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EXTREME SEXUAL SIZE DIMORPHISM, SEXUAL SELECTION, AND THE FORAGING ECOLOGY OF MONTEZUMA OROPENDOLAS

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ABSTRACT.—Sexual differences in body size usually are considered to be a product of either sexual selection or ecological divergence between the sexes. I tested the predictions of these hypotheses to explain extreme sexual dimorphism in size in a Neotropical blackbird, the Montezuma Oropendola (*Psarocolius montezuma*). Sexual dimorphism was more pronounced in wing length and relative mass, traits that appear to be important in courtship and competition for mates, than in bill length or tarsus length. Male dominance rank, which is an indicator of mating success, was positively associated with body size (i.e. high-ranking males were larger than low- ranking males). These results suggest that sexual selection acts to increase male body size, and hence contributes to sexual size dimorphism in this species. Differences in foraging behavior and diet also existed between the sexes and were related to sexual size differences. The small size of females allowed them to forage on food resources that were difficult for the larger males to reach (e.g. insects in rolled leaves at the ends of branches). Females, though, did not appear to be restricted from those resources exploited by males (primarily epiphytal bromeliads). Although it was not possible to reject the ecological-divergence hypothesis, my results suggest that sexual foraging differences are a consequence rather than a cause of sexual dimorphism in size in this species. *Received 23 August 1996, accepted 18 March 1997.*

SEXUAL DIFFERENCES IN SIZE AND SHAPE are widespread among animals, and attempts to explain them represent a major theme in evolutionary biology that dates back to Darwin (1871). For birds and mammals, two main hypotheses have been proposed to explain body-size differences between the sexes. The first of these, the sexual-selection hypothesis, proposes that large body size in one sex (usually males) is favored because it confers an advantage in intrasexual competition for mates and/or because females prefer large males. Natural selection, acting through ecological factors such as foraging efficiency and predation, is assumed to favor the same size in both sexes, but sexual selection is thought to push males toward larger sizes. Alternatively, the ecological-divergence hypothesis postulates that foraging and/or other ecological factors favor different body sizes in the two sexes. For example, different sizes might result because the sexes differ in their nutritional requirements (such that they use different food resources) or in their reproductive roles (e.g. incubation vs. nest defense). Intersexual divergence also might arise if it reduces intersexual competition for food resources (sexual foraging-niche divergence), a process analogous to interspecific niche partitioning and character displacement (Selander 1972, Slatkin 1984, Hedrick and Temeles 1989, Shine 1989).

The sexual-selection hypothesis has received a great deal of attention and is widely accepted as an explanation for sexual size dimorphism. This hypothesis is supported by both theoretical genetic models (Lande 1980) and interspecific studies demonstrating an association between sexual dimorphism and the intensity of competition among males for mates (e.g. Clutton-Brock et al. 1977, Alexander et al. 1979, Oakes 1992, Webster 1992, Fairbairn and Preziosi 1994; but see Höglund 1989; Björklund 1990, 1991). For intraspecific studies, this hypothesis predicts that large males have an advantage in obtaining matings, and that large male size carries with it an ecological cost. Some studies of size-dimorphic birds have demonstrated a large-male mating advantage (see Andersson 1994, Searcy and Yasukawa 1995), but several have not. Relatively few studies of birds have demonstrated an ecological cost of large male size. For example, some studies have demonstrated that large males have

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lower survival than small males (e.g. Yasukawa 1987), whereas others have found no such relationship (Weatherhead et al. 1987, Björklund and Lindén 1993, Weatherhead and Clark 1994).

The ecological-divergence hypothesis is the standard alternative to sexual selection (Darwin 1871, Selander 1972, Shine 1989) and is supported by theoretical models (Slatkin 1984). Although many ecological differences between the sexes could lead to sexual size dimorphism, most theoretical and empirical studies have focused on foraging differences between the sexes (e.g. Wallace 1974, Schoener et al. 1982, Askins 1983, Camilleri and Shine 1990, Shine 1991, Houston and Shine 1993). Support for this hypothesis requires that the sexes partition food in a way that favors size differences in body parts associated with foraging.

In this paper, I test predictions of the sexual-selection and ecological-divergence hypotheses for the Montezuma Oropendola (*Psarocolius montezuma*), one of the most sexually size-dimorphic of all birds (see below). I follow other studies of the ecological-divergence hypothesis and focus on foraging ecology. To distinguish between the alternative hypotheses, I examine sexual dimorphism and the role body size plays in both competition for mates (males) and foraging (both sexes) in this species. Because the relatively inaccessible nests of Montezuma Oropendolas made it difficult to monitor female reproductive success, I do not consider potential evolutionary forces that might push female size away from the ecological optimum, such as social competition or fertility selection (Ralls 1977, Price 1984, Robinson 1985a, Langston et al. 1990).

METHODS

Study species.—The Montezuma Oropendola is a Neotropical member of the New World blackbird family (Icteridae). It inhabits lowland rain forest habitats from southern Mexico to the Canal Zone in Panama, and breeds during the dry season (January to May in Costa Rica; Skutch 1954). I studied a color-marked population of these birds during the 1986 to 1990 breeding seasons at the La Selva Biological Station in Costa Rica (see McDade et al. 1993).

Male and female Montezuma Oropendolas differ greatly in body size but not in plumage coloration. Individuals of both sexes have bare patches of skin in the face; in adult males these patches are brightly colored and swollen to form wattles, whereas in females and juvenile males the skin patches are pale and not swollen. In addition, the outermost primaries of adult males are extremely elongated and twisted relative to those of females and juvenile males. Air rushing between these modified primaries produces a deep "whooshing" sound used by males during agonistic and courtship displays (Webster 1991).

Montezuma Oropendolas have been described as frugivorous or omnivorous (Skutch 1954, Orians 1985). Like most members of their subfamily, oropendolas forage for animal prey by "gaping" (Beecher 1951, Orians 1985). A gaping bird inserts its bill into the leaves or stem of a plant (e.g. an epiphytal bromeliad) and opens its bill to pry apart the plant parts and expose potential prey hiding within.

Female oropendolas nest colonially in free-standing trees isolated from the surrounding forest (Skutch 1954, Fraga 1989, Webster 1994b). Previous results have shown that the mating system of the Montezuma Oropendola is one of harem-defense polygyny (sensu Emlen and Oring 1977) characterized by high levels of intrasexual competition between males for access to sexually receptive females (Webster 1994a). Males compete for positions at nesting colonies and, based on the outcome of aggressive interactions, can be ordered in a linear dominance hierarchy. Top males in this hierarchy (those winning the most aggressive interactions) physically exclude other males from nest-building females. Typically, a single male defends an entire colony of 10 to 30 females, although lower-ranking males often remain in nearby trees and enter the nesting colony when higher-ranking males are absent. Observed male mating success within a colony is extremely biased toward high-ranking males; alpha and beta males obtain virtually all observed copulations (Webster 1994a). Further, genetic studies have shown that although subordinate males obtain some fertilizations by copulating away from the nesting colony, top-ranking males (alpha and beta) sire more offspring than do other males (Webster 1995).

Capture and marking.—I captured a total of 76 males and 73 females using elevated mist nets (Mease and Mease 1980) placed near nesting colonies and at foraging sites baited with bananas. At the time of capture, I measured (flattened wing length, culmen length, tarsus length), weighed, and individually marked birds with colored leg bands (body-mass data were not collected in 1986). Although sample sizes were small, body mass did not appear to vary substantially within a season; three males that were captured twice in the same season differed by only 2 to 5 g between their first and second captures. For analyses, I used mean body mass for individuals captured more than once ($n = 6$).

I determined the sex of captured individuals based on body size. Measures of museum skins showed no overlap in tarsus length between the sexes; male tarsi exceed 60 mm in length, whereas female tarsi are shorter than 60mm. Subsequent observations of marked individuals revealed no cases in which an individual classified as a male behaved as a female (i.e. nest building, incubation, feeding nestlings) or vice versa. I used the presence of swollen face wattles to distinguish adult males from juvenile males.

Colony observations.—I monitored activity at a focal colony (La Selva Colony) during the peak of breeding activity each year (total of 1,200 h), and recorded colony attendance, aggressive interactions between males, and copulation attempts during these periods. In addition, I visited all known colonies near the focal colony several times throughout a season (Webster 1994a, 1994b). On each visit to one of these colonies, I noted the males present and the outcome of any aggressive interactions that occurred.

As an estimator of male mating success, I measured male dominance rank at breeding colonies because this measure has been shown to be a strong correlate of observed male mating success (Webster 1994a, 1995). Males at each colony were assigned a dominance rank based on the outcome of aggressive interactions (Webster 1994a). The alpha male was that male able to aggressively displace all other males, the beta male was that male able to displace all males except the alpha, and so forth. Male ranks seemed stable throughout the course of a breeding season; no case of two males changing relative rank were recorded. Based on dominance rank, adult males at the focal colony were placed into one of two categories: (1) "upper" males were higher-ranking than at least half of the marked males at the colony, and (2) "lower" males were lower-ranking than half or more of the marked males at that colony. For colonies that I visited but did not intensively observe during the season, "upper" males were marked males observed to win at least half of their aggressive interactions, and "lower" males were marked males that lost half or more of their aggressive interactions. Finally, "noncolony" males were those males that were rarely (fewer than 5% of scans made) or never observed at any of the nesting colonies.

Foraging observations.—I searched for oropendolas along forest trails. When a foraging bird was encountered, I recorded its sex, age class (males only), the item it was foraging on, its method of foraging, and the location and approximate diameter of the limb where the bird was standing. The location of the bird on the limb was noted using a categorical system that divided the limb into five zones of approximately equal length from base to tip end. The approximate diameter of the limb was noted with reference to the bird itself: "thin" limbs were thinner than the diameter of a male's tarsus (ca. 1.5 times the diameter of a female's tarsus); "medium" limbs were thicker than the diameter of a male's tarsus, but less than approximately 3.75 cm (i.e. 1.5 inches) in diameter; and "thick" limbs were greater than 3.75 cm in diameter. During the 1990 season, if I encountered a bird foraging in epiphytal bromeliads (a common food for oropendolas; see below), I also noted the approximate size of the bromeliad. I classified bromeliads as "small" if they were smaller than the size of a female (ca. one-half the body size of an adult male), "medium" if they were larger than a female but smaller than an adult male, and "large" if they were larger than an adult male. I recorded foraging data for only the first foraging observation after an individual was encountered. If I encountered a group of birds foraging together on the same food item, I collected data only on the first foraging individual of each sex that I observed in order to avoid problems of nonindependence.

RESULTS

Body size and sexual dimorphism.—Relative to females, male oropendolas were approximately 30% larger in most of the linear measures and more than 100% larger in body mass (Table 1). The distribution of body mass for adult males did not overlap that for females (Fig. 1). This size difference between males and females makes this species one of the most sexually size-dimorphic of all birds (Fig. 2). Juvenile males were intermediate in size between adult males and females. The size differences between males and females were evident at the time of fledging (Table 2). Analyses of covariance indicated that both tarsus length and sex were independently associated with wing length and body mass (although the significance of the effect of sex on mass was marginal), and there was a significant interaction between sex and tarsus length for these measures (Table 3). If tarsus length is taken as a general indicator of overall body size (see Rising and Somers 1989, Freeman and Jackson 1990), then these results suggest that relative mass and wing length are greater in males than in females. In contrast, the relationships between sex and tarsus length versus culmen length were not significant.

Male size, dominance rank, and mating success.—Male body mass was associated with dominance rank category (ANOVA, $F = 7.72$, df $= 2$ and 29, $P = 0.002$; Fig. 3A). Similar results were obtained using body condition (mass/tarsus, $F = 5.22$, df $= 2$ and 29, $P = 0.012$) and tarsus length ($F = 3.74$, df $= 2$ and 29, $P = 0.036$) as a size measure, but not using wing length ($F = 1.54$, df $= 2$ and 28, $P = 0.233$) or culmen length ($F = 0.39$, df $= 2$ and 29, $P =$

TABLE 1. Size measures ($\bar{x}$ ± SD, n in parentheses) and dimorphism scores ($\bar{x}$ ± SE) of captured Montezuma Oropendolas. All differences between males (adults and juveniles combined) and females are significant (t-tests, Ps < 0.001), as are all differences between adult and juvenile males (t-tests, Ps ≤ 0.01) except for culmen/tarsus ($t = 0.887$, $P = 0.380$).

Measure	Females	Adult males	Juvenile males	Dimorphism[a]
Mass (g)	245.8 ± 14.4 (58)	515.9 ± 40.8 (33)	418.8 ± 30.4 (14)	2.09 ± 0.037
$\text{Mass}^{1/3}$	6.26 ± 0.12 (58)	8.01 ± 0.21 (33)	7.47 ± 0.18 (14)	1.28 ± 0.008
Tarsus (mm)	53.71 ± 1.54 (56)	67.37 ± 2.27 (33)	66.03 ± 1.83 (14)	1.25 ± 0.009
Culmen (mm)	60.01 ± 2.53 (54)	77.65 ± 3.28 (33)	75.69 ± 3.27 (14)	1.30 ± 0.012
Wing (cm)	20.18 ± 0.97 (50)	26.76 ± 1.14 (32)	23.32 ± 1.44 (12)	1.33 ± 0.013
Mass/tarsus	4.58 ± 0.21 (54)	7.64 ± 0.49 (33)	6.35 ± 0.48 (14)	1.67 ± 0.021
Culmen/tarsus	1.12 ± 0.05 (54)	1.15 ± 0.06 (33)	1.15 ± 0.07 (14)	1.03 ± 0.012
Wing/tarsus	0.38 ± 0.02 (50)	0.40 ± 0.02 (32)	0.35 ± 0.03 (12)	1.06 ± 0.011

[a] Dimorphism is the ratio of mean value of adult male to that of female. SE estimates were made using a bootstrap method (Lanyon 1987). Dimorphism scores were obtained by randomly choosing (with replacement) a subset of males from the total pool of males and a subset of females from the total pool of females (the number chosen was equal to the number in the original sample), calculating a mean size measure from the subset for each sex, and then calculating a dimorphism score as the male/female ratio. Values are means from 100 repetitions.

0.679). Fisher's LSD post-hoc tests showed that all differences in size measures were due to statistically significant differences ($P < 0.05$) between "upper" versus "lower" and "noncolony" males; "lower" and "noncolony" males did not differ significantly from each other in any of the size measures ($P > 0.10$ in all cases).

I was able to examine male body size and rank within a single colony, Crocodile Point, in 1988 (Fig. 3B). Male dominance rank was significantly correlated with body mass ($r_s = -0.661$, $n = 10$, $P = 0.024$) and mass/tarsus ($r_s = -0.697$, $P = 0.018$), but not with tarsus length ($r_s = -0.285$, $P = 0.195$). Except for two males (ranks 5 and 11), all size measures used in this analysis were obtained in 1988, the same year that dominance ranks were determined; size measures for the other two males were obtained in the previous season (1987). If the two males whose masses were recorded in 1987 are excluded from the analysis, the correlations drop slightly (mass vs. rank, $r_s = -0.595$, $P = 0.057$; mass/tarsus vs. rank, $r_s = -0.619$, $P = 0.051$). The marginal significance in these latter analyses may be due to small sample sizes ($n = 8$ males).

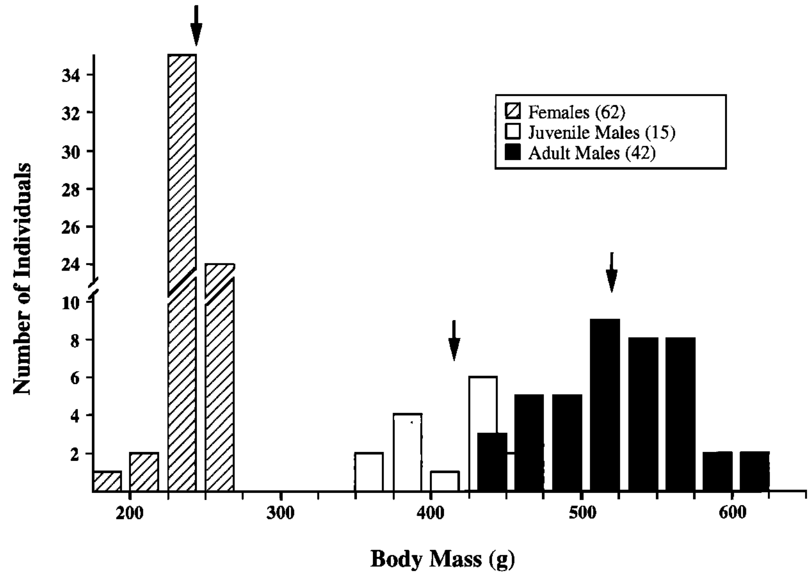

FIG. 1. Distribution of body mass for captured female, juvenile, and adult male Montezuma Oropendolas. Arrows indicate mean body mass for each group; sample sizes in parentheses.

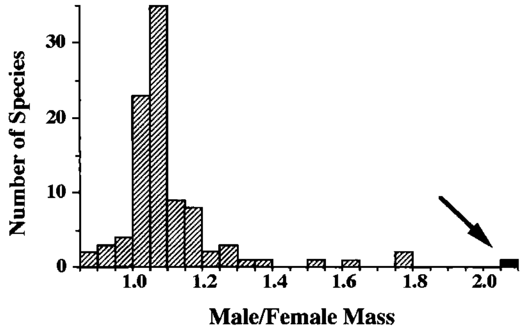

FIG. 2. Distribution of sexual size dimorphism scores (male/female mass) for 97 species of North American passerines for which data on male and female body mass were available (hatched bars; from Dunning 1984) and for Montezuma Oropendolas (arrow; this study).

TABLE 2. Size measures ($\bar{x}$ ± SD) of male and female Montezuma Oropendolas based on five males and six females at or near the age of fledging.

Measure	Males	Females	t
Tarsus (mm)	65.47 ± 2.13	52.55 ± 1.50	11.81**
Culmen (mm)	40.11 ± 3.79	33.97 ± 1.92	3.49*
Mass (g)	252.8 ± 30.0	181.2 ± 19.9	4.75**

*, $P < 0.01$; **, $P < 0.001$.

Males RRR and OMO were the alpha and beta males, respectively, at the focal colony during the 1987 to 1989 breeding seasons. Together, these two males accounted for 81 of 84 observed copulations (Webster 1994a, 1995). These two males also were heavier than most other males caught during this study (Fig. 3A). Indeed, RRR, who accounted for 88% of all observed copulations during the course of this study, was the heaviest male ever captured; his mass was nearly two standard deviations above the mean for adult males.

General foraging behavior and diet.—Oropendolas were extremely omnivorous and consumed a wide variety of plant (both fruit and nectar), invertebrate, and vertebrate prey (Table 4). Individuals gaped for animal prey primarily in the leaves and roots of epiphytes (58.2% of 261 gaping observations), particularly bromeliads (83.5% of 152 observations of gaping at an epiphyte), and in curled leaves at the end of limbs (27.6% of 261 gaping observations). Arthropods and small vertebrate prey were taken at these sources. Occasionally, oropendolas were observed gaping open rotted wood and twig stems, and gaping also was the method used to open large fruits, such as bananas and papayas.

In contrast to animal prey, oropendolas obtained most plant foods either by plucking (pulling small fruits from the ends of branches) or nectar-drinking (inserting the bill into a flower, followed by raising and tilting the head back). Although less frequently observed than gaping, plucking and nectar-drinking accounted for a substantial number of the foraging observations (18.3% and 15.5% of 394 foraging observations, respectively).

Size and sexual foraging differences.—Males and females differed in the thickness of perches used during foraging (Fig. 4). Adult males tended to use thick perches, whereas females perched more on thin limbs. Perch choice, in turn, was associated with sexual differences in foraging location along the length of the limb; females foraged more than twice as often as males at the thin tip end of the limb (Fig. 5). Females did not forage toward the tips of branches because they were forced to do so by males; the distribution of foraging locations when females foraged alone did not differ from that when females foraged in the presence of males ($\chi^2 = 0.59$, $P = 0.444$). Juvenile males, who are intermediate in size between adult males and females, did not differ significantly in foraging location from adult males ($\chi^2 = 7.03$, df = 4, $P = 0.134$) or females ($\chi^2 = 4.57$, df = 4, $P = 0.335$), indicating that they were intermediate between the adults in location of

TABLE 3. Results of analysis of covariance on size measure of male and female Montezuma Oropendolas.

Source	F	P
Body mass		
Tarsus length	19.98	<0.001
Sex	3.36	0.070
Tarsus length × sex	5.20	0.025
Wing length		
Tarsus length	4.12	0.045
Sex	4.59	0.035
Tarsus length × sex	6.05	0.016
Culmen length		
Tarsus length	1.66	0.201
Sex	0.95	0.331
Tarsus length × sex	0.06	0.807

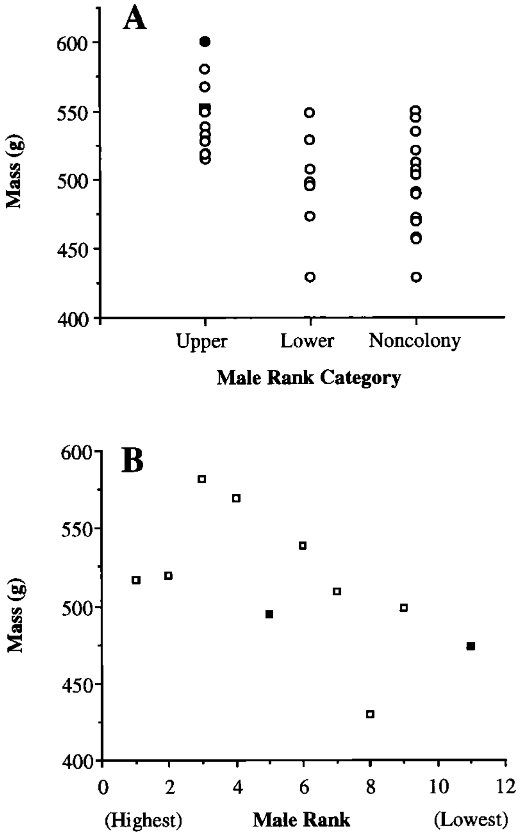

FIG. 3. Association between body mass and dominance rank in male Montezuma Oropendolas. (A) Body mass of males in different categories of dominance rank (see text) at all observation colonies. Filled symbols represent the alpha (circle) and beta (square) males at the focal colony. (B) Body mass versus dominance rank for male Montezuma Oropendolas at the Crocodile Point Colony, 1988. Body mass was measured in 1988 (open squares) or 1987 (shaded squares).

foraging (n = 60 observations of foraging juvenile males).

Adult males and females differed significantly in the amount of time they spent foraging on rolled leaves and epiphytes (Fig. 6). Almost all (67 of 72) individuals observed gaping open rolled leaves to search for insect prey were females. Normally, rolled leaves are located at the very tip of branches, where the diameter of the limb presumably is too thin to support the greater bulk of a male. Four of the five observations of males foraging on rolled leaves were cases in which the male was able to reach the leaves while perched on a thick limb. Males foraged more on epiphytes than did females, but the sexes did not differ in their foraging on other food resources (Fig. 6).

As was the case for rolled leaves, small fruits and flowers tended to occur near the ends of branches. Therefore, it is surprising that males foraged on these resources as often as did females. However, males tended to perch on thick- and medium-sized perches while foraging on small fruits and flowers more often than did females (n = 154 observations; $\chi^2 = 6.12$, df = 2, $P = 0.047$). Males often foraged on fruit from one limb while perched on another, or distributed their mass between two or more small branches, suggesting that they were able to forage on fruits and flowers by taking advantage of thick perches near the food resource. Females did not appear to be less able to forage in bromeliads and other epiphytes than were males. Females gaped as often in epiphytes as they did in dead leaves, and they foraged on each of these food sources more often than they did on any other food source (Fig. 6). Moreover, females did not forage less on large bromeliads than did males ($\chi^2 = 0.44$, df = 4, $P = 0.979$; Fig. 7).

DISCUSSION

Sexual size dimorphism and sexual selection.—The body-mass ratio between male and female Montezuma Oropendolas exceeds 2:1 (Fig. 2), which places the species among the most sexually size-dimorphic of all birds (see Ralls 1976). My results support a critical prediction of the hypothesis that sexual selection is responsible for the evolution and/or maintenance of extreme sexual dimorphism in this species: body mass and tarsus length were positively associated with male dominance rank, and rank is an indicator of male success in copulations (Webster 1994a) and fertilizations (Webster 1995) in this species.

The hypothesis that sexual selection is a general cause of sexual dimorphism in size in blackbirds and other higher vertebrates is supported by interspecific studies showing an association between degree of polygyny and degree of dimorphism, and by intraspecific studies showing an association between male size and mating success (see Introduction). However, for several size-dimorphic and highly polygynous birds, the association between male

TABLE 4. Food items eaten by adult Montezuma Oropendolas.

Food item	Source	Frequency[a]
Lepidoptera larvae	Curled leaves	High
Scorpions	Epiphytes	Low
Lizards	Epiphytes	High
Frogs	Epiphytes	Moderate
Orthopterans	Leaves and epiphytes	High
Large spiders	Leaves and epiphytes	High
Fruits	Bromeliads (Bromeliaceae)	Moderate
	Hampea appendiculata (Malvaceae)	Moderate
	Miconia impediolaris (Melastomataceae)	Low
	Topobea durandiana (Melastomataceae)	Low
	Cecropia sp. (Moraceae)	High
	Coussapoa panamensis (Moraceae)	High
	Ficus spp. (Moraceae)	High
	Elaeis guineensis (Palmaceae)	Moderate
	Bactris gasipaes (Palmaceae)	Moderate
	Zanthoxylum sp. (Rutaceae)	Low
	Carica papaya (Papaya, Caricaceae)	Moderate
Nectar	*Ochroma lagopus* (Bombacaceae)	Moderate
	Erythrina cochleata (Fabaceae)	High
Fruit and nectar	*Musa* spp. (Banana, Musaceae)	High

[a] High, > 10 observations; Moderate, 5 to 10 observations; Low, < 5 observations.

size and mating success is weak or absent altogether (Payne and Payne 1977, Searcy 1979, Yasukawa 1981, Gibson and Bradbury 1985, Weatherhead et al. 1987, Pruett-Jones and Pruett-Jones 1990). The latter results suggest that sexual selection may not favor large male size in some species. Alternatively, confounding factors such as extrapair copulations (e.g. Gibbs et al. 1990, Westneat 1993, Weatherhead and Boag 1995) may make the connection between size and mating success difficult to detect in many systems.

Ecological hypotheses for sexual dimorphism in size, particularly the niche-partitioning hypothesis, have proven notoriously difficult to test, primarily because it is difficult to determine whether observed differences in diet between the sexes are a cause or an effect of

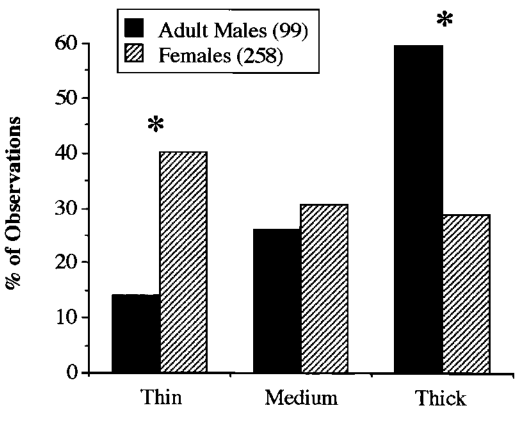

FIG. 4. Thickness of perches (see text) used by foraging adult male and female Montezuma Oropendolas. Sample sizes in parentheses; *, $P < 0.001$ (χ^2 tests comparing males and females).

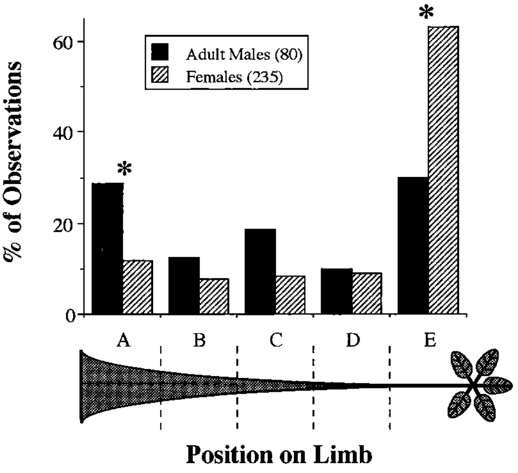

FIG. 5. Location of perches used by adult male and female Montezuma Oropendolas. The sections of the limb run from the base (A) to its tip (E). Sample sizes in parentheses; *, $P < 0.001$ (χ^2 tests comparing males and females).

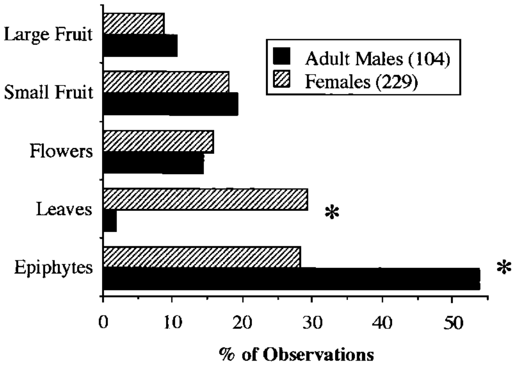

FIG. 6. Food resources exploited by adult male and female Montezuma Oropendolas. Sample sizes in parentheses; *, $P < 0.001$ (χ^2 tests comparing males and females).

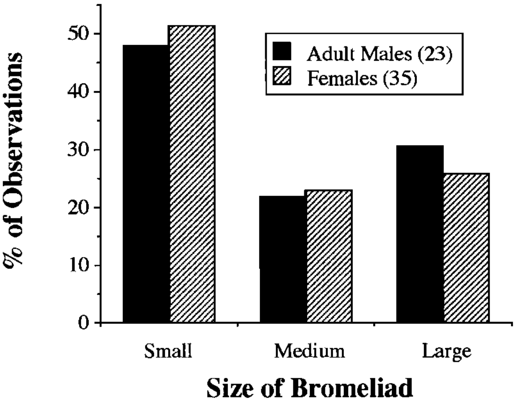

FIG. 7. Size of bromeliads (see text) foraged upon by adult male and female Montezuma Oropendolas. Sample sizes in parentheses.

sexual dimorphism (Hedrick and Temeles 1989, Shine 1989). Selander (1972) argued that the only reliable evidence that would support the ecological-divergence hypothesis would be a demonstration that foraging structures are relatively more dimorphic than other body parts. Because Montezuma Oropendolas search for prey by using their bill to pry open various substrates, it is likely that the bill is a primary foraging structure. My results do not indicate that the bill is any more dimorphic in size than are other body parts (Table 1). Indeed, the greatest sexual dimorphism was found in measures of traits likely to be important in sexual competition among males, i.e. wing length (the elongated, modified primaries of males are used in agonistic and courtship displays) and relative body mass (mass/tarsus). However, using Selander's criterion is difficult because often it is not possible to know which morphological traits are important in foraging (i.e. for oropendolas, structures other than the bill may be important), and the test is highly conservative (Shine 1989, 1991).

Two critical predictions of the foraging-niche divergence hypothesis were supported in this study. First, males and females differed significantly in the microhabitats exploited for food resources, with females foraging more often in leaves at the end of limbs and males taking more animal prey by gaping in epiphytal bromeliads. Similar sexual foraging differences have been reported in the Russet-backed Oropendola (*P. angustifrons*; Robinson 1985b) as well as in other birds (Selander 1966, Williams 1980, Askins 1983, Holmes 1986, Noske 1986). Second, observed sexual foraging differences appeared to result from body-size differences, because adult males used significantly thicker perches than did females, and this difference was not a result of males forcing females to forage in suboptimal areas (as has been suggested for other species; Kodric-Brown and Brown 1978, Puttick 1981, Peters and Grubb 1983, Temeles 1986). Juvenile males, which are intermediate in size between adult males and females, also were intermediate in the amount of time spent foraging at the ends of limbs. Interspecific comparisons also suggest that large size prevents foraging on curled leaves: Chestnut-headed Oropendolas (*P. wagleri*) and Scarlet-rumped Caciques (*Cacicus uropygialis*), closely related species that are sympatric but smaller than Montezuma Oropendolas, search for insects in curled leaves more often than do Montezuma Oropendolas (Orians 1985, pers. obs.). Indeed, most bird species that specialize on foraging in aerial leaf litter and leaves at the ends of limbs are extremely small (Greenberg 1979, 1987; Gradwohl and Greenberg 1984; Remsen and Parker 1984). Together, these observations indicate that the greater mass of male oropendolas prevents them from reaching the rolled-leaf resources used by females.

Although the small size of female oropendolas appears to allow them to exploit food resources in rolled leaves, it is not clear whether large size assists males in foraging on their primary food resource, epiphytal bromeliads. It is conceivable that being large and having a long bill is beneficial when foraging in larger, deeper bromeliads. However, females foraged on bromeliads approximately as often as they did in curled leaves, suggesting that they did not specialize on leaves at the expense of reduced ability to forage in bromeliads, and males did not forage on larger bromeliads than did females. Interspecific comparisons suggest that large size is not necessary to foraging by gaping in bromeliads: most avian species that use epiphytal bromeliads, including smaller species of oropendolas and caciques that forage by gaping, are smaller than female Montezuma Oropendolas (Orians 1985, Nadkarni and Matelson 1989, pers. obs.). Indeed, the Jamaican Blackbird (*Nesopsar nigerrimus*), a species less than half the size of the Montezuma Oropendola, forages almost exclusively by gaping in bromeliads (Wiley and Cruz 1980, Orians 1985). Therefore, although additional studies are needed to make firm conclusions, large size probably does not assist males in obtaining food from bromeliads or other epiphytes.

The above results suggest that the observed foraging differences between male and female Montezuma Oropendolas are a consequence rather than a cause of sexual size dimorphism. However, the results are not conclusive and must be considered with two caveats. First, as discussed above, detailed studies of foraging efficiency on different food resources are needed to determine whether large males are better able to forage in bromeliads than are small males or females. Second, ecological differences between the sexes other than foraging may favor sexual size dimorphism. For example, different parental roles, risk of predation (if different predators prey on the two sexes), or parasitism (if niche separation reduces transmission rates) could lead to sexual size dimorphism even if competition for food resources does not. These alternatives require further testing.

In summary, my results show that sexual selection is at least partially responsible for the extreme sexual size dimorphism in Montezuma Oropendolas, and that the sexes differ in the microhabitats that they exploit for animal prey. These results also suggest that sexual foraging differences are a consequence rather than a cause of sexual size dimorphism in this species, and that sexual foraging differences represent an ecological cost of large male size. However, I could not reject the ecological-divergence hypothesis completely. These possibilities require further study in this and other sexually dimorphic species.

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