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ECOLOGY, BEHAVIOR AND SOCIAL ORGANIZATION OF SAFFRON-COWLED BLACKBIRDS (*XANTHOPSAR FLAVUS*)

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Resumen. – Ecología, comportamiento y organización social del Tordo Amarillo (*Xanthopsar flavus*). – La ecología de la conducta y la organización social del Tordo amarillo (*Xanthopsar flavus*) se investigó entre 1995 y 2004, principalmente en Argentina y Paraguay; también se obtuvo información de una pequeña población cautiva. Según una reciente filogenia molecular, este ictérido y ambas especies del genero *Pseudoleistes* forman un clado monofilético bien definido (clado *Pseudoleistes*). El Tordo Amarillo muestra un mínimo dimorfismo sexual en tamaño, pero un marcado dimorfismo sexual en coloración, concordando y discordando, respectivamente, con los *Pseudoleistes.* El Tordo Amarillo se alimenta principalmente de artrópodos obtenidos por "gapeo" en el suelo o en vegetación baja. Nidifica como parejas monógamas en la vegetación acuática emergente de humedales, o en la vegetación herbácea en sitios secos. La nidificación puede ser solitaria o en pequeñas colonias de hasta 40 parejas. Los machos alimentan a los pichones tanto como las hembras, y se observaron machos ayudantes (helpers) en dos de seis nidos o grupos aislados con volantones. El repertorio vocal del Tordo Amarillo es relativamente exiguo (menos de 10 vocalizaciones) y mayormente compartido por ambos sexos. En todos estos aspectos, el Tordo Amarillo se asemeja a los *Pseudoleistes*, aunque su organización parece menos compleja. Una hipótesis basada en la distribución filogenética del uso de humedales y conducta parental en ictéridos predijo que tanto la poliginia como un cuidado paterno mínimo se deberían dar en el clado *Pseudoleistes*, pero la predicción se basa en una categorización floja del hábitat y conducta territorial de estas especies.

Abstract. – The behavioral ecology and social organization of Saffron-cowled Blackbirds (*Xanthopsar flavus*) was investigated between 1995 and 2004, mostly in Argentina and Paraguay. In addition, some data were obtained from a small captive population. According to a new molecular phylogeny, this blackbird, plus the two *Pseudoleistes* marshbirds, forms a well-defined monophyletic clade (marshbird clade). Sexes of Saffron-cowled Blackbirds show minimal size dimorphism and marked color dimorphism, agreeing and disagreeing with the marshbirds. The blackbird feeds mostly on arthropods by gaping in the ground or in low vegetation, and breed as monogamous pairs either in marsh emergent vegetation, or in herbaceous vegetation in dry soil. Nesting occurs solitarily, or in small colonies of up to 40 pairs. Males feed chicks at similar rates than females. Male helpers were observed in two of six isolated nests or postfledging groups. The vocal repertory of Saffron-cowled Blackbirds is comparatively small (less than 10 vocalizations) and mostly shared between the sexes. Saffron-cowled Blackbirds closely resemble the marshbirds in all those aspects, but their social organization seems less complex. An hypothesis based on the phylogenetic distribution of marsh nesting and parental behavior in icterids predicted that polygynous mating and minimal male care should occur in the marshbird clade, but the prediction was based on weak categorizations of habitats and territorial behavior. *Accepted 22 November 2004.*

Key words: Saffron-cowled Blackbird, *Xanthopsar flavus*, displays, vocalizations, breeding organization, behavioral evolution, molecular phylogeny.

INTRODUCTION

The Saffron-cowled Blackbird (*Xanthopsar flavus*), a red data book species, survives in fragments of its former distribution in Argentina, Brazil, Paraguay and Uruguay (BirdLife International 2002). Recent literature on the species is mostly concerned with conservation issues (Fraga *et al.* 1998, Azpiroz 2000, Dias & Maurício 2002). Natural history and behavioral data is included in some of those papers, as well as in Belton (1985) and in the older literature (e.g., Gibson 1885, Hudson 1920). However, a detailed account of the behavioral ecology (including vocalizations) of this icterid has not been published. This paper presents new behavioral data on Saffron-cowled Blackbirds, obtained in Argentina, Uruguay and Paraguay, and summarizes our knowledge on the social organization of the species.

The behavioral ecology of some icterid species has been intensively studied, with important reviews that summarize data and propose ideas on the evolution of social behavior and organization within the family (e.g., Orians 1985a, 1985b; Robinson 1986). The information on behavior and ecology of Saffron-cowled Blackbirds is discussed in this context. Thanks to a new molecular phylogeny of the family (Lanyon & Omland 1999, Johnson & Lanyon 1999), more rigorous approaches to behavioral evolution in the Icteridae are now possible (Searcy *et al* 1999). Scientific names in this paper follow the last version of the South American Checklist Committee of the American Ornithologists' Union (Remsen *et al.* 2004). Lowther *et al.* (2004) cover the nomenclatural history of the genus *Agelaius* (formerly including *Xanthopsar*) and state the reasons for the recent generic changes.

The phylogenetic analysis of Searcy *et al.* (1999) suggested that a switch to marsh-nesting was crucial for the evolution of polygynous mating and unequal parental care in the icterids. In the new phylogenetic tree (Lanyon & Omland 1999, Johnson & Lanyon 1999), Saffron-cowled Blackbirds are ancestral to an exclusively South American clade containing also the marshbirds of the genus *Pseudoleistes* [Brown-and-yellow (*P. virescens*), Yellow-rumped (*P. guirahuro*)]. The clade containing Saffron-cowled Blackbirds and the marshbirds (marshbird clade) was classified as marsh-nesting and, by being monogamous, it was a clear exception to the trend. On the other hand, the nearest icterids outside this clade, the Yellow-hooded (*Chrysomus icterocephalus*)and Chestnut-capped Blackbirds (*C. ruficapillus*), agreed with the hypothesis, as both species (formerly included in *Agelaius*) are marsh-nesting, polygynous and have unequal parental care (Lowther *et al.* 2004). The poverty of information on South American icterids, even on basic subjects like habitat, food and general ecology, made more difficult the analysis of Searcy *et al.* (1999). The subject is discussed here using more updated comparative data.

MATERIALS AND METHODS

Saffron-cowled Blackbirds were observed at 36 localities in Argentina (provinces of Corrientes and Entre Ríos), Uruguay (departamento Rocha) and Paraguay (departamentos Misiones, Caazapá and Itapúa). Coordinates of localities where the species was observed were obtained with a GPS receiver, and distances between localities and occupied areas were estimated with Arc View GIS. The area most frequently visited was located around Perdices (33º16´S, 58º34´W) in southeastern Entre Ríos. A total of 127 days and approximately 500 h of field observations (from October 1995 to March 2004) are included in this report. A total of 17 nestlings and fledglings were color banded for individual identification.

Data were also obtained from a group of

TABLE 1. Body masses (g), sexual size dimorphism and color dimorphism in Saffron-cowled Blackbirds and their four closely related species, according to molecular phylogeny. Sample sizes are given for males and females. Size dimorphism is expressed as the ratio of mean male body mass/mean female body mass.

Species	Mass		N		Sexual dimorphism	
	Male	Female	Male	Female	Size	Color
Chestnut-capped Blackbird (*Chrysomus ruficapillus*)	41.5	32.0	5	3	1.297	Yes
Yellow-headed Blackbird (*C. icterocephalus*)	34.5	26.7	11	14	1.292	Yes
Safron-cowled Blackbird (*Xanthopsar flavus*)	41.1	38.3	11	10	1.073	Yes
Yellow-rumped Marshbird (*Pseudoleites guirahuro*)	91.2	81.9	6	3	1.113	No
Brown-and-yellow Marshbird (*P. virescens*)	79.6	72.9	62	56	1.092	No

Sources: Personal unpubl. data; publications: Belton (1985), Darrieu & Camperi (1998), Magalhaes (1999), Fraga & Di Giacomo (2004); label data on specimens at the American Museum of Natural History, New York, the Field Museum of Natural History, Chicago, and, for Yellow-headed Blackbirds, the Colección Ornitológica Phelps, Caracas.

nine captive blackbirds (seven males and two females, all color banded for individual recognition) donated by bird catchers in Buenos Aires, and captured at unprecise localities of Corrientes and Entre Ríos provinces. This captive population was kept in a 64 m^2 outdoor aviary near Luján, Buenos Aires Province, Argentina, from 15 May to 23 October 1998, with a special permission from the provincial government. The rehabilitated blackbirds were afterwards released in a private nature reserve in Buenos Aires Province (BirdLife International 2000), and monitored for some weeks.

Sexes of adult Saffron-cowled Blackbirds are easily recognizable by differences in coloration (Ridgely & Tudor 1984). Chicks out of the nest and dependent juveniles resemble females and cannot be sexed in the field, but differ from adults of both sexes in having yellowish gray rumps (versus bright yellow) and pinkish-red palates (versus black) (Fraga *et al.* 1998).

My body mass data for Saffron-cowled Blackbirds (including some adults of the aviary population) were obtained with Pesola scales. Body mass values for Saffron-cowled Blackbirds and other icterids were obtained from the literature (Belton 1985, Darrieu & Camperi 1998, Magalhaes 1999, Fraga & Di Giacomo 2004) and label data on specimens at the American Museum of Natural History (New York), Field Museum of Natural History (Chicago), and the Colección Ornitológica Phelps (Caracas).

I recorded bird vocalizations with an AKG C568 EB shotgun microphone and a Sony Walkman Professional cassette recorder. All vocalizations used in this paper were spontaneous, i.e., no playback was used. One vocalization of each recognizable type, and with a minimum background noise, was selected for each individual; if more than one good sonogram were available for one individual, I used the mean measurements. For each vocalization I measured the following variables: total duration (s) and emphasized (or peak) frequency (kHz); these two variables are little affected by sound volume or recording quality. Temporal and acoustic variables were measured with the Cool Edit 2000 and Syrinx 2001 softwares, and sonograms printed with the last software (obtained from the Cornell Laboratory of Ornithology, Ithaca, NY, USA).

Comparative data on behavior, vocaliza-

tions and nesting of the marshbirds and the *Chrysomus* blackbirds are often taken from my unpublished field observations and tape recordings, obtained in NE Argentina (Buenos Aires, Entre Ríos, Chaco, Corrientes), Paraguay (Bajo Chaco, Ñeembucú, Misiones, Itapúa), Brazil (Minas Gerais, Amazonas) and Venezuela (Sucre). Names of icterid displays follow Orians & Christman (1968). Definitions of terms describing social organization, like "monogamy" and "territory" follow Searcy *et al.* (1999). Helpers are individuals other than a mated pair that participate in the feeding and care of the chicks.

RESULTS

Body mass and sexual dimorphism. Data on body mass, sexual dimorphism in mass, and plumage dimorphism of Saffron-cowled Blackbirds and its four related species are in Table 1. Clearly, Saffron-cowled Blackbirds resemble the *Chrysomus* blackbirds in having sexual dimorphism in plumage, but are similar to the marshbirds in their slight size dimorphism.

Five males in the captive population had scattered brownish feathers (instead of orange yellow) in the front, and likewise brownish feathers in the otherwise black nape and back, suggesting a gradual acquisition of the adult plumage. By the presumed dates of capture indicated by the bird dealers, those males were probably yearlings.

Habitat. In Argentina, Saffron-cowled Blackbirds have been found in grasslands and marshes in open environments (Fraga *et al.* 1998). In the southern Pampas of Buenos Aires (37º15´S), the species formerly occupied treeless areas (Doering & Lorentz 1879), sharing the habitat with Brown-and yellow Marshbirds. At the northern end of its range in Paraguay (upper bassin of the Río Tebicuary, 26º30´S), Saffron-cowled Blackbirds are found in the abrupt interface between open grasslands (campos) and the interior Atlantic forest (López de Kochalka 1996, Madroño *et al.* 1998, pers. observ.). The "campos" are apparently an edaphic formation in this region (Cabrera 1970). Paraguayan populations of *Xanthopsar* may live and breed in large (50–100 ha) natural patches of grassland and marsh surrounded by dense subtropical forest, or stands of the tree-sized bamboo *Bambusa angustifolia*. This habitat is shared by Yellow-rumped Marshbirds. The Saffron-cowled Blackbird population in the upper Tebicuary may well exceed 1000 individuals.

The Perdices population in Entre Ríos, estimated to 120 individuals, occupies rolling countryside with fertile agricultural and pasture soils, limited to the south by the floodplain of the Río Paraná delta. By plotting all my records, the area occupied by the Perdices population is estimated to 282 km^2. Saffron-cowled Blackbirds are seldom seen in the floodplain of the delta , but a small population of about 80 individuals was recently found at Ibicuy (33º44'S, 59º06´W), within the delta; this population lives in a small elevated area covered by old sand dunes, remnants of a mid-Holocene coastline (Iriondo 1991).

Diet . The diet of *Xanthopsar* has been examined mostly in Paraguay (López de Kochalka 1996), using faecal analysis; it is mostly composed of insects and spiders (95% of the items), with a small percentage of seeds. My own observations agree with those data; I observed only three cases of seed consumption, two involving cultivated plants. Sorghum seeds were taken from the plants, and small groups of individuals sometimes consumed rice seeds left on rural roads by harvesting machines. The aviary population rejected seeds (even rice), but readily accepted insects (larvae of *Tenebrio*). Insects consumed (López de Kochalka 1996) include Hemiptera,

Coleoptera, Diptera, Lepidoptera (caterpillars) and Hymenoptera (ants).

Flying ants were captured when available, by mean of short sallies, and were offered to chicks. Otherwise, most prey were obtained on the ground, the top soil, or in low vegetation, with much use of gaping. Gaping was not only used in the soil, but also to search in the basal leaves of *Eryngium* and other plants. In the aviary, some individuals squatted on the ground while probing and gaping. Foraging flocks were rather compact (small inter-individual distances) and, when moving, often exhibited "rolling" behavior, with the rear individuals flying on top of the first ones.

Flocks and flocking behavior. With four exceptions, I found Saffron-cowled Blackbirds in groups or flocks of 2 to 240 individuals. Flock sizes of Saffron-cowled Blackbirds varied considerably between seasons and localities (Fraga *et al*. 1998, Dias & Maurício 2002). Flocks of up to 470 individuals have been reported from Paraguay (BirdLife International 2000). The largest flock I observed in Argentina (approximately 240 individuals) was found around a winter roost in Corrientes.

Sentinel behavior has been reported for the species (Hudson 1920, López de Kochalka 1996) and I observed some cases. However, more frequently Saffron-cowled Blackbirds depended on the sentinel behavior of associated bird species (López de Kochalka 1996, Fraga *et al* 1998, and below). In presence of avian predators like Sharp-shinned Hawks (*Accipiter striatus*) or Aplomado Falcons (*Falco femoralis*), flying flocks in Perdices moved in a compact, spheroid-shaped formation.

Interactions with other birds. Most authors (Belton 1985, Fontana & Voss 1995, Azpiroz 2000) have stressed the remarkable association of Saffron-cowled Blackbirds with the Black-and-white Monjita (*Xolmis dominicana*). In Argentina, this association occurs mostly in Corrientes, because Black-and-white Monjitas are rare and local in Entre Ríos (Fraga 2003). The monjita is a hypothetical species in Paraguay (Hayes 1995) so this association does not occur everywhere within the range of Saffron-cowled Blackbirds.

Besides the Black-and-white Monjita, I saw foraging flocks of blackbirds following the movements of other birds (icterids and tyrant flycatchers) and landing near them. The icterids more frequently followed were the two marshbirds (Fraga *et al* 1997). The aviary population joined a flock of Brown-and-yellow Marshbirds within 15 min of being released in the wild. Flycatchers followed by Saffron-cowled Blackbirds included the Streamer-tailed Tyrant (*Gubernetes yetapa*) in Paraguay and Corrientes, and rarely the Scissor-tailed Flycatcher (*Tyrannus savanna*) in Entre Ríos. On the other hand, Gray Monjitas (*Xolmis cinerea*) attacked and expelled two groups of blackbirds that landed below their perch.

Concerted attacks on birds (other than predators and parasites) by groups of Saffron-cowled Blackbirds have been reported (Madroño *et al*. 1998). In Entre Ríos, I once saw attacks on Eared Doves *Zenaida auriculata* that foraged on the ground. Male Saffron-cowled Blackbirds sometimes attack other birds when setting a nesting colony (Belton 1985).

Agonistic behavior. Saffron-cowled Blackbirds threat conspecifics with a "bill up" display, raising the head and bill, and often walking or flying in this position towards other individual. I saw both sexes using this display. Most agonistic behavior is seen in breeding colonies (Belton 1985). Fighting and chasing in the aviary population occurred during the first three months (May–July), and was afterwards replaced by threat displays and avoidance. As expected, males with brownish feathers

(subadults) were displaced from perches or foraging positions by adults. No special appeasement displays (e.g., allopreening) from the subordinate individuals were seen.

Sexual behavior. Aerial courtship flights (sexual chases), similar to those of other icterids (Orians & Christman 1968), were seen in Paraguay and Argentina. Perched courting males showed a display partially resembling the "song spread" of other icterids (Orians & Christman 1968): the wings were lowered and curved, exposing the yellow rump, and the tail feathers were spread like a fan. However, differing from similar displays in Nearctic *Agelaius*, the head of Saffron-cowled Blackbirds pointed upwards, and the body feathers were not fluffed. Song is usually delivered in this posture, which sometimes preceded copulation. One male in Entre Ríos displayed on the ground to a female perched above it, clearly showing its bright yellow rump surrounded by black plumage.

Pairing behavior between two dominant males and the two females took place in the captive population towards July. When the birds were released, the paired males flew to their respective females and performed standard courtship behavior. Data from Corrientes and Entre Ríos also indicate that pair formation occurs before the females select nesting sites, as in the Yellow-rumped Marshbirds (Fraga & Di Giacomo 2004).

The main sexual display of females was silent: the female crouched on the ground or on a perch, raised the tail and quivered the wings. This display was not always followed by copulation, and was observed months before the breeding season (e.g., late August). As noted by Belton (1985), the display was seen also in agonistic contexts, particularly in conflicts between neighbor nesting pairs.

Nesting behavior. Most nests were built in small colonies of 3 to 40 pairs (Fraga *et al* 1998). Colonial nesting is also the rule in Paraguay (Madroño *et al*. 1998, pers. observ.) and Brazil (Belton 1985, Dias & Mauricio 2002). Solitary or colonial nesting occurs in Entre Ríos province, where I found four solitary nests in the incubation or nestling stages, built on low shrubby vegetation along rural roads. Besides, at least six isolated pairs were seen during the early breeding season, apparently looking for similar nest sites along roadsides in this province. Solitary nesting seems more frequent in Uruguay, reflecting perhaps population declines (Azpiroz 2000). Nevertheless, two blackbird colonies of 10 and 12 pairs were reported from that country (Gibson 1885, A. Azpiroz pers. comm.)

Preliminary data on colony locations for Argentina can be found in Fraga *et al*. (1998). Updating that information, all the 11 nesting colonies I observed in Perdices were in dry or upland terrain; nests were built in either native herbaceous plants or introduced weeds (once also on the ground). Elsewhere in Entre Ríos, historical sources mention a colony in a marsh (Barrows 1883) and another in thistles and low shrubs along a roadside hedgerow (Klimaitis 1984, I visited the site in 1996). Before extinction, the population around Buenos Aires city also nested on dry ground (Hudson 1920, Pereyra 1933). One historical record for western Uruguay indicates a colony in dry terrain (Gibson 1888), and local people interviewed in 2003 in this area mentioned this fact. Elsewhere in Corrientes, Argentina (Fraga *et al*. 1998), Brazil (Belton 1985, Dias & Mauricio 2002), eastern Uruguay (Azpiroz 2000) and Paraguay (Madroño *et al*. 1998, pers. observ.) Saffron-cowled Blackbirds nest in emergent vegetation in marshes and bogs, including abandoned ricefields. Arboreal nesting has not been reported for Saffron-cowled Blackbirds.

In Perdices, most colonies were located within or near nesting groups of White-

browed Blackbirds (*Sturnella superciliaris*), which have a similar breeding season. This icterid could also be considered a colonial nester, although its nests were more scattered than those of Saffron-cowled Blackbirds (pers. observ.). Both species tolerated each other, and even attacked together avian predators like Long-winged Harriers (*Circus buffoni*), and Shiny Cowbirds (*Molothrus bonariensis*). In Paraguay nesting colonies were often close to nests of Yellow-rumped Marshbirds, which are aggressive to raptors (Fraga & Di Giacomo 2004). Persistent (or traditional) use of specific nesting areas or sites by Saffron-cowled Blackbirds was not observed in Entre Ríos, where agricultural practices constantly changed the landscape. However, an abandoned rice field in Corrientes was used for a minimum of four breeding seasons. Similar data exists for some sites in Paraguay.

Nest clumping in Saffron-cowled Blackbirds reached a density of almost 56 nests/ha in one colony (Fraga *et al* 1998). Inter-nest distances ranged from 3 to 18 m. Saffron-cowled Blackbirds have been classified as territorial breeders (Searcy *et al* 1999). However, nesting pairs in colonies defended (at most) small areas around the nest, and did not defend feeding territories. In all the Perdices colonies, nesting birds foraged and gathered most of the food for chicks outside the colony, often flying hundreds of meters to do so. Solitary pairs feeding nestlings also collected food at similar distances.

Breeding season and nesting synchrony. Based on egg-laying dates, Saffron-cowled Blackbirds nested from October to December. Data on clutch sizes, incubation and nestling periods can be found in Fraga *et al.* (1998). The breeding season is brief and no second broods were detected. Data from Perdices also indicate nesting synchrony within colonies, with 80% of the clutches laid within an interval of about 10 days. Colonies were occupied for 30 to 45 days.

Parental behavior. Breeding Saffron-cowled Blackbirds appear to form monogamous pairs. Only the females build the nest, incubate eggs and brood chicks. Males perform most nest guarding and most attacks on avian nest predators and parasitic Shiny Cowbirds (*Molothrus bonariensis*); however, females were also observed attacking nest predators like Chimango Caracaras (*Milvago chimango*). A male was seen feeding its incubating mate in Entre Ríos; as few nests were intensively watched during this stage, this behavior may be more widespread. Males were observed performing other parental behavior, like guiding a recently fledged brood away from the nest (and myself), by repeatedly landing with quivering wings near the chicks.

During non-systematic observations at six broods or nests (Argentina and Paraguay) chicks in and out of the nest were fed by both sexes at roughly equal proportions (29 feeding trips for males, 33 for females). By contrast with most South American icterids (Orians 1980), provisioning adults frequently carried several prey items per feeding trip. All identified items were insects, including Orthoptera (Tettigoniidae, Acrididade, mostly green-colored), Mantidae, Hymenoptera (reproductive alates of ants) and larvae of Lepidoptera (mostly green-colored). Emergent aquatic insects, prominent in the diet of other marsh-nesting blackbirds (Orians 1980), were not observed. Similar observations (equal sexual roles and food items) have been reported from Uruguay (Azpiroz 2000).

Azpiroz (2000) first reported helpers at the nest in Uruguayan Saffron-cowled Blackbirds. His sample comprised 10 isolated nests, but no information on the frequency and sex of the helpers was given. Colonial nesting (the rule in Argentina and Paraguay) make more difficult the observations of helping; without

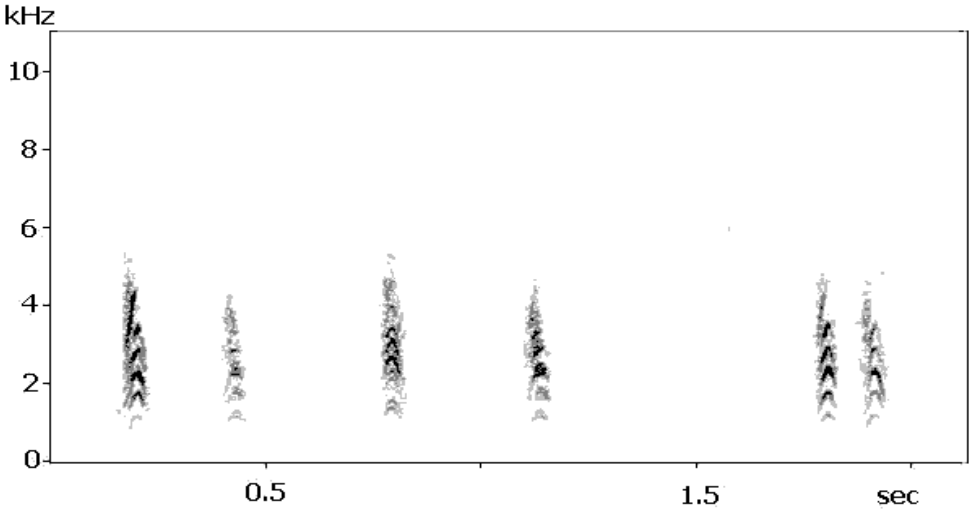

FIG. 1. Calls ("*chucks*") from departing individuals of both sexes, 12 km NE from Santo Tomé, Corrientes province, Argentina (26 June 1999).

banded individuals it was difficult to determine how many individuals were carrying food, and to which nests or chicks. The same comment applies to postfledgling groups produced by colonies with multiple successful nests.

My best data are therefore based on 6 isolated nests or postfledging groups (five from Entre Ríos, one from Corrientes); these breeding units were located at distances of more than 5 km from the nearest conspecifics. Two solitary nests in Entre Ríos which survived to the late incubation stage were attended by unassisted pairs of blackbirds. The postfledging groups contained one female and no more than three chicks of similar age; they could have originated from undetected isolated nests, or from small colonies where a single nest survived (this last information was available in two cases). Two of three isolated postfledging groups in Entre Ríos, observed for periods of 40 min or more, had helpers. One group found on 3 December 2000 consisted of two recent fledglings (color banded as nestlings), escorted by two males and one female. Both males were seen carrying insects in their bills. On 28 December 2000, I observed another isolated group of four adult Saffron-cowled Blackbirds (three males, one female) and three fledglings; all the adults caught flying ants that were delivered to the begging juveniles. At least one male lacked full adult plumage. The only isolated postfledgling group from Corrientes (30 November 1995) consisted of a pair attending one chick still barely able to fly. The loud alarm calls of the adults attracted other conspecifics (two males and one female), but these were chased and threatened by the male parent. However, this pair tolerated two Brown-and-Yellow Marshbirds near its chick.

Vocal behavior. Individuals of both sexes in departing flocks usually exchange sonorous "*chuk*" calls when flying away (Fig. 1). Other contact calls for both sexes sound like "*cheg*" or "*kuk*". In sonograms the calls look like stacks of chevron-shaped elements, lasting 0.04 to 0.08 s, and with mean emphasized fre-

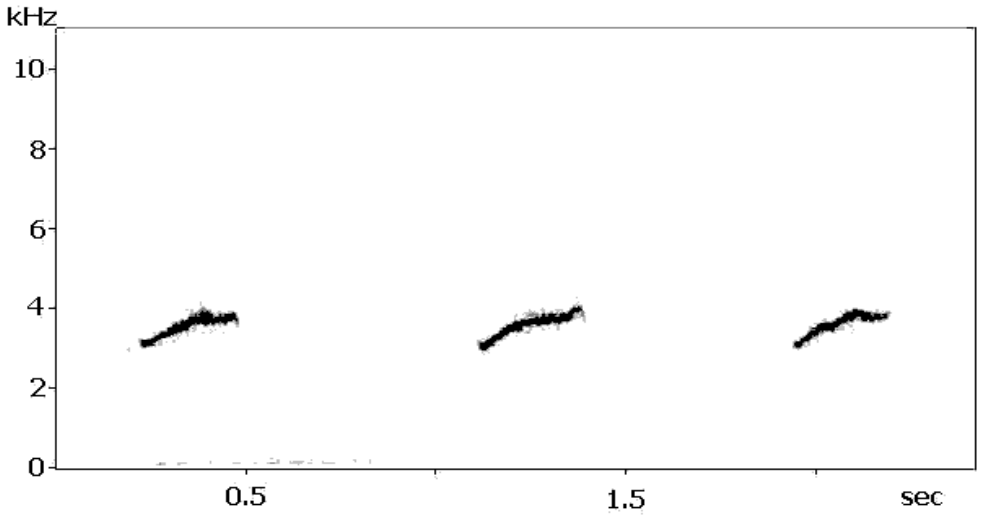

FIG. 2. Alarm whistles of a male in a breeding colony, Perdices, Entre Ríos province, Argentina (7 December 1997).

quencies ranging from 2.01 to 4.36 kHz (n = 22 individuals, both sexes). There is some variation in frequency and structure of the contact calls, possibly related to context.

A loud ascending whistle (Fig. 2) was commonly heard from males during the breeding season, apparently alarmed because of my presence near a nest or a fledged chick. I also heard this whistle while a snake (*Philodryas patagonica*) was raiding a nesting colony in Entre Ríos (Fraga *et al.* 1998). I did not hear this call from females. Whistles (n = 7 males) lasted 0.25 to 0.44 s, with a range of emphasized frequencies covering 2.94 to 4.43 kHz. When I approached recently fledged chicks, attending females produced fast series of harsher calls "*kuk*", perhaps a variant of the contact call that functions like an alarm.

Individuals in the hand or trapped in mist nests produced series of rasping calls (no recordings available), similar to "distress calls" of other icterids I have trapped [e.g., Baywings (*Agelaioides badius*)].

The five fledged chicks I recorded produced two main calls, a soft contact "*chew*" and the begging call, a longer, nasal "*chwaaa*" (Fig. 3). One individual combined both in repeated series, and intermediate calls between both vocalizations commonly occur. Both chick calls, particularly the "*chwaaa*", show considerable variation in length, frequency and harmonic structure, probably related to context and motivation. The "*chwaa*" calls may have up to 12 harmonics, with mean emphasized frequencies ranging from 2.29 to 5.46 kHz .

The song is produced by both sexes (Belton 1985) but it is more frequent among males. I obtained satisfactory song recordings from 26 males, but only from two females (Fig. 4). Most singing was produced by perched individuals, and singing in flight was heard mostly during sexual chases. The songs comprise fast introductory notes, followed by one to three loud rasping notes, either ascending or descending. As defined by Marler (1969), songs are frequency modulated, with a marked dissonant quality. The number of elements in a song range from one to six or

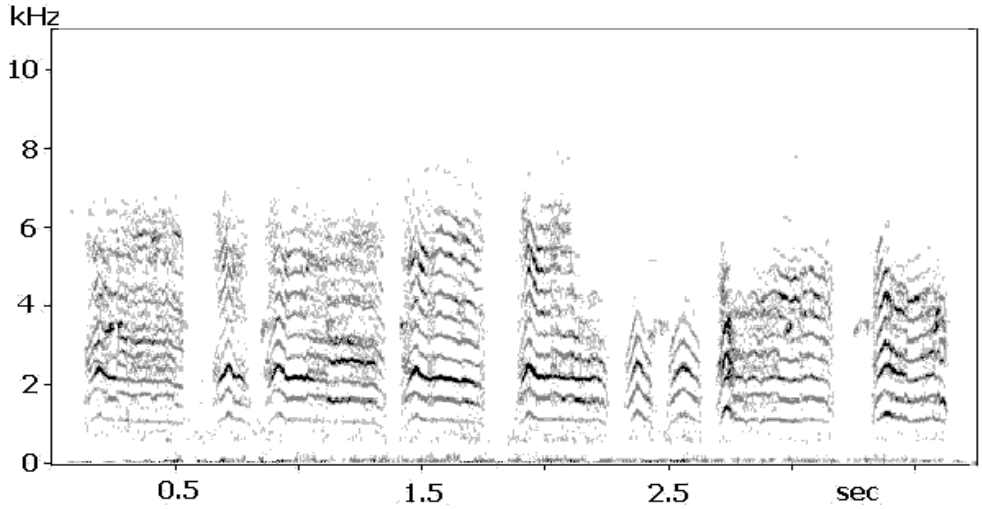

FIG. 3. Calls of a fledged chick, Perdices, Entre Ríos province, Argentina. The short calls at 2.5 s are contact calls, the others are food-begging calls directed to the male (1 December 2001).

seven; however, pauses between elements are not well defined in the sonograms, even during sudden changes in pitch.

Songs showed considerable variation in duration and emphasized frequencies. Songs of 28 individuals lasted from 0.29 to 1.13 s, with a mean (SD) of 0.85 (0.16) s. The emphasized frequencies ranged from 2.94 to 7.16 kHz, with a mean (SD) of 4.33 (1.12) kHz. Each marked male in the aviary population had a distinctive song, clearly recognizable in the sonograms. Likewise, songs of neighbor males in nesting colonies were different (Fig. 5). I could recognize in the field the most distinctive song variants.

Male songs occur throughout the year, and are produced even by individuals attending fledged chicks. Group singing is frequent among males, as noted by Hudson (1920). In the aviary population, song bursts involved up to five of the seven males, and were started by the two paired males. Female singing was heard mostly during the nesting season, and once in a flock with many fledged chicks. In nesting colonies, it apparently occurred in response to the presence of another female near the nest, or (rarely) a male other than the mate. Mated pairs produced song duets after conflicts with neighbor pairs; the duets were sometimes initiated by the female.

DISCUSSION

Saffron-cowled Blackbirds are similar to the two *Pseudoleistes* marshbirds in their mainly insectivorous diet (Darrieu *et al.* 1996 for Brown-and-Yellow Marshbirds) and in foraging mostly on the ground. This similarity possibly explains their frequent interspecific association (Fraga *et al.* 1998). Contrasting with Saffron-cowled Blackbirds, both *Chrysomus* blackbirds consume large amounts of seeds, even in the breeding season, and are regarded as important pests of rice crops (e.g., ffrench 1976, Bello Falavena 1988, Bruggers & Zaccagnini 1994). The most unusual aspect of the foraging ecology of Saffron-cowled Blackbirds is their frequent association with tyrant flycatchers and the marshbirds, best interpreted as an antipredator strategy (Fon-

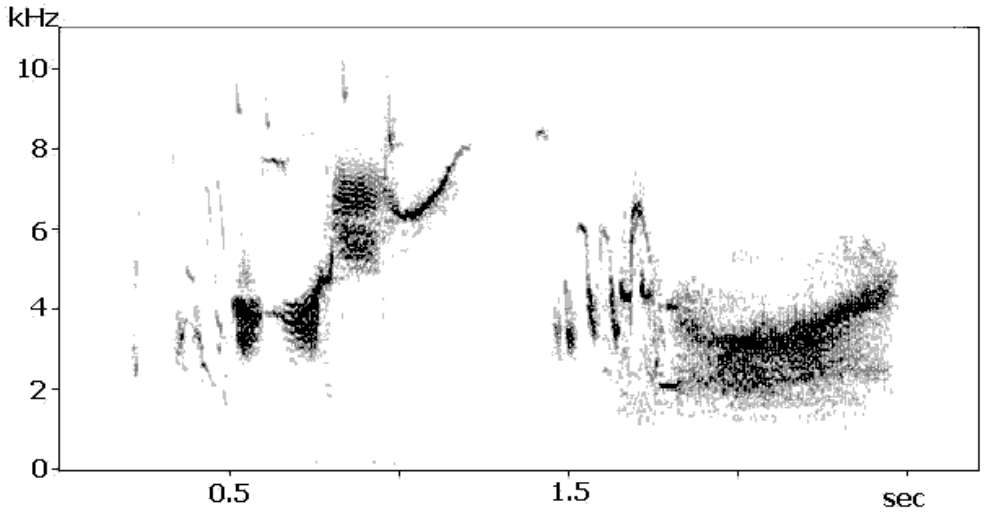

FIG. 4. Songs of two neighboring males in a breeding colony, Perdices, Entre Ríos province, Argentina (25 November 2000).

tana & Voss 1995, Fraga *et al* 1998). Possibly the blackbirds' conspicuous coloration and relatively small size make them particularly vulnerable to avian predators in open habitats.

In their social organization, breeding Saffron-cowled Blackbirds closely resemble the two marshbirds (Orians *et al*. 1977, Fraga & Di Giacomo 2004), in nesting solitarily or in small colonies. By contrast, the two *Chrysomus* blackbirds commonly nest in large colonies reaching up to 350 nests (Bruggers & Zaccagnini 1994); perhaps this degree of clumping is related to their granivorous diet. Pairing in Saffon-cowled Blackbirds appears to be monogamous, as in the marshbirds (Orians *et al*. 1977, Fraga & Di Giacomo 2004.). Male Saffron-cowled Blackbirds provide a considerable fraction of chicks´ food, as in the marshbirds. This contrasts with the reduced provisioning role of *Chrysomus* males (Wiley & Wiley 1980, Lyon 1997).

Helpers are regularly present in the nests of both marshbirds (Orians *et al*. 1977, Fraga & Di Giacomo 2004), from the incubation to the postfledging stages. My limited data suggest that cooperative breeding is less frequent among Saffron-cowled Blackbirds, with helpers occurring mostly during the late nestling and postfledging stages. However, a more extensive research with color banded adults could reveal a higher frequency of helping. Non-breeding groups of both marshbirds show seemingly "altruistic" behaviors like the presence of flock sentinels, and the persistent mobbing of avian predators (Mermoz & Reboreda 1998, Fraga & Di Giacomo 2004), far more regularly than Saffron-cowled Blackbirds. Saffron-cowled Blackbirds appear to be in a more simple stage of social organization than the marshbirds.

Data presented here show that ecological and behavioral categorizations (marsh-nesting and territoriality) of the marshbird clade in the analysis of Searcy *et al*. (1999) should be reconsidered. Belton (1985) stressed the fact that the narrow boggy swales used as nesting habitat by Saffron-cowled Blackbirds in the southern Brazilian highlands are not typical marshes, having little standing water. The nesting habitat of Saffron-cowled Blackbirds

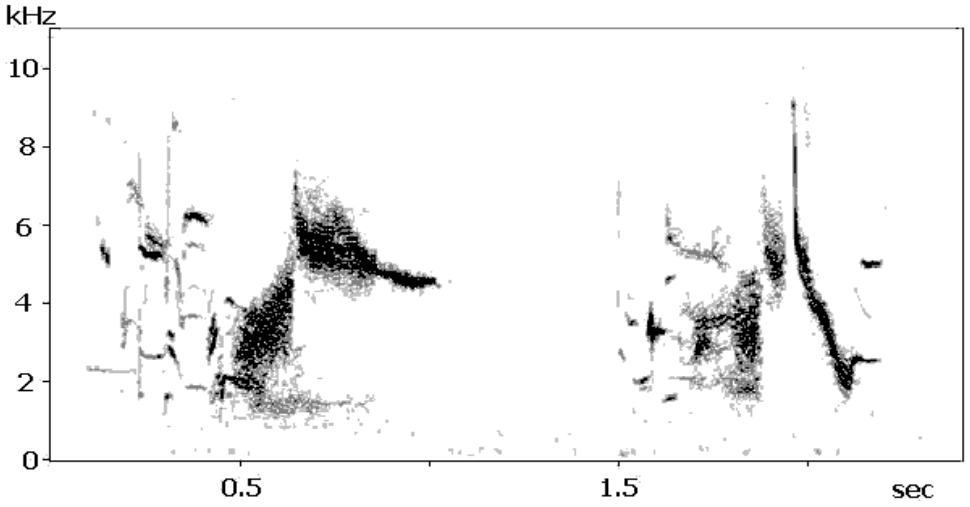

FIG. 5. Male-female song duet in a breeding colony, Perdices, Entre Ríos province, Argentina (25 November 2000).

also includes grassland and even open savanna on dry terrain, and the same comment applies to the marshbirds (Orians *et al.* 1977, Mermoz & Reboreda 1998, Fraga & Di Giacomo 2004). The three species rarely forage in water or aquatic plants, and may breed in emergent marsh vegetation to escape nest predators, or the human-induced grassland fires so frequent in Paraguay and Corrientes. My data indicate that Saffron-cowled Blackbirds are non-territorial, and that pair formation takes place in the mobile non-breeding flocks rather than in fixed male territories visited by females. The same pattern occurs in marshbirds (Orians *et al.* 1977, Mermoz & Reboreda 1998, Fraga & Di Giacomo 2004). Monogamy may prevail in the marshbird clade by a combination of habitat and behavior. By contrast, males defend fixed territories and display to visiting females in the two *Chrysomus* blackbirds (Wiley & Wiley 1980, Lyon 1997, pers. observ.), showing the predicted association between marsh habitat, territorial behavior and polygynous mating.

The agonistic displays found in both sexes of Saffron-cowled Blackbirds are widespread in the family (Orians 1985b). The courtship display of male Saffron-cowled Blackbirds, less complex than the song spread display of Nearctic *Agelaius* blackbirds (Orians & Christman 1968), is similar to the perched courtship display of singing male Yellow-rumped Marshbirds, which also exhibit their bright yellow rumps (Jaramillo & Burke 1999, pers. observ.).

Buzzing, nasal or rasping sounds similar to those of Saffron-cowled Blackbirds occur in the songs of a large number of icterid species, Nearctic and Neotropical (Hardy *et al.* 1998, Orians 1985a), including the two *Chrysomus* blackbirds and the Yellow-rumped Marshbird (Hardy *et al.* 1998, my own recordings). The songs of Saffron-cowled Blackbirds are characterized by being shorter, simpler and with a peculiar tonal quality. Contact and distress calls of Saffron-cowled Blackbirds are similar to equivalent calls of other icterids (Orians 1985a). Begging calls of Saffron-cowled Blackbird chicks sound and look (in sonograms) much like those of

Pseudoleistes marshbird chicks, particularly the Yellow-rumped Marshbird.

Even if I missed some types of vocalizations, the vocal repertory of Saffron-cowled Blackbirds appears small (less than 10 vocalizations) and mostly shared by both sexes. *Xanthopsar* blackbirds strikingly differ from North American *Agelaius* blackbirds, where male Red-winged (*A. phoeniceus*) and Tricolored (*A. tricolor*) blackbirds have 18 and 17 different voices, respectively, versus six for females (Orians 1985a). This extensive male repertory is presumably correlated with their non-monogamous mating system. Within the five Neotropical icterids discussed here, the most elaborate songs are produced by males of the polygynous Chestnut-capped Blackbird (Hardy *et al.* 1998, my own recordings). The songs, usually in contrasted sequences, last up to 9 s, and include nasal buzzing sounds, musical trills, thin whistles, ascending scales, sustained notes, and soft staccatto chords. As in the polygynous oropendolas (Price & Lanyon 1992), this song complexity may have evolved through sexual selection.

The small repertory size of Saffron-cowled Blackbirds is comparable with the repertoires of 8–9 vocalizations reported for both sexes in the two marshbirds (Orians 1985a, pers. observ.). Saffron-cowled Blackbirds are markedly dimorphic in plumage, but almost monomorphic in vocal behavior. This paradoxical situation should be the subject of further study.

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