

VOCAL MIMICRY IN THE EPAULET ORIOLE¹

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Abstract. The Epaulet Oriole (*Icterus cayanensis*) imitated calls of seven species of birds (models) at six localities in northeastern Argentina. The models occurred in the same habitats. At one site 92% of 61 tape recorded calls were imitations. Calls of hawks, alarm calls, and mobbing calls were frequently copied. Both sexes imitated year round.

Epaulet Orioles reacted to playbacks of conspecifics, even those from distant localities. Models, however, were seldom attracted to playbacks and/or to the vocalizing orioles. The available data is consistent with the idea that mimicry is used as an "interspecific threat" directed to potential predators.

Key words: Vocal mimicry; Epaulet Oriole; *Icterus cayanensis*; alarm calls; Roadside Hawk; Argentina.

INTRODUCTION

Interspecific vocal mimicry or copying is of widespread occurrence in some groups of birds, notably the oscine passerines (Baylis 1982, Kroodsma and Baylis 1982). Despite the considerable literature on the subject (summarized in Dobkin 1979 and Baylis 1982), its meaning and possible adaptive values are not well known. In this paper I describe vocal mimicry in the Epaulet Oriole (*Icterus cayanensis*), a South American icterine. The species was not included in the list of avian vocal mimics compiled by Kroodsma and Baylis (1982).

Some common names of the Epaulet Oriole in Argentina (e.g., "calandria negra" = "black mockingbird") suggest that country people have noticed that it imitates other birds. The first written description of vocal mimicry in this species occurs in a letter written by W. H. Hudson in 1869 and published in 1870 (Hudson 1951). W. Voss (in Belton 1985) and F. Silva (pers. comm.) have stated that the Epaulet Oriole is also a vocal mimic in Rio Grande do Sul, Brazil. Vocal mimicry occurs in other species of the genus (Kroodsma and Baylis 1982).

Imitations often make up most of the oriole's repertoire. Hawk calls, as well as varied alarm and mobbing calls that the hawks could elicit from other birds, are often copied. These facts made the possible adaptive significance of such pervasive copying particularly interesting.

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STUDY AREAS AND METHODS

I tape recorded and/or noted calls of Epaulet Orioles in six localities in eastern Argentina. In the province of Buenos Aires at: (1) Estancia La Candelaria, Lobos; habitat was mainly planted woodlands (described in Fraga 1980), and (2) Estancia El Destino, Magdalena, with a mixture of natural and planted woodlands, near the shore of the Río de La Plata. In the province of Entre Ríos I observed orioles mainly at (3) Estancia Humaitá, Colón, in the gallery forest of the Río Uruguay, and (4) Parque Nacional El Palmar, Colón, in the same habitat. In the province of Corrientes I observed orioles at (5) Estancia Las Tres Marías, not far from the town of Virasoro, Santo Tomé; the place was a (largely) natural patch of subtropical forest. In Misiones I studied orioles at (6) Parque Nacional Iguazú; there the birds were found around natural or man-made clearings in the subtropical forest. At La Candelaria there were 1 to 2 pairs of orioles in 60 ha, and the density at other sites was similar. At El Palmar, however, groups of up to 10 birds were seen.

I have carried out extensive research on birds at La Candelaria (e.g., Fraga 1980, 1985), and I was well acquainted with the vocalizations of the local avifauna. I visited El Palmar eight times during this study, spending about a month there. I spent 1 to 15 days in the other sites. Samples of 50 or more recorded oriole calls were obtained only from La Candelaria, El Palmar, and Iguazú. I recorded orioles usually while studying vocalizations of other birds and/or while making avifaunal lists with the use of playbacks. At all sites

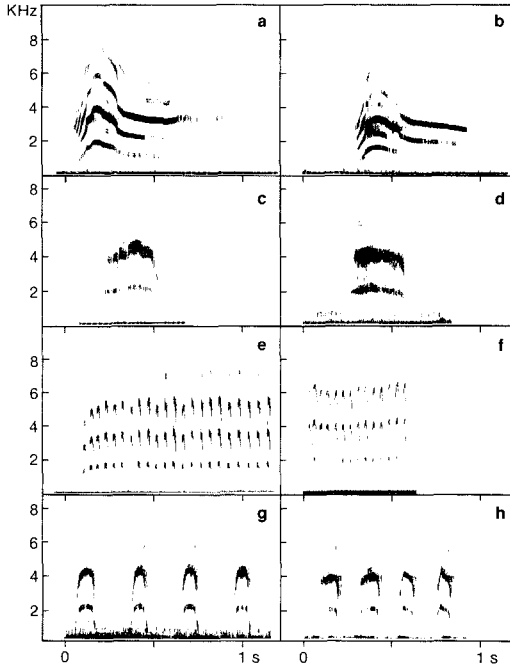


FIGURE 1. (a) Call of perched Roadside Hawk. (b) Imitation by Epaulet Oriole. (c) Call uttered by a Great Kiskadee while mobbing a Chimango Caracara (*Polyborus chimango*). (d) Imitation by Epaulet Oriole. (e) Alarm call of Guira Cuckoo. (f) Imitation by Epaulet Oriole. (g) Alarm notes of Rufous Hornero. (h) Imitation by Epaulet Oriole. Vocalizations (a) to (f) from La Candelaria, (g) and (h) from El Palmar.

(except El Palmar) I recorded every Epaulet Oriole seen within 30 m, as long as there was no major background noise. At El Palmar orioles were more abundant, and my sample of vocalizations is certainly biased towards the rarer calls.

For recording I used a Uher 4000 IC tape recorder with a shotgun Electrovoice DL42 microphone. The tapes were studied with a Uniscan Real Time Spectrum Analyzer, and sonograms made with a Kay Sona-Graph 6061-B, using wide band filter. I used both aural and visual evidence for making judgements on resemblance. Sonograms in Figure 1 are representative of the average quality of the oriole's mimicry. For playbacks I used a 7 W outdoor speaker, plugged to the Uher recorder with a 20 m cable.

I played back sequences of oriole calls from La Candelaria, Parque Nacional El Palmar and Las Tres Marías, and containing, respectively, 52, 48, and 47 calls. All calls from La Candelaria and El Palmar were mimetic. The three sequences were constructed to last 250 sec. All

playback experiments were performed at El Palmar. At the start of each experiment no oriole was present within a radius of 20 m of the speaker; if orioles subsequently approached within 5 m of the speaker the response was judged positive.

I found Epaulet Orioles nesting in late September (nest building, at Iguazú) and December to January (La Candelaria). Data in the literature (Barrows 1883, Pereyra 1938, Belton 1985) indicate a similar breeding season. Orioles recorded during February to August were regarded as nonbreeders (Table 1).

RESULTS

GENERAL HABITS OF EPAULET ORIOLES

Epaulet Orioles are almost monomorphic (Belton 1985), largely black icterids found in several types of woodlands in Argentina and neighboring countries. They were seen year round in Buenos Aires (contra Hudson 1951), Entre Ríos (see also Barrows 1883), and Misiones. Epaulet Orioles feed on insects, berries and nectar, and forage in trees.

THE MODELS

All the species in this list were year-round residents, and could be found in the same habitats with the orioles.

Roadside Hawk (*Buteo magnirostris*). This was a frequent diurnal raptor in all the study areas, particularly at La Candelaria. Epaulet Orioles copied (Fig. 1B) the calls of perched hawks (Fig. 1A); these are referred to as "complaint" calls by Wiley and Wiley (1981). Imitations of calls of soaring hawks ("song" in Wiley and Wiley 1981) were heard only three times (vs. 40 imitations of the other call), and only at La Candelaria (Table 1).

Guira Cuckoo (*Guira guira*). This species was abundant in Buenos Aires and Entre Ríos, less so in Corrientes and Misiones. Epaulet Orioles copied (Fig. 1F) their main alarm call (Fig. 1E). Although imitations of Guira Cuckoos were not detected at El Palmar, orioles mimicked this bird at Humaitá, 15 km to the north.

Green-barred Flicker (*Colaptes melanochloros*). A species present at all sites. Orioles imitated its sharp "keep," a note that is probably a contact call (pers. observ.).

Rufous Hornero (*Furnarius rufus*). Horneros were common passerines in all localities, except Iguazú (for La Candelaria, see Fraga 1980). Ori-

TABLE 1. Recorded vocal repertoire of Epaulet Orioles at 3 localities in East Argentina. Status of individuals: B = Breeding or nesting; NB = nonbreeders. Models: RH = Roadside Hawk; GC = Guira Cuckoo; GF = Green-barred Flicker; RF = Rufous Hornero; GK = Great Kiskadee; CM = Chalk-browed Mockingbird; BC = Black Cacique. Other calls = Nonmimetic, or doubtful imitations.

Site	Status	Models							Total imitations	Other calls	Total calls
		RH	GC	GF	RF	GK	CM	BC			
La Candelaria	NB	9	—	1	—	—	2	—	12	1	13
La Candelaria	B	25	4	7	—	2	5	—	43	5	48
El Palmar	NB	6	—	10	39	14	—	4	73	25	98
Iguazú	NB	3	—	—	—	2	—	—	5	19	24
Iguazú	B	—	—	—	—	4	—	—	4	30	34

oles imitated (Fig. 1H) the hornero's alarm call (Fig. 1G), but in bouts that lasted less than 1 sec. By contrast, horneros may repeat alarm calls for minutes (pers. observ.).

Great Kiskadee (*Pitangus sulphuratus*). Kiskadees were common in all the study sites. Epaulet Orioles copied (Fig. 1D) their mobbing call (Fig. 1C), used by kiskadees when mobbing perched hawks and owls (pers. observ.).

Chalk-browed Mockingbird (*Mimus saturninus*). This mockingbird was relatively common in Buenos Aires and Entre Ríos. Epaulet Orioles mimicked their scolding call, a loud, rasping "cht."

Solitary Black Cacique (*Cacicus solitarius*). This cacique was seen only in the Entre Ríos sites. Orioles imitated one of the cacique's calls, a harsh, rather low pitched vocalization; its function in the model is unknown.

CONTEXT OF VOCAL MIMICRY

The imitations I heard and recorded were not part of the Epaulet Oriole's song. Oriole songs (Hudson 1951, Belton 1985) are possibly nonmimetic, but no satisfactory recordings could be obtained. I heard at La Candelaria only three to four songs from one nesting individual, that sang while its mate was building. Elsewhere I heard songs only in Iguazú.

The orioles that imitated were foraging, attending nests, or feeding fledglings. Possibly these orioles were mildly alarmed by my presence, as some were tail-flicking (an indication of alarm in icterines, Orians and Christman 1968). At other times I observed silent orioles, usually foraging.

PERSISTENCE AND FREQUENCY OF VOCAL MIMICRY

Epaulet Orioles are "persistent" mimics (Baylis 1982), as all the individuals I observed (more

than 50), in all localities, imitated. At La Candelaria interspecific imitations comprised 56 of 61 tape-recorded oriole calls (91.8%, see Table 1). At El Palmar, where my experience with the avifauna was briefer, 73 imitations occurred in 98 recorded oriole calls (74.5%, Table 1). This is a conservative estimate, as I was not able to obtain recordings of models of all the apparent imitations. Probably because of my relative lack of familiarity with the local avifauna, the proportion of recognizable imitations was still lower at the sites in the provinces of Misiones and Corrientes. Still, recorded sequences of 58 calls from Iguazú included 9 recognized imitations. The number of species imitated in a single sequence was at least five, for La Candelaria. Usually orioles alternated the imitations of different models.

At times the imitations were mixed with sharp notes (sounding like "kit"), that are nonmimetic. These were the only nonmimetic calls of adult Epaulet Orioles at La Candelaria (begging calls of fledgling orioles were also distinctive). Sequences with "kits" were immediately recognizable as oriole vocalizations. In all cases the imitations were less loud than the copied model's calls.

Hudson (1951) indicated that both sexes of a nesting pair of orioles were vocal mimics. My

TABLE 2. Responses (positive or negative) of Epaulet Orioles of El Palmar to playbacks of conspecific calls.

Origin of calls	Season*	Play-backs	Responses	
			Pos.	Neg.
La Candelaria	Nonbreeding	7	5	2
El Palmar	Breeding	4	4	0
	Nonbreeding	6	6	0
Las Tres Mariás	Breeding	6	6	0

* Season of experiments: nonbreeding = June to August; breeding = October.

experience with 2 nesting pairs (La Candelaria and Iguazú) was similar. Epaulet Orioles used vocal mimicry at all seasons. At La Candelaria I heard imitations during all months, except May and August. Orioles mimicked in winter (June to September) at El Destino, El Palmar, and Iguazú.

PLAYBACK RESULTS

Orioles at El Palmar reacted positively to playbacks (Table 2), even of sequences from other sites that included different imitations. Once the approach of an individual was apparently aggressive, and I was "mobbed" while moving the speaker, the oriole fluttering twice just over my head. This individual was primarily attracted by the playback. Experiments done in October (breeding season) attracted mostly pairs (7 out of 10 cases).

RECOGNITION OF MODELS BY EPAULET ORIOLES (AND VICE VERSA)

Epaulet Orioles reacted to calls of Roadside Hawks. In a recorded sequence at El Palmar, an oriole was not imitating hawks during a bout of 16 vocalizations (0/16). When a soaring pair of hawks started to call in the area, the oriole produced six copies of the "perched" hawk's call (6 of 10 calls). These were the only copies of hawk's calls in the sample recorded at El Palmar (Table 1). Interestingly, the oriole copied the call of a perched hawk, not the song of the flying pair (the actual stimulus).

Model species did not approach the speaker during playbacks of oriole imitations at El Palmar. Two common models included in the playbacks (Rufous Horneros and Great Kiskadees) were present in the area of the experiments; Kiskadees usually react vocally to playbacks of their own calls (pers. observ.). Orioles may impart some distinctive character to their imitations, perhaps in the temporal sequence. I have seen only two possible cases of attraction of models to imitating orioles in the wild, involving Green-barred Flickers. The woodpeckers were seen within 15 m of the orioles. In one case a flicker apparently responded to "keep" notes of an oriole with others of its own.

DISCUSSION

Dobkin (1979) and Baylis (1982) have suggested some plausible functions (intra and interspecific) for vocal mimicry. These functions are not al-

ways mutually exclusive. No functional hypotheses are clearly supported by my data, but some ideas are more plausible than others.

Among intraspecific functions of vocal mimicry, a hypothesis of sexual selection seems unlikely. Both sexes in the Epaulet Oriole imitate. As far as is known the species is monogamous, and both sexes feed the nestlings (Hudson 1951, pers. observ.).

The use of mimicry for integration and cohesion of monospecific flocks is perhaps more plausible. Small, loose flocks of orioles were seen at El Palmar in winter, and vocal imitations occur year round there, as well as in La Candelaria and Iguazú (for winter flocks, see also Belton 1985). The results of playback experiments indicate that orioles are attracted to imitations by conspecifics. This hypothesis will not explain the use of interspecific mimicry, particularly during the breeding season.

The use of imitations for cohesion in mixed species flocks is unlikely. At La Candelaria orioles occasionally joined flocks of Bay-winged Cowbirds (*Molothrus badius*) in winter, but they did not imitate baywing calls. However, imitations of baywings have been reported from Brazil (Voss in Belton 1985). At El Palmar I saw groups of 4 to 6 orioles with 1 to 2 Black Caciques; the caciques, however, were seldom imitated (Table 1). It is unlikely that imitations of hawks, or of alarm calls of birds that do not form mixed flocks, will promote flock cohesion of Epaulet Orioles and these other species. At El Palmar, the most imitated species (Rufous Horneros) did not join mixed flocks.

The hypothesis of interspecific territoriality, with orioles excluding competitors with imitations of their calls, is also implausible. With the exception of the cacique, all models belonged to different families and orders of birds. I find it hard to believe that the exclusively arboreal orioles could be competing with the terrestrial horneros and mockingbirds. It is possible that orioles could exclude competitors that are not models with imitations of hawks and alarm calls, but I have no evidence for this. Although other nectarivorous and frugivorous passerines occur in this area, the Epaulet Oriole is the only species of its genus in eastern Argentina, Uruguay and southern Brazil (Olrog 1979, Belton 1985).

Thick-billed Euphonias (*Euphonia lanirostris*) of both sexes imitate mobbing calls of other species when their nests are threatened, attract-

ing the models to the site; these join the mimic in mobbing the nest predator (Morton 1976). Epaulet Orioles imitated mobbing calls of Great Kiskadees, but rather infrequently (Table 1), and even in the nonbreeding season. These imitations occurred, but did not predominate, among two nesting pairs in La Candelaria and Iguazú. At the last site, nonmimetic "kit" calls comprised 14 of the 34 calls uttered by orioles while I was close to their nest. Although the orioles were alarmed, showing insistent tail flicking, mobbing calls were imitated only four times. At La Candelaria Epaulet Orioles were nesting in a tall royal palm, and did not seem alarmed by my presence. This sample may be irrelevant for a test of the hypothesis.

Epaulet Orioles could avoid predation by Roadside Hawks with their vocal mimicry. Stomach contents indicate that Roadside Hawks prey on birds (Schubart et al. 1965), up to the size of a *Turdus* thrush. In La Candelaria, I have twice seen this hawk attacking birds (Rufous Horneros and Bay-winged Cowbirds) in wooded areas. At La Candelaria the oriole imitations often gave the impression that the hawk was alarming and/or being mobbed by two to four species of birds. This could function as an "interspecific threat" to the hawk (Robinson 1974, Baylis 1982); probably experiments with playbacks to captive hawks will be needed to test the idea.

If vocal mimicry has an interspecific function at all, the hypothesis of a general interspecific threat directed to predators (Baylis 1982) is more consistent with the data. Epaulet Orioles could have been alarmed by my presence, and perhaps most of their mimicry was directed to me.

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