

## ASPECTS OF THE BREEDING BIOLOGY OF AUDUBON'S ORIOLE

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**Abstract.**—Several pairs of Audubon's Oriole (*Icterus graduacauda*) breeding in northeastern Tamaulipas were studied in 1984 and 1985. Eight birds were banded and measured, five nests were located, and behavior observed for a total of 34 h. Songs of three individuals were recorded and analyzed spectrographically. The sexes have similar plumage and song and show little size dimorphism. Audubon's Oriole breeds in various habitats and nests in a variety of tree species and locations. Nests are well concealed and, compared to those of other oriole species, are small relative to female body size. Only females incubate, but both sexes feed the young. Nest success is low, due in part to parasitism by Bronzed Cowbird (*Molothrus aeneus*). Pair members communicate with each other frequently. Typical Audubon's Oriole song is longer, but shows less frequency modulation, and is less complex than Northern Oriole (*I. galbula*) song.

### ASPECTOS DE LA BIOLOGÍA REPRODUCTIVA DE *ICTERUS GRADUACAUDA*

**Sinopsis.**—Varias parejas de *Icterus graduacauda* que se reprodujeron en el noroeste de Tamaulipas fueron estudiadas durante el 1984 y 1985. Ocho aves fueron capturadas, medidas y anilladas. Se localizaron 5 nidos y se observó la conducta de las aves por 34 horas. Se grabó y se analizó espectrográficamente el canto de tres individuos. Las especies muestran muy poco dimorfismo, siendo el plumaje muy similar en ambos sexos al igual que el canto. Este oriol se reproduce en diversos habitats y anida en diferentes tipos de árboles y localidades. Los nidos están bien escondidos y comparado con otras especies de orioles, son pequeños en relación al tamaño de la hembra. Sólo la hembra incuba pero ambos sexos alimentan a los pichones. El éxito de anidamiento es bajo debido en parte al parasitismo reproductivo por parte de *Molothrus aeneus*. La comunicación entre los miembros de la pareja es frecuente. La canción de esta especie es más larga pero es menos compleja y muestra menor frecuencia modular que la de *Icterus galbula*.

Audubon's Oriole (*Icterus graduacauda*) is perhaps the least familiar of the six oriole species that breed north of Mexico and is among the least-known of the approximately 25 species of New World orioles (*Icterus* spp.). Indeed, the recently published Birder's Handbook (Erlich et al. 1988), refers to Audubon's Oriole as, "little known and virtually unstudied." Here, I present data on aspects of the species' breeding biology that have not been previously described. To my knowledge, these are the first relatively long-term, systematic observations of Audubon's Oriole.

Audubon's Oriole is resident from southern Texas through eastern and southern Mexico to the Isthmus of Tehuantepec (A.O.U. 1983). Throughout its range, it breeds during the rainy season, roughly April to September. Although they often feed in small, mixed-species flocks during the dry winter months (Harrell 1951, Sutton and Pettingill 1942), many apparently stay on or near the breeding grounds; the species is, therefore, relatively sedentary, and is frequently found in pairs throughout the year (Oberholser 1974, Harrell 1951).

## STUDY AREA AND METHODS

I studied Audubon's Oriole in the state of Tamaulipas, Mexico, at Rancho del Cielo, a biological station near the town of Gómez Farías, situated at 1160 m elevation in cloud forest habitat (an oak-sweet gum-beech [*Quercus-Liquidamber-Ficus*] association), and at Rancho Cielito, which is located on the banks of the Río Sabinas, near the town of El Encino. The two sites are less than 10 km apart, but the lower-elevation Rancho Cielito habitat is characterized by cultivated fields, scattered palmettos (*Sabal* spp.), areas densely packed with 1-2 m high vines and thorn-bearing shrubs (*Acacia* spp. and *Leucaena* spp.), and woods dominated by cypress (*Cupressus* spp.) and other large tree species, as well as native bamboo (*Bambuseae* spp.). (The habitat typical of this area is described in more detail by Sutton and Pettingill 1942.) Audubon's Oriole is as common in winter as it is in summer at both locations (Harrell 1951).

I banded a total of eight Audubon's Orioles, five at Rancho del Cielo (four females and one male) and three at Rancho Cielito (one female and two males). All birds identified as females had full brood patches and some were obviously about to lay eggs. None had a swollen cloaca. In contrast, the three birds identified as males had substantially distended and swollen cloacae, and no brood patches. Each of these eight birds was given a unique combination of a U.S. Fish and Wildlife aluminum band and one or more colored plastic leg bands.

I concentrated most of my observations on the pairs at four nests: one at Rancho del Cielo (nest 1, observed for 8 h during both the incubation and nestling periods, from 11 to 17 Jun. 1984) and three at Rancho Cielito (nest 2, observed for 5 h during laying and incubation from 1 to 11 Jul. 1984; nest 3, observed for 8 h during the incubation and nestling periods, from 9 to 21 Jul. 1984; nest 4, observed for 13 h during the incubation and nestling periods, from 24 Jun. to 10 Jul. 1985). At least one member of the pair at each of the 1984 nests was banded, and the sexes identified on that basis. The pair observed in 1985 was somewhat unusual in that one bird was noticeably duller in coloration than the other; since observations began on this nest during incubation, and only the drabber bird incubated, this individual was considered to be the female. (In the sexed pairs of this species, as well as in all other oriole taxa that have been studied, only the female incubates [Orians 1985, pers. obs.].) All activities of the pairs (and other birds) occurring at or near these nests during 1-h long watch periods were timed and recorded. All observations were made from a blind placed at least 15 m away from the nest.

At Rancho del Cielo, I recorded varying numbers of the songs of three different individuals. Recordings were made at 4.76 cm/s with a M645 Uher microphone mounted in a parabola (46 cm in diameter) and attached to a Sony TCD5M tape recorder. Sonagrams of these recordings were made on a model 7800 Kay Elemetrics Corp. sound spectrum analyzer.

## RESULTS AND DISCUSSION

*Habitat.*—The Gómez Farías region of southwestern Tamaulipas has been described by several authors as being essentially tropical in both its flora and its fauna, including its birdlife (Eaton and Edwards 1948, Sutton and Pettingill 1942, Webster 1974). Lying along the eastern slope of the Sierra de Guatamela (a segment of the Sierra Madre Oriental), it receives moisture-laden winds from the Gulf of Mexico, approximately 90 km to the east. Upon reaching the mountains, these winds rise and drop sufficient moisture to produce Middle America's northernmost cloud forest at elevations between 900 and 1200 m. Below this lies tropical, semi-evergreen forest, and at even lower elevations, tropical deciduous and thorn forests occur. Particularly along the banks of rivers, forested areas are interspersed with cultivated and/or cleared fields. Above the cloud forest lie humid pine-oak forest and dry pine-oak forest; montane chaparral appears at 2100 m, the highest elevation of the range.

Audubon's Oriole is unusual among the birds of this area in that it breeds at all but the highest elevations, and in all of the above mentioned forest types (Webster 1974, pers. obs.). It is found most commonly near forest edges, or in trees bordering rivers or fields, and enters clearings (natural or man-made) to feed on cultivated fruits, wild berries, and insects (Harrell 1951, pers. obs.). Thus, like other oriole taxa, Audubon's Oriole is an "edge" species, although it frequents densely vegetated areas more often than other members of the genus (Bent 1958, pers. obs.). Most authors' anecdotal descriptions of its apparent habitat preferences have been similar to this, confirming Sennett's (1878, quoted in Bent 1958) early impression that, "If I were to go in search of [Audubon's Oriole], I should seek dense woods, near an opening, with plenty of undergrowth."

*Banding data.*—As Table 1 shows, based on this small sample, there is little sexual size dimorphism in the species. The only variable for which males are significantly larger than females is wing length ( $\bar{x}_s = 9.77$  cm,  $\bar{x}_s = 8.90$  cm; Wilcoxon rank sum test,  $U = 15$ ,  $P \leq 0.05$ ). For the six linear measurements, the average difference between the sexes was 5.9%, similar to the sexual size difference for Audubon's Oriole reported by Lowther (1975). Based on consideration of the same linear measurements, the average difference between the sexes is 4.2% for Northern Orioles (*I. galbula*) and 4.8% for Scott's Orioles (*I. parisorum*) (Flood 1980, unpubl. data). These, as well as other data (Lowther 1975), suggest that the extent of sexual size dimorphism exhibited by Audubon's Oriole is typical of members of the genus *Icterus*.

There were also no consistent plumage differences between the sexes in this sample. Although subtle sexual differences have been described by some authors (e.g., Harrell 1951, Oberholser 1974), they do not involve characters that could easily be used to distinguish between the sexes in a field situation (i.e., at a distance). While on average, females may be slightly duller in coloration than males (and the members of some pairs may be conspicuously different), age effects further obscure sexual dif-

TABLE 1. Field measurements of Audubon's Oriole from the Gómez Farías region, Tamaulipas, Mexico.

Sex	Weight (g)	Tarsus length (cm)	Culmen			Wing length (cm)	Tail length (cm)
			Exposed length (cm)	Nostril to tip (cm)	Depth (cm)		
♂	42.9	2.48	2.20	1.49	0.75	10.1	10.2
♂	42.1	2.65	2.19	1.44	0.71	9.4	9.5
♂	—	2.62	2.15	1.44	0.68	9.5	10.1
♀	41.1	2.59	2.16	1.35	0.65	9.1	9.4
♀	42.9	2.51	2.02	1.38	0.60	8.8	9.5
♀	41.9	—	2.02	1.33	0.64	9.2	9.6
♀	36.5	2.63	2.03	1.39	0.68	9.0	9.4
♀	44.8	2.63	2.14	1.44	0.66	8.5	9.1

ferences (Pyle et al. 1987, Oberholser 1974) so that the species should probably be considered monomorphic, as many authors have in fact described it (e.g., Edwards 1972, Lowther 1975, Peterson and Chalif 1973).

In 1985, a non-systematic program of mist-netting at Rancho del Cielo, recovered two of the four females banded there, in almost the same spots they had been in the previous year. One of these was recorded as still present in the same area in 1986 (S. Boykin, pers. comm.).

*The nest.*—According to Bendire, in Texas Audubon's Oriole usually builds its nests, "in mesquite trees, 1.8–4.3 m above the ground" (1895: 470; also in Bent, 1958). My data on Mexican nests, however, although limited, indicate a far more variable pattern of nest placement (Table 2). The five Gómez Farías nests for which I have relevant data were all built in different tree species (one of which was unknown to me), and were placed 12.9–33.0 m above the ground, much higher than the nests Bendire described. While most nests were situated in mature trees, one was placed in a sapling.

Compared to the nests of other oriole species, which are relatively easy to find (Pleasants 1981, pers. obs.), those of Audubon's Oriole are very difficult to locate. Quite different from the familiar pendant structures of the Altamira (*I. gularis*) and Northern (*I. galbula*) orioles, they are cup-like. While semi-pensile (attached at the rim and sides rather than below), some nests are also supported, and therefore partially concealed, by twigs beneath the nest (Bendire 1895, pers. obs.). None of the five nests that I located (nest and nest tree measurements were not obtained for one of them) were placed near the tips of branches as is common for other oriole species (Bent 1958); all were located among the abundant twigs and leaves on the central portions of the limbs. One of the five nests I found was built in, and well-concealed by, a hanging clump of spanish moss.

The few descriptions of Audubon's Oriole that have been published almost all remark on its small size (Bendire 1895, Harrison 1978, Ober-

TABLE 2. Characteristics of Audubon's Oriole nests.

Characteristics of						
Nest tree				Nest		
Nest	Species	Height (m)	Dbh (m)	Height (m)	Distance from trunk (m)	Quadrant of nest tree
a <sup>a</sup>	<i>Liquidamber styraciflua</i>	≈33.0	0.75	≈21.0	—	—
1 <sup>b</sup>	?	12.9	0.08	11.7	1.0	—
2	<i>Cupressus moctezumae</i>	31.6	0.63	13.9	8.0	NE
3	<i>Ficus cotinifolia</i>	29.7	0.95	4.8	7.5	NW
5 <sup>c</sup>	<i>Enterolobium cyclocarpum</i>	23.1	0.70	12.7	4.5	NW

<sup>a</sup> Nest described by Harrell (1951).

<sup>b</sup> At Rancho del Cielo; remaining nests at Rancho Cielito.

<sup>c</sup> Female observed building, but not later active.

holser 1974). Compared to other *Icterus* species with cup-shaped nests, Audubon's Oriole nests are indeed small relative to the body size of the birds that build them. For example, the average wing length of female Scott's Orioles (*I. parisorum*) breeding in a population in Texas (Flood, unpubl. data) is 9.4 cm (SD = 3.17 cm,  $n = 63$ ), and the mean maximum inner diameter of the nests in this area is 8.7 cm (SD = 1.04 cm,  $n = 85$ ). The corresponding values for a single subspecies of the Hooded Oriole (*I. cucullatus nelsonii*) are 8.1 cm (SD = 0.07 cm,  $n = 2$ ) for female wing length and 7.5 cm (SD = 0.71 cm,  $n = 2$ ) for nest diameter. Similarly, the average wing length of 10 Orchard Oriole (*I. spurius*) females collected in Ontario is 7.5 cm (SD = 0.13 cm) and the average maximum inner diameter of Orchard Oriole nests in that province is 6.7 cm (SD = 0.47 cm,  $n = 14$ ). (The measurements of both birds and nests for the Hooded and Orchard orioles are of specimens housed in the collection of the Royal Ontario Museum, Toronto, Canada.) The ratio of female wing length to inner nest diameter is thus 1.08 for both Scott's and Hooded orioles, and 1.12 for Orchard Orioles. For the Audubon's Oriole in this study population, on the other hand, this ratio is 1.21, indicating that these latter nests are, in fact, smaller relative to the average size of the birds that build them. Although the difference is not substantial, it may nonetheless contribute to the comparatively greater concealment of the nest.

Although previous authors have described the nest of Audubon's Oriole as being made up of, and lined with, various types of grasses (Bendire, 1895; Erlich et al. 1988, Harrison, 1978), I suggest that they are more commonly constructed of fibers pulled from the leaves of palmetto plants. The two previously active nests that I examined closely were made of such fibers (which, when dry, might have been mistaken for grasses) and were not conspicuously lined. On several occasions I observed individuals of Audubon's and Altamira orioles working to pull strands from the edges

TABLE 3. The behavior of males and females during the incubation period. The data provided are mean values for each nest (i.e., averaged over the total number of hours each nest was watched, as given in the text). Vocalizations other than song include alarm calls and other single note calls of uncertain function. Males were recorded as <50 m from the nest when they were seen and/or heard in that area; they could have spent much more time near their nests, but if silent and out of sight they would go undetected.

	Nest 1		Nest 2		Nest 3		Nest 4	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Behavior of males								
No. of songs	5.3	3.10	3.0	3.46	2	—	0	—
No. of other vocalizations	9.0	8.04	91.3	97.5	95	—	0	—
% of period spent <50 m from nest	15.5	8.46	47.7	41.03	31.3	—	0	—
Behavior of females								
No. of songs	6.8	2.98	6.5	6.40	0	—	0	—
No. of songs from nest	4.0	1.83	3.8	3.30	0	—	0	—
No. of other vocalizations	7.5	6.14	5.0	6.78	3	—	0	—
% of period on nest	66.1	16.11	81.0	7.38	68.9	—	82.9	15.4

of palmetto leaves. It took one Audubon's Oriole 7.5 min, from the time it landed on the plant, to pull a single long fiber from the edge of such a leaf, at which point it flew off carrying the strand. The use of such plant fibers as nest material has been described for various other oriole species (Bent 1958, Harrison 1978, Sutton and Pettingill 1943).

*Nesting behavior.*—The first four nests described above were watched during the incubation period for 4, 4, 1, and 3 h, respectively. These 12 1-h observation periods encompassed 11 complete bouts of incubation, as well as 11 of the intervals between such bouts. (Often bouts or rest intervals started or ended outside of the observation periods and thus were of uncertain duration.) The average incubation bout was 27 min 12 s (SD = 12 min 32 s) in length, and the intervals between bouts averaged 13 min 11 s (SD = 7 min 55 s).

At all four nests, only the female incubated. In general, males spent much of their time less than 50 m from the nest; they were often heard (and their locations roughly pinpointed) or seen in this vicinity throughout the observation periods. At three nests the members of the pair communicated frequently with each other, the female singing (often full, male-like songs) or uttering single notes, often from the nest, and the male responding, usually with the same type of vocalization (Table 3). In fact, there was no difference between the males and female at these nests with respect to the number of full songs given per hour during the incubation period (Wilcoxon matched pairs, signed ranks test,  $n = 10$ ,  $n[\text{differences}] = 8$ ,  $P > 0.05$ ). At the fourth nest, the pair was essentially silent. However, frequent communication and unusually close (relative to most other oriole species [pers. obs.]) contact between members of a pair seems to be fairly

typical of Audubon's Oriole (Bendire 1895, Bent 1958). This may be because of their preference for habitats in which the vegetation is relatively more dense than that preferred by other oriole species.

Nest 2 failed during incubation, but nests 1, 3, and 4 were watched for 4, 7, and 10 h, respectively, during the nestling period. At nest 3, only the female fed the young. This is unusual, not only for Audubon's Oriole, but for orioles in general, since in all species that have been carefully studied, both parents feed the young (Bent 1958, Flood 1984, Pleasants 1981). A male was caught and banded in the same net and at the same time the female from this nest was captured, 2 d before her eggs hatched. Although seen and heard in the area of the nest less frequently than the males of the other observed pairs, this male appeared periodically and four times chased intruding cowbirds from the area of the nest. This nest was the latest of the four nests to be initiated (in terms of time since the beginning of the rainy season) and could very easily have been a second nest. Fledged, almost fully grown Audubon Oriole young had been seen elsewhere on the study area as early as 11 Jul. in 1984. Various authors have speculated that Audubon's Oriole probably tries to raise two broods per year (Bent 1958) and this male may have been caring for a first set of young. Alternatively, the female may have lost her original mate and this may have been a replacement male who was not the father of these young. The failure of replacement males to feed a widow's nestlings has been observed in other oriole species (Flood 1980, unpubl.).

At the two nests where both parents fed the young, there was no difference in the number of trips per hour made by males and females (Wilcoxon matched pairs signed ranks tests,  $n = 13$  h,  $n$  [differences] = 7,  $P > 0.1$ ). The average number of trips per hour made by females was 2.85 (SD = 1.72), and the average number made by males was 2.31 (SD = 1.49). The female feeding alone at nest 3 apparently compensated successfully for her lack of male assistance. She made an average of 4.9 (SD = 4.14) trips per hour, producing fledged young after 11 d of feeding. The pair at nest 4, which were similarly watched from hatch to fledging (a period of 11 d in this case as well), together made an average of 5.2 (SD = 2.73) feeding trips per hour. There was no significant difference between these feeding rates (Mann-Whitney  $U$ -test,  $U = 46$ ,  $P > 0.1$ ).

Parents fed their young various invertebrates, including spiders and a large number and variety of insects, particularly larval forms. At nest 4, whenever possible, the approximate size of food items brought by the parents was assessed relative to the bill size of adults. Items ranged in size from  $\frac{1}{2}b$  ("bill unit") to  $3b$ , with a modal size of  $2b$ . (An item  $1b$  in size was the same length as the bill of the adult carrying it, i.e., roughly 2 cm long.) There was no difference between the sexes with respect to the size of the items delivered to nestlings (Mann-Whitney  $U$ -test,  $n_2 = 16$ ,  $n_3 = 20$ ,  $U = 187.5$ ,  $P > 0.05$ ). Both sexes removed fecal sacs, usually eating them during the first 2 d of the nestling period, but later carrying them off to be dropped at some distance from the nest.

*Nest success.*—Unfortunately, I had to leave Rancho del Cielo shortly

after the eggs in nest 1 hatched; the outcome of this nesting attempt is thus unknown. Nest 2 failed during the egg stage, and nest 5 was observed under construction on 10 Jul. 1984 (and appeared to be more or less complete) but was not later active. Two cowbird young (and no orioles) fledged from nest 4, while the pair (or at least the female) at nest 3 produced an unknown number of fledged young, some of which may also have been cowbirds. Bronzed Cowbirds (*Molothrus aeneus*) pose a serious problem for Audubon's Oriole. Each of the four nests I watched was visited at least once, and usually more often, by cowbirds. At nest 3, a flock of 15–30 cowbirds spent several days in the nest tree; during four hour-long observation periods, over the same number of days, cowbirds (often 5–10 at a time) visited (went up to or into) the oriole nest 10 times. Both members of the pair chased these intruders, one or the other of them engaging in 23 separate chases over the 4 h; 10 feeding trips were interrupted or abandoned in order to expel the cowbirds.

Bronzed Cowbirds have long been recognized as detrimental to the reproductive success of Audubon's Oriole (Bendire 1895, Bent 1958). They seem to have had a particularly deleterious effect in the northernmost portions of the oriole's range, specifically in South Texas, which has only recently been invaded by substantial numbers of this cowbird species (Oberholser 1974). The combined effects of habitat loss (as woodlands in the Río Grande Valley are cleared for agriculture) and cowbird parasitism have reduced the numbers of Audubon's Oriole in Texas to dangerously low levels (Oberholser 1974).

*Song.*—Often described as a “mellow,” “humanlike,” whistle (e.g., Bendire 1895, Oberholser 1974), the song of Audubon's Oriole consists of a long series of separate “figures” (the individual syllables comprising a vocalization), each differing from the one preceding it (Fig. 1; Table 4). In structure and sound, it is quite different from songs of the more familiar North American orioles. Perhaps the best way to describe the song in words is to compare it to that of the Northern Oriole, a more common and widespread member of the genus, whose song has been frequently recorded and is thus commercially available on a variety of records and tapes. The Northern Oriole is also the only oriole species whose vocalizations have been described in detail and analyzed quantitatively.

Neither Audubon's Oriole song, nor the figures that comprise it, show as much frequency modulation as is characteristic of the song and song figures of Northern Orioles. For example, the average frequency range for the songs of the three individuals represented in Figure 1 is significantly less than that of either male or female Northern Orioles (Beletsky 1982a,b). Whereas the majority of these Audubon's Oriole figures are almost pure tones, Northern Oriole figures are more typically modulated in frequency, often over the entire bandwidth of the song (Beletsky 1982a). Audubon's Oriole song is also much lower in frequency than that of the Northern Oriole (Table 5). These particular contrasts between the two species' songs reflect typical differences between birds breeding in forested



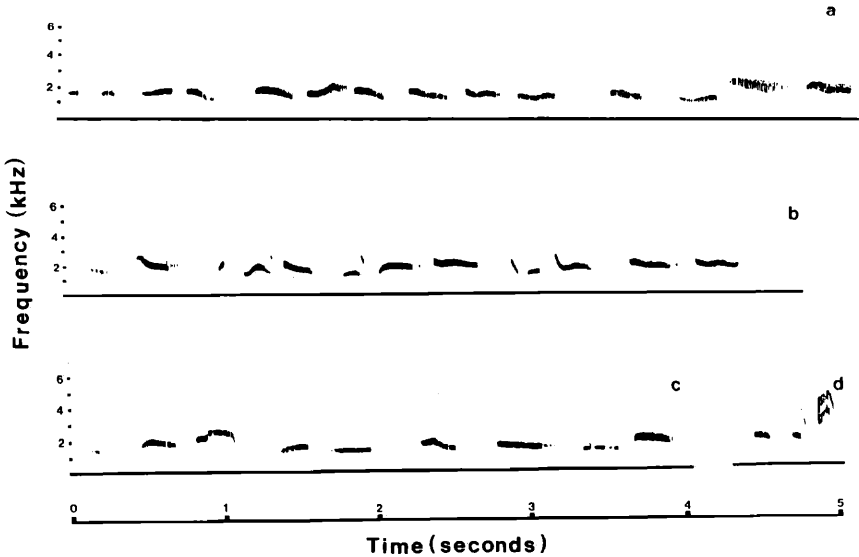


FIGURE 1. Typical songs of three different *Icterus graduacauda* individuals (1-c) and an example of the species' alarm call (d).

as opposed to more open habitats. Because the acoustical properties of habitats differ, attenuation of high frequency and frequency modulated songs is greater in forest than in grassland. As one might predict, therefore, forest-dwelling species (particularly those in neotropical forests) often sing lower, less frequency modulated songs than do grassland birds (Morton 1975, Wiley and Richards 1982). Although both Northern and Audubon's orioles can be considered edge species, the former is associated with open habitats (e.g., riparian habitats of the great plains), more than the latter, which, as described above, typically spends much of its time in densely vegetated areas. It is perhaps not surprising, therefore, that the differences between their songs should follow this same pattern.

In addition, Audubon's Oriole songs are typically much longer than those of the Northern Oriole. This greater length is probably due to a combination of factors, including more figures per song, and an increase in the average duration of figures: the mean length of the 150 different Northern Oriole figures recorded by Beletsky (1982a) was 107 (SD = 52) ms, whereas the average duration of 37 Audubon's Oriole figures is 230 (SD = 52) ms. The result of all this is a long, slow-sounding, whistled song that seems to drift lazily from one note to the next. In addition to this song, Audubon's Orioles frequently utter single-figure vocalizations, using (at least in the case of these three birds) the first syllable of their song. Also they produce relatively high-frequency alarm calls when the situation merits (Fig. 1).

TABLE 4. Features of the song of Audubon's Oriole.

Individual	No. of songs	Length of songs (s)		No. of figures per song		Frequency range (kHz)
		$\bar{x}$	SD	$\bar{x}$	SD	
A	7	5.58	1.129	13.7	1.98	1.1 - 2.8
B	10	3.74	0.892	10.4	2.10	1.3 - 3.1
C	3	3.97	0.061	9.0	0.00	1.2 - 3.0

Perhaps the major contrast between the vocalizations of these two oriole species lies in features related to the complexity of their songs. In Northern Oriole song, individual figures are often repeated, or sequentially rearranged, to produce different songs or "song patterns" (Beletsky 1982a). Audubon's Orioles, on the other hand, do not repeat figures and apparently always sing their particular repertoire of figures in the same order. Instead, they alter their song patterns by deleting certain notes, or by stopping before reaching the end of their longest songs. Whereas individual C for example, always sang the same nine figures in the same order, B sang only the first eight of its repertoire of 12 figures in four of the analyzed songs. (It sang all 12, always in the same order in the remaining six analyzed songs.) Individual A had 16 different figures in its longest song, but sometimes deleted particular figures (usually #12), or left off the last few.

As a result, the overall complexity of Audubon's Oriole song, measured in terms of the average repertoire size of an individual, is probably much less than that of the Northern Oriole. Various authors have suggested that among-species variation in the intensity of sexual selection might be responsible for such differences in song complexity. Kroodsma (1977), for example, in a comparative study of nine North American wren species, noted that the taxa with the most complex songs (a) were polygynous (whereas most of the nine species were monogamous) and, (b) bred in very high densities in areas with otherwise relatively depauperate avi-faunas (i.e., in which wrens would have high intraspecific encounter

TABLE 5. Comparison of the songs of Audubon's Oriole and Northern Oriole (calculated from data provided in Beletsky 1982a).

Feature	Audubon's Oriole	Northern Oriole
Frequency range (kHz) (mean $\pm$ SD)	1.8 $\pm$ 0.06	2.0 $\pm$ 0.24*
Lowest frequency (kHz) (mean $\pm$ SD)	1.2 $\pm$ 0.10	1.8 $\pm$ 0.17**
Highest frequency (kHz) (mean $\pm$ SD)	3.0 $\pm$ 0.15	3.8 $\pm$ 0.24**
No. of figures/song (mean $\pm$ SD)	8.5 $\pm$ 2.63	11.0 $\pm$ 2.41
No. of figure types/song (mean $\pm$ SD)	5.5 $\pm$ 1.73	11.0 $\pm$ 2.41**
Length of song(s) (mean $\pm$ SD)	4.4 $\pm$ 1.00	1.4 $\pm$ 0.44**

Mann-Whitney *U* tests, \**P* < 0.05, \*\**P* < 0.001.

rates). Such conditions, Kroodsma reasoned, implied high levels of intrasexual competition, which he proposed had selected for increased song complexity. Catchpole (1980), investigated a similar gradient in song complexity among European *Acrocephalus* warblers. Although he agreed that an increase in the intensity of sexual selection had probably played a major role in the evolution of complex songs, he felt that this effect was mediated primarily through inter- rather than intrasexual selection. In the genus *Acrocephalus*, it is the monogamous species, in which males defend small, nesting-only territories and contribute substantially to parental care, that have the more complex songs. Males of the regularly polygynous taxa, on the other hand, which defend large, nesting-and-feeding territories in which several females may settle, have relatively simple songs. These males play a comparatively reduced role in parental care. Catchpole thus reasoned that females of the monogamous species should be influenced more by the quality of the male himself than by features of his territory, and that the complex songs of these males might have been selected for as a means to advertise this quality. (Territorial song, he felt, useful for contests between males, should be short and simple.) In addition, those members of the genus that spent the shortest time on the breeding grounds, and in which selection should therefore presumably favor traits promoting rapid mate attraction, had relatively more complex songs. Catchpole (1980) regarded this as further evidence implicating intersexual selection as a factor in the evolution of signal complexity. Since Audubon's Oriole is resident on its breeding grounds, whereas the Northern Oriole is migratory, the difference in song complexity between the two species is at least partially consistent with Catchpole's (1980) hypothesis. It is also true, however, that Northern Orioles commonly breed in much higher density than Audubon's Orioles (e.g., 1.2–2.4 pairs/ha in a Kansas breeding population of the former species [Flood 1980], compared to 0.1 pairs/ha for the latter in the Gómez Farías area [Harrell 1951]). Thus, Kroodsma's hypothesis may also provide a plausible explanation for complexity differences in the species' vocalizations. Additional research is obviously necessary to resolve this question. Collection of data that would provide the basis for a comparative analysis of additional oriole species might prove particularly fruitful.

Unfortunately, none of these three birds was banded, and their sex is thus unknown. However, the primary reason why so few of the many recordings of C's song were analyzable, was that it often overlapped with, and was in the background to, B's song. In other words, B and C were often recorded in the same spot, and appeared to be communicating with each other, much like most of the pairs described above. Their behavior during the recording bouts resembled that of a mated pair. A, on the other hand, was recorded nearby, but not in the same spot, and its songs never overlapped with those of either B or C. I suspect, therefore, that A and B are the songs of males, whereas C is that of a female. The song of Northern Oriole females has in fact, been shown to be structurally similar to that of males, but is apparently uttered much less frequently

(Beletsky 1982b). Audubon's Oriole females, on the other hand, seem to sing as often as males, and to produce songs that, at least to a listener, sound structurally the same. This is interesting in light of the fact that in Audubon's Oriole the sexes also look similar, whereas the Northern Oriole has sexually dimorphic plumage coloration. Noting that female Northern Orioles sometimes sing in the presence of their mates, or in response to their mate's vocalizations, Beletsky (1982b) suggested that female song in this species could play a role in pair bond maintenance. He noted, however, that females had been observed chasing conspecifics of the same sex, presumably in an attempt to exclude intruders from defended territories, and that females sometimes sang in such aggressive contexts. He was unable, therefore, to make any conclusive statements about the function of female song in Northern Orioles, and remarked that detailed behavioral studies of other species were necessary before the subject could be adequately addressed. The same situation still pertains. The fact that male and female Audubon's Oriole appear to sing similar songs with the same frequency has interesting implications for questions relating to the role of the sexes in monomorphic vs. dimorphic species. Additional research, particularly to provide comparative data on other *Icterus* species (both dimorphic and monomorphic) is needed, however, to successfully approach the issue.

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## ERRATA

Two statements in my paper "Colony sizes and nest trees of Montezuma Oropendolas in Costa Rica" (*J. Field Ornithol.* 60:289-295, 1989) should be corrected as follows.

The first statement indicates that above 500 m in Costa Rica palm trees contained fewer nests per tree than dicot trees, but gives no supporting data. Data for all colonies in the highlands (Turrialba) show that palm trees ( $n = 11$ ) contained fewer nests per tree than dicot trees ( $n = 4$ ) ( $U = 43$ , 2-tailed,  $P = 0.007$ ; the respective medians are 5 and 24.5 nests per tree).

The second statement indicates that in the lowlands there was no difference between palms and dicot trees in numbers of nests per tree. The statement cannot be proved with my data.—Rosendo M. Fraga