at colony had occurred. However, observations of aggressive interactions and male attendance at colony indicate that male RRR was the unmarked male at colony that obtained all copulations.

[c] Copulation data from first half of season (on or before 21 February) and second half (after 21 February) reported separately.

ter male EJ's arrival, the former alpha (RRR) obtained more copulations than the new alpha. The majority of copulations obtained by RRR during this period (11 of 12) occurred within eight days of male EJ's first appearance at the colony. In total, the alpha male obtained 77.3% of all copulations, or 90.3% if the data from the latter half of 1988 are excluded. Virtually all other copulations were obtained by the beta male; only a single observed copulation was obtained by a lower-ranking male in all four years of study.

Several males visited colonies even though they were not observed to copulate. The mean number of marked males that visited a colony site (present >5% of all scans made) increased with the number of females nesting there (Fig. 1; *rho* = 0.94, $Z = 2.49$, $P = 0.01$). This number gives a minimum estimate for the number of males competing for mates at each colony.

Female mate choice.—The success or failure of a copulation attempt appeared to be under the female's control; no forced copulations were observed, and females terminated 209 copulation attempts (54.1% of all copulation attempts, 70.8% of all unsuccessful attempts) by moving away or acting aggressively toward the male. Although males sometimes persisted in following and courting a female that had moved away, females mated with such persistent males only nine times (4.3% of all initial rejections). On most other occasions the female left the colony area entirely or bit the male and pecked at him until he left her alone. In addition, females occasionally approached and solicited copulations (i.e. raising her tail) from a male before he be-

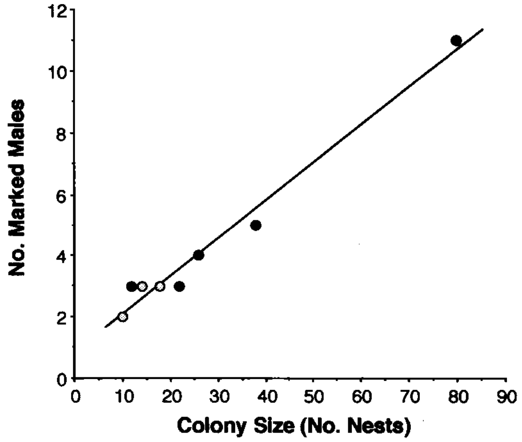

Fig. 1. Colony size (number of completed nests) versus total number of marked males present at colony for 5% or more of scans. Filled circles indicate colony observed more than 100 h. Number of marked males visiting colony is minimum estimate of number of males competing for mates there, as it excludes unmarked males and males that rarely visited colony, but courted females away from it.

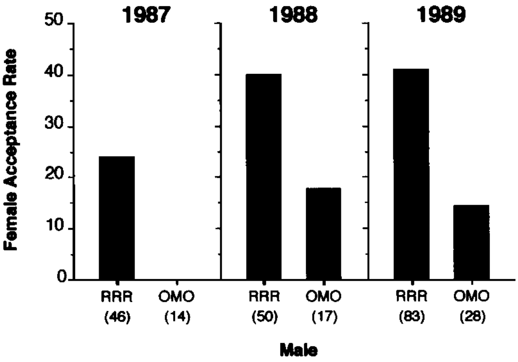

Fig. 2. Proportion of copulation attempts accepted by females for alpha male (RRR) and beta male (OMO) at Coop (1987 and 1988) and Comando (1989) sites of La Selva Colony. Number of copulations attempted by each male (excluding attempts interrupted by other males) in parentheses. Height of each bar shows proportion of these attempts that led to cloacal contact. Difference between RRR and OMO significant ($P < 0.05$) in 1987 and 1989, and approaching significance ($P < 0.10$) in 1988.

gan courtship displays (11.4% of 88 successful copulations).

Females at the focal nesting colony appeared to copulate preferentially with the alpha male (RRR), as this male had a significantly higher female acceptance rate (number of successful copulations per attempted copulation) than the only other male to obtain numerous copulations, the beta male (Fig. 2). This was not because the alpha male was better able to monitor the nesting stage of females in the colony; the proportion of copulation attempts directed toward sexually-receptive females (58%, $n = 84$ copulation attempts for which the female involved could be identified) did not differ significantly between males of different rank ($X^2 = 0.08$, df = 1, $P = 0.778$). Furthermore, copulation attempt rates did not appear to be associated with male rank; the relative number of copulations attempted by RRR and OMO did not differ from expectation based on amount of time each spent in the colony (Table 2; $X^2 = 0.125$, df = 1, $P = 0.723$, 1987-1989 data combined).

Interactions away from colony.—Away from nesting colony, female oropendolas formed scattered, loosely organized groups that usually foraged high in the canopy. The mean number of females in foraging groups was 5.3 ± SD of 4.0 ($n = 48$ female groups whose composition could be determined). This probably underestimates female group size, as the dense canopy made it difficult to determine the composition of most groups, particularly large ones.

Adult males followed and appeared to defend females in foraging groups; 26 (54.2%) female groups were accompanied by a single male, and 12 (25%) were accompanied by more than one male. The adult male in a group displayed frequently and chased other males that flew into the area. Males of all ranks were observed accompanying females, including alpha males from nearby colonies, and males rarely or never observed at nesting colonies. Most males not accompanying females (69.7% of 132 males sighted) traveled alone and attempted to join female groups.

Males frequently were observed courting females in the forest. However, due to the difficulty of observing birds high in the canopy, no successful copulations were observed away from the nesting colonies.

DNA-profile comparisons.—Both Jeffreys 33.15 and M13 probes produced individual-specific banding patterns. The mean number of scorable bands per lane was somewhat higher for M13 (32.9 ± 4.8) than for Jeffreys 33.15 (21.0 ± 6.2). Below, I treat the banding patterns produced by each probe separately and in combination

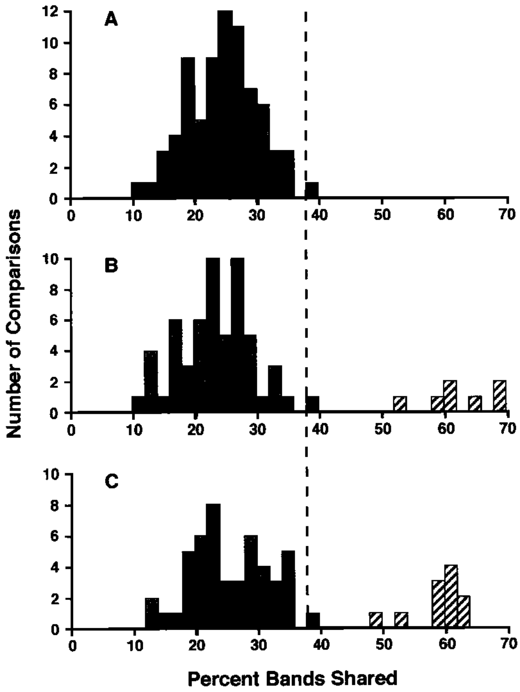

Fig. 3. Distribution of band sharing (both probes combined) for comparisons among: (A) adults; (B) females and nestlings; and (C) males and nestlings. Comparisons between presumably unrelated individuals shown with gray bars. Hatched bars show comparisons between nestlings and dams (in B) or between nestlings and males presumed to have sired them (in C). Dashed vertical line corresponds to upper 99% limit for sharing between unrelated individuals.

(single band-sharing score calculated using all bands scored).

Adult samples run near each other on the same gel shared few bands in common (Table 3), with scores being approximately normally distributed (Fig. 3A). Assuming that most of these adults were unrelated to each other, and using the definition of a normal distribution (Snedecor and Cochran 1980), the probability that two unrelated individuals will have a band-sharing score more than 2.33 standard deviations above the mean is less than 0.01. This upper 99% limit for band sharing between unrelated individuals corresponds to a band-sharing score of 37.8% for both probes combined (for M13 and Jeffreys 33.15, upper limits were 39.1% and 41.0%, respectively).

Band sharing between nestlings and nondams (Fig. 3B) did not differ significantly from band sharing between adults (Table 3). In con-

TABLE 3. Band-sharing scores and estimates of relatedness. Mean percent of bands shared among *n* comparisons of individuals in various groups, with standard deviations corrected for multiple comparisons among individuals (after Lynch 1990). Estimates of average within-group relatedness calculated using combined results of both probes (after Reeve et al. 1992).

Probe	*n*	Percent band sharing[a]	Relatedness	
			Expected	Estimated
		Adults		
Both	75	24.7 ± 5.6	0.000	—
M13	84	25.0 ± 6.1		
33.15	77	23.1 ± 7.7		
		Nestlings and nondams		
Both	57	23.2 ± 5.7^{ns}	0.000	−0.020
M13	57	23.8 ± 6.8^{ns}		
33.15	58	22.0 ± 9.6^{ns}		
		Nestlings and dams		
Both	7	62.0 ± 5.7*	0.500	0.495
M13	7	60.9 ± 8.4*		
33.15	7	64.2 ± 10.0*		
		Nestlings and nonsires		
Both	47	25.4 ± 12.0^{ns}	0.000	0.009
M13	48	26.0 ± 10.0^{ns}		
33.15	48	24.0 ± 17.8^{ns}		
		Nestlings and sires		
Both	11	59.1 ± 4.4*	0.500	0.457
M13	11	59.4 ± 5.7*		
33.15	11	59.2 ± 7.3*		
		Unrelated nestlings		
Both	20	26.7 ± 5.1^{ns}	0.000	0.027
M13	20	25.6 ± 9.9^{ns}		
33.15	20	28.3 ± 9.7^{ns}		
		Half-sib nestlings[b]		
Both	8	43.3 ± 6.2	0.250	0.247
M13	8	44.5 ± 4.9		
33.15	8	40.8 ± 10.7		
		Colony B nestlings[b,c]		
Both	9	32.3 ± 4.3	—	0.101
M13	9	33.7 ± 6.0		
33.15	9	28.8 ± 8.8		
		Milagro nestling[b,c]		
Both	8	42.4 ± 5.6	—	0.235
M13	8	42.5 ± 6.1		
33.15	10	44.9 ± 7.6		

[a] Asterisk (*) indicates average band sharing was significantly different ($P < 0.05$) from band sharing among adults (*t*-tests using SE corrected for multiple comparisons among individuals). An "ns" indicates not significant ($P > 0.05$), and lack of superscript indicates that band-sharing scores not compared to those for adults.

[b] Due to small sample size, SD not corrected for multiple comparisons.

[c] Includes only comparisons between nestlings from different nests and for which father is unknown.

TABLE 4. Male fertilization success (number of nestlings sired) and observed copulation success.

Male rank	Fertilization success (by colony site)					Copulation success (%)[a]
	Comando	Ingrid's	Milagro	Colony B	Total (%)	
Alpha	2	3	0	2	7 (33.3)	66 (90.4)
Lower	2	2	0	0	4 (19.0)	7 (9.6)
Unsampled[b]	0	0	5	5	10 (47.6)	—

[a] Based on four years of observed copulations at the La Selva Colony (Table 2), with latter half of 1988 excluded.

[b] Number of young at each colony that did not show high band-sharing scores with any sampled male (i.e. apparently sired by unsampled male[s]).

trast, comparisons between nestlings and dams gave band-sharing scores that were statistically significantly higher than for comparisons between adults (Table 3). All seven band-sharing scores for dam-offspring comparisons were greater than the 38% expected upper limit for band sharing between unrelated individuals (Fig. 3B).

As with comparisons between females and nestlings, band-sharing scores between adult males and nestlings were distributed in two distinct groups (Fig. 3C). The majority of comparisons gave band-sharing scores that were indistinguishable from scores for adults (Table 3). However, 11 comparisons between nestlings and adult males yielded band-sharing scores above the 99% limit for sharing between unrelated adults (for each probe considered separately and the two combined). These 11 scores did not differ significantly from band sharing between nestlings and their dams (M13, $t = 0.43$, df = 9, $P > 0.10$; Jeffreys 33.15, $t = 1.15$, df = 10, $P > 0.10$; both probes, $t = 1.14$, df = 10, $P > 0.10$). Thus, I conclude that these 11 nestlings were sired by the male with whom they share this high number of bands. One nestling shared a proportion of bands that fell at the cut-off for sharing between unrelated adults with M13 (39%) and both probes combined (38%; see Fig. 3), but was below the cut-off for unrelated individuals based on Jeffreys 33.15 (37%). This nestling was not assigned to the male in question.

Of the 11 nestlings that could be assigned to individual males, 7 were sired by the alpha male at their colony site and 4 were sired by a lower-ranking male (Table 4). These latter four nestlings were from the Comando and Ingrid's sites of the La Selva Colony and were sired by the beta male at those sites (male OMO). The remaining 10 nestlings did not match up with any of the males sampled at or near their colony site and, so, were apparently sired by an unsampled male. The paternity of these 10 nestlings is considered below.

Assignment of paternity allowed some pairs of nestlings to be classified as half-sibs if they shared one parent, or unrelated if they were produced by different pairs of adults. The band-sharing scores for nestlings that could not be assigned to a sampled male can be compared to those for nestlings of known relationship. At Colony B, band-sharing scores among unassigned nestlings from different nests (i.e. both mother and father are potentially different) were significantly lower than those between known half-sibs (Table 3; M13, $t = 4.10$, df = 15, $P < 0.01$; Jeffreys 33.15, $t = 2.50$, df = 14, $P < 0.05$; both probes, $t = 4.20$, df = 12, $P < 0.01$), but did not differ significantly from band sharing among unrelated nestlings (M13, $t = 1.47$, df = 24, $P > 0.10$; Jeffreys 33.15, $t = 0.07$, df = 27, $P > 0.10$; both probes, $t = 1.11$, df = 22, $P > 0.10$). This suggests that, although some of the Colony B nestlings may have been sired by the same male, most probably were not. This result is supported by estimates of average relatedness (r) among nestlings at Colony B. The method of Reeve et al. (1992), which closely estimates r for several groups of known relationship (Table 3), indicates that average relatedness among unassigned Colony B nestlings was quite low and approached that of unrelated individuals.

Results were different for nestlings at Milagro Colony. None of these nestlings matched with either of the two males sampled at that colony site, yet they showed a very high degree of band sharing with each other (Table 3). Band sharing among Milagro nestlings differed significantly from sharing between unrelated nestlings (M13, $t = 3.06$, df = 24, $P < 0.01$; Jeffreys 33.15, $t = 2.88$, df = 26, $P < 0.01$; both probes, $t = 3.42$, df = 26, $P < 0.01$), but not from sharing between known half-sibs (M13, $t = 0.73$, df = 14, $P > 0.10$; Jeffreys 33.15, $t = 0.91$, df = 12, $P > 0.10$; both probes, $t = 0.53$, df = 16, P

> 0.10). Furthermore, average relatedness among Milagro Colony nestlings was as high as r for half-sibs (Table 3), strongly suggesting that most or all of the nestlings sampled at this colony site were sired by a single male.

Paternity of unassigned young.—Although all of the young sampled at Comando and Ingrid's sites of the La Selva Colony were attributed to the alpha or beta males at those colony sites, several of the nestlings produced at Colony B and Milagro were not assignable to any of the males sampled. Before proceeding to estimates of fertilization success, it is first necessary to determine which males might have sired these young. I do this here for each of the colony sites considered separately.

At Colony B, the low genetic similarity among unassigned young makes it unlikely that they were sired by any single male, such as a previous alpha male (if a change in alpha status occurred between laying and sample collection) or a highly successful subordinate male. Furthermore, the alpha male at Colony B (male SH5) was identified before three of the seven sampled eggs had been laid (SH5 sired only one of these three nestlings). It also is unlikely that any of these nestlings were sired by the alpha male from another colony, as the degree of band sharing between each of these seven nestlings and the alpha male at the nearest neighboring colony (male RRR at Comando/Ingrid's; M13 only, $\bar{x} = 28.48\%$, range 10 to 37%), indicated that this male did not sire any. Therefore, it is most likely that these nestlings were sired by several different, low-ranking males.

The high coefficient of relatedness among nestlings at Milagro Colony strongly suggests that most were sired by the same male, yet the alpha male sampled at this colony site did not match with any. Possibly, a change in alpha status had occurred; the alpha male at Milagro was not identified until after all of the sampled eggs had been laid. Furthermore, the Milagro Colony was located very close to a much larger colony (see Methods), and it would have been relatively easy for males and females from either colony to visit and copulate with individuals at the other. Unfortunately, nestlings at the Milagro Colony could not be compared to the alpha male at Chilamate Colony, as no DNA sample was obtained from the latter. It is unclear as to which male(s) sired the young birds sampled at Milagro Colony. Therefore, the analyses presented below were performed both including and excluding this colony.

Fertilization success vs. observed mating success.—Alpha males sired 33.3% of the young sampled at all four colony sites. Because results obtained from the Milagro Colony are difficult to interpret, a better estimate of alpha male fertilization success is 43.8% (i.e. Milagro excluded) to 60% (i.e. highest proportion of young sired by alpha male at any single colony site). At the La Selva Colony (both Comando and Ingrid's sites), all sampled young not sired by the alpha male were sired by the beta male, and at Colony B several low-ranking males seem to have sired young. The distribution of fertilization success can be compared to the distribution of observed copulation success (Table 4); the proportions of young sired by alpha males at the Comando site, Ingrid's site, and Colony B were significantly lower than expected based on the observed copulation success of alpha males ($X^2 = 16.3$, df = 1, $P < 0.001$). These results do not change if the Milagro Colony is included; alpha males at the four colony sites sired fewer young than expected if one assumes that all nestlings at Milagro were sired by low-ranking males ($X^2 = 27.4$, df = 1, $P < 0.001$), or if it is assumed that a change in alpha status occurred and all nestlings at Milagro were sired by a previous alpha male (57.1% sired by alphas; $X^2 = 10.5$, df = 1, $P = 0.001$).

DISCUSSION

Copulation vs. fertilization success of alpha males.—Several studies have demonstrated clearly that, for monogamous birds (reviewed in Westneat et al. 1990, Westneat and Webster 1994) and polygynous birds that form social pair bonds (Gibbs et al. 1990, Bollinger and Gavin 1991, Westneat 1993), a male's success at obtaining social mates does not necessarily reflect his success at siring young. My results indicate that the same may be true for polygynous species in which no pair bond is formed; a male's observed success at obtaining copulations may not necessarily reflect his success in siring progeny. Although alpha male oropendolas monopolize matings at nesting colonies, the fertilization success of alpha males was substantially lower than their observed copulatory success.

It is possible that the discrepancy between observed copulatory success and fertilization success is an artifact of the way in which this study was conducted. Specifically, most of the copulation data were gathered at a single focal colony, whereas the fertilization data were collected at four separate colony sites in a single year. If the focal-observation colony was not representative of most oropendola colonies, the observed results would not be surprising. However, observations at other colonies in the La Selva area suggest that the focal colony was typical. In particular, all colonies observed were dominated by a single alpha male that prevented other males from approaching females (Webster 1991, 1994a; see also Skutch 1954, Fraga 1989), and limited observations of copulations at other colonies indicate that they are biased toward top-ranking males (Webster 1994a). Furthermore, two of the colony sites where blood samples were collected (Comando and Ingrid's) were sites of the focal observation colony. Nevertheless, it is possible that the copulatory success of alpha males varies according to factors such as colony size, a supposition that requires further testing.

If copulatory patterns observed at the focal colony were typical, some factor must limit the alpha male's ability to monopolize fertilization success. At least two possibilities exist—female mate choice, and copulations away from the colony. I examine each of these possibilities below.

Female mate choice.—The hypothesis that success in intrasexual competition is the sole or primary determinant of male oropendola mating success predicts that females should accept male copulation attempts without regard to the male's rank. This prediction was not supported; female oropendolas at the focal-observation colony were more likely to accept a copulation attempt of the alpha male than one of the beta or lower-ranking male. This difference was not due to differences in the rate of copulation attempts by males of different rank, or to some males being better able to monitor female receptivity. Thus, female mate choice appears to reinforce the outcome of intrasexual competition. Similar results have been obtained in other systems characterized by high levels of competition among males for mates (Cox and Le Boeuf 1977, Borgia 1981).

Female mating preferences do not seem to explain the discrepancy between observed male mating success and fertilization success: females appeared to prefer to copulate with alpha males, at least at the nesting colony. These results are somewhat paradoxical, as female cooperation appears to be necessary for successful copulation; no forced copulations were observed in this study. At least two hypotheses might explain this apparent paradox. First, some females might be willing to mate with low-ranking males, but the presence of the alpha male prevents them from exerting this preference while at the nesting colony. Alternatively, the costs and benefits of mate choice may be different away from the colony. For example, if courting males interfere with a female's ability to forage, then females foraging in the forest might copulate with low-ranking males in order to reduce harassment.

Copulations away from nesting colony.—Female oropendolas frequently left the colony to forage in the forest, and low-ranking males frequently were observed following them. Observations of aggressive interactions and the composition of foraging groups (i.e. usually a single male accompanying several females) suggest that males are defending females at locations away from the colony. Although no copulation was observed in the forest, males were observed courting females there. With the possible exception of the Milagro Colony, those young not sired by alpha males apparently were sired by low-ranking males. Because low-ranking males obtained few if any copulations at nesting colonies, they must have sired young by copulating with females in the forest.

Many studies of mammalian female-defense systems have shown that low-ranking males attempt to copulate with females who leave the harem or who are near the edge of it (Wilkinson 1985, Le Boeuf and Mesnick 1990). Although few studies have employed genetic techniques to determine the reproductive success of these males, those that have done so show that the monopolization of fertilizations by the harem-holding male can vary considerably among species. In some species of pinnipeds (Harris et al. 1991, Amos et al. 1995) and bats (McCracken and Bradbury 1981, Wilkinson 1985), top-ranking males sire fewer young than would be expected based on observed copulatory success, apparently because low-ranking males are able to copulate with females at the edge of and/or away from harem sites. In contrast to these results, harem-holding males were found to have sired nearly all young in two species of ground squirrel (*Maromota flaviventris*, Schwartz and Armitage 1980; *Cynomys ludovicianus*, Hoogland and Foltz 1982), and observed mating success appears to be a good predictor of male fertilization success in the female-defense system of red deer (*Cervus elaphus*, Pemberton et al. 1992). However, even in these latter studies, low-ranking or behaviorally unsuccessful males are able to sire some young.

The ability of harem-holding or alpha males to monopolize fertilization success may be related to the grouping behavior of females. For many species, including many ground squirrels and ungulates, female groups are relatively small and discrete. In contrast, for oropendolas, pinnipeds, and some bats, female aggregations can be extremely large and, consequently, difficult to defend. Furthermore, for some of these species, females frequently leave colony sites to forage; an alpha male that remains at the colony and defends females there cannot simultaneously defend females who are foraging. As a consequence, low-ranking males are able to approach, court, and apparently copulate with females away from the colony.

Male fertilization success and rank.—Although alpha males sired fewer young than expected from observed mating success, rough estimates of male reproductive success indicate that alpha males are much more successful than lower-ranking males. Assuming that the proportion of young the alpha male sires at his colony is between 44 and 60%, and given one fledgling per nest and a median colony size of 24 nests (Webster 1991), an alpha male would sire 10 to 15 young per season. In this study, the alpha male at the largest colony (Colony B, 61 nests) sired the lowest proportion of young (29%), suggesting that the fertilization success (proportion of young sired) of alpha males may decrease with increasing colony size. Nevertheless, such an alpha male can expect to sire about 18 young per year (29% of 61 young). Furthermore, alpha males seem able to maintain their status for several seasons; male RRR was the alpha male at the main study colony from 1987 through 1990 (Table 2), and may have been alpha before or after this period. An alpha male that maintains his status for four or more years could sire 50 or more offspring.

In contrast, males lower-ranking than alpha or beta probably have quite low reproductive success each season. Excluding the Milagro Colony, most of the young sampled in this study were sired by known alpha and beta males (11/16 = 69%) and, apparently, several lower-ranking males, rather than a single such male, accounted for the remaining young. Subordinate males apparently sired the most young at Colony B. The relationship between colony size and number of males competing for mates at a colony (Fig. 1) indicates that at least nine males (including the alpha) were competing for mates at that colony site. Excluding the alpha male and the two nestlings he sired, the remaining five nestlings sampled at Colony B were spread among eight or more males. Given the size of Colony B (61 nests) and the estimated success of these eight males, each low-ranking male at a colony the size of Colony B could expect to sire five young per year. This figure probably greatly overestimates the success of low-ranking males because (1) the estimated number of males competing at the colony is a minimum and refers only to the number of males actually appearing at the colony, and (2) the beta male probably obtains more fertilizations than lower-ranking males.

Thus, observed copulatory successes at colonies of the Montezuma Oropendola are a rough indicator of male fertilization success. Fertilizations apparently are biased toward those males able to exclude other males from nesting colonies (i.e. high-ranking males), and at small- and medium-sized colonies the two highest-ranking males may account for most of the fertilizations. At larger colonies lower-ranking males appear able to sire some progeny. While each individual low-ranking male is probably siring a small number of young, their combined effect is to reduce significantly the alpha male's monopolization of mating success.

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