NATURAL HISTORY AND BREEDING BEHAVIOR OF THE OLIVE (PSAROCOLIUS YURACARES) AND YELLOW-BILLED (P. ANGUSTIFRONS ALFREDI) OROPENDOLAS IN CHAPARE PROVINCE, BOLIVIA

Rosendo M. Fraga¹ & Stefan Kreft²

CICYTTP, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Matteri y España, (3105) Diamante, Entre Ríos, Argentina. E-mail: chfraga@yahoo.com
Faculty of Forestry, Univ. of Applied Sciences Eberswalde, Alfred-Moeller-Str. 1, D-16225 Eberswalde, Germany. E-mail: stefan_kreft@gmx.de

Resumen. – Notas sobre la historia natural de las oropéndolas Psarocolius yuracares y P. angustifrons alfredi en la provincia Chapare, Cochabamba, Bolivia. - Se aportan datos de historia natural para dos oropéndolas o tojos (Psarocolius yuracares y P. angustifrons alfredi) poco estudiadas de la provincia Chapare, Departamento Cochabamba, Bolivia. P. yuracares resultó ser la más escasa, y se la encontró, generalmente desplazándose en bandadas monoespecíficas, hasta los 900 m s.n.m. Se encontraron tres colonias de nidificación, dos pequeñas de 5-6 nidos en palmas Socratea en la selva (Agosto y Noviembre), y una colonia mayor (Octubre), cerca de plantaciones, con más de 30 nidos activos en un gran árbol leguminoso de unos 35 m. Esta fue un colonia mixta con nidos de otra oropéndola (P. decumanus). Los nidos de P. yuracares, más cilíndricos y de tejido más tosco que los de P. decumanus, estaban agrupados en dos núcleos (clusters), cada uno con un macho que cantaba y efectuaba despliegues, los cuales no colaboraban ni con la construcción ni con la alimentación de pichones, pero sí en alejar al Tordo Gigante (Molothrus oryzivorus). P. angustifrons alfredi resultó la oropéndola más abundante del Chapare, y se encontró en abundancia en plantaciones, pueblos y aldeas, donde nidifica a partir de Julio. No encontramos sus nidos arriba de los 700 m s.n.m. De 15 colonias, nueve fueron construidas en la palma tembe (Bactris gasipaes), nativa y cultivada en el Chapare. Las colonias nunca excedieron los 14 nidos, dando un promedio de 6,7 nidos simultáneamente activos por colonia. Los nidos, de tejido tosco, estaban bien espaciados y nunca encimados. Esta oropéndola expulsó agresivamente de sus colonias a Psarocolius yuracares y al Tojito (Cacicus cela). Se observaron desde uno a cuatro machos en las colonias, en un caso dos de éstos alternando en despliegues y cantos. Sólo las hembras efectuaron todas las actividades de nidificación. Pichones dependientes se observaron junto con hembras hasta el comienzo de la temporada de cría siguiente. No se detectó parasitismo por el Tordo Gigante.

Abstract. – We present natural history data for the little-known Olive (*Psarocolius yuracares*) and Yellow-billed (*P. angustifrons alfredi*) oropendolas from Chapare Province, Cochabamba department, Bolivia. The Olive was the scarcest oropendola, usually traveling in monospecific flocks up to 900 m a.s.l. We found only three nesting colonies, two with 5–6 nests in *Socratea* palms in dense forest (August and November), and one with about 30 active nests (October), close to plantations, in an emergent, 35-m high legume tree. This last colony was mixed, having active nests of Crested Oropendolas (*P. decumanus*). Nests of Olive Oropendolas were located in two separate, dense clusters, and were more cylindrical and coarsely woven than those of Crested Oropendolas. One singing and displaying male was present at each cluster, which did not participate in nesting activities, but helped to expel Giant Cowbirds (*Molothrus oryzivorus*) from the colony.

The Yellow-billed was the most abundant oropendola in the Chapare, visiting and nesting in plantations, villages and towns, from July onwards. No nests were observed above 700 m a.s.l. Nine of 15 colonies were built in peach palms (*Bactris gasipaes*), a native species cultivated in Chapare. Colonies did not exceed 14 nests, and had a mean of 6.7 simultaneously active nests. Nests were coarsely woven, well spaced and never clustered. This oropendola agressively expelled Olive Oropendolas and Yellow-rumped Caciques (*Cacicus cela*) from their nesting trees. One to four males visited the colonies and, in one case, two males alternated in songs and displays. All nesting activities were carried out by females. Dependent chicks may remain with females up to the start of the following breeding season. We did not detect parasitism by Giant Cowbirds on this species. *Accepted 20 January 2007*.

Key words: Olive Oropendola, *Psarocolius yuracares*, Yellow-billed Oropendola, *P. angustifrons alfredi*, Russetbacked Oropendola, foraging, breeding ecology, colonial nesting, taxonomy, Chapare, Bolivia.

INTRODUCTION

Three species of oropendolas and one colonial nesting cacique breed in the Andean foothills and adjacent lowlands (200-1000 m a.s.l.) of Chapare Province, Cochabamba Department, Bolivia. The species are the widespread Crested Oropendola (Psarocolius decumanus), the Olive Oropendola (P. yuracares), a distinctive subspecies of the Russet-backed Oropendola known as the Yellow-billed Oropendola (P. angustifrons alfredi), and the Yellow-rumped Cacique (Cacicus cela). A fifth species, the Dusky-green Oropendola (P. atrovirens), nests mostly above 1000 m a.s.l. (Jaramillo & Burke 1999, MacLeod et al. 2005), and some individuals visited our study area during the austral winter.

Two of the nesting oropendola species remain relatively unknown. The Olive Oropendola, a species mostly found in the Amazon basin, reaches its southern limit in the Chapare and nearby Santa Cruz Department. The most extensive data on its nesting behavior has been obtained from just two colonies in Venezuela (Rodríguez-Ferraro 2006). The Yellow-billed Oropendola occurs in the eastern Andean slopes from Ecuador to Bolivia (Jaramillo & Burke 1999). Published information on its behavior and ecology is minimal (Jaramillo & Burke 1999).

We present new information and summarize the behavioral and nesting data available for each species, comparing our information with that available for closely related species. The Yellow-billed Oropendola is a member of the Russet-backed Oropendola complex, a group of subspecies with a complex and controversial taxonomy (Jaramillo & Burke 1999, Remsen *et al.* 2006), and our behavioral comparisons involve two other forms within the complex, currently regarded as subspecies.

STUDY AREA AND METHODS.

The province of Chapare is located in central Cochabamba, Bolivia. We studied the icterids mostly at elevations of 200–1200 m, in the foothills of the Andes and the adjacent low-lands. Our main localities were Villa Tunari (290–430 m a.s.l.) and surroundings, including Parque Machía, Hotel El Puente and its surroundings (16°59'S, 65°24'W), Cruce Avispas (17°01'S, 65°33'W; 450–750 m), Chocolatal (17°04'S, 65°39'W; 660–1000 m) and the lower northwestern sections of Parque Nacional Carrasco (17°04'S, 65°29'W, 500–1200 m) (Fig. 1).

The study area lies almost entirely within the Southwest Amazon ecoregion, which reaches up to 1000 m (Ibisch et al. 2003). Several large rivers (Espíritu Santo, Chapare, Chimoré, Ichilo) drain the region via the Río Mamoré towards the Río Madeira and the Amazon. Annual average temperatures lie between 24° and 28°C. However, during the

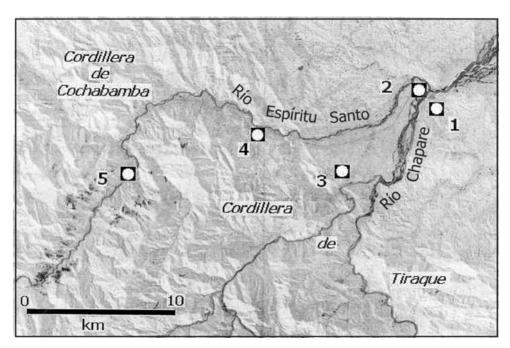


FIG. 1. Our study sites in the Chapare: 1, Hotel El Puente; 2, Villa Tunari; 3, Parque Nacional Carrasco; 4, Cruce Avispas; and 5, Chocolatal.

austral fall and winter (April-August), temperatures sometimes drop suddenly to 12–15°C or less during the passage of cold fronts from the south. Annual average rainfall in Villa Tunari is 5676 mm (Ibisch 1996), with the heaviest rains falling between October and March. However, the Chapare climate is also characterized by a nearly complete lack of dry months (Mueller *et al.* 2002).

The natural vegetation is humid evergreen forest of 30 m and (few) emergent trees reaching 45 m height. Even in the upper parts, Amazonian dominate over Andean elements (Ibisch et al. 2003). The indigenous Yuracaré were semisedentary, warrior agriculturists with an Amazonian culture (Sánchez 2002); their population was relatively small. Systematic colonization of the region by highland Bolivians started in the 1960s, and coca was the main cash crop of the colonists (Henkel 1995). In the last decade, coca cultivation has

been discouraged and replaced by plantations of tropical and subtropical fruits (mostly citrics), diverse species of palms, and cattle pastures. Large tracts of early successional forest occur naturally along the main rivers, but anthropogenic secondary forest is nowadays quite widespread, depending on the accessibility of the terrain. Recent shifts of political gravitude may bring more tolerance towards, or even encourage, coca growing.

SK worked in the study area from January 2000 until January 2003 and visited Villa Tunari more than 10 times that included at least one complete day dedicated to observation, with longer stays of 3–5 observation days in February, May and September 2001 and in January 2003. His observations took place also at Cruce Avispas in May 2001 and August and November 2002, in Chocolatal in March and August 2001 and May and November 2002, and finally in Parque Nacio-

nal Carrasco at 1200 m in February 2001. RF intensively studied oropendolas in all the sites excepting Chocolatal during 31 field days, in July and October of 2004, and in July 2005; on average he spent 8 h/day in the field. Observations were aided by binoculars, and often complemented by tape recordings. SK's recordings are housed at the Archive of Animal Sounds, Humboldt Univ. Berlin, Germany; RF's recordings are in his private collection. Sonograms were prepared with the Cool Edit 2000 (Syntrillium Corporation) and Syrinx (www.syrinxpc.com) softwares. In addition to field data, information on specimens (including body mass and stomach contents) and nests was obtained from the following museums: Field Museum of Natural History (Chicago), Museum of Zoology of the Louisiana State Univ. (Baton Rouge), Colección Boliviana de Fauna (La Paz) and the Museo de Historia Natural Noel Kempff Mercado (Santa Cruz). Specimen numbers and locations are available from the first author.

RESULTS

Olive Oropendola. This species was the least abundant oropendola at our study sites. It was also the largest and most strikingly colored. Hellmayr (1937) commented on the color variation found in the upper body plumage of this oropendola. Most individuals in the Chapare were olive green, but others were brighter, almost lemon vellow. This plumage variation was found in both sexes. Olive Oropendolas showed an obvious size dimorphism. Body mass data in museum specimens from Bolivia gave a mean (± SD) for males of 457.8 ± 39.1 g (n = 6), and 250.5 g ± 7.8 g (n = 4) for females. The size dimorphism score (mean male mass/mean female mass) was 1.83. Males also had a small crest that females lacked.

Stomach contents from museum speci-

mens included fruits and insects. Olive Oropendolas usually foraged near the canopy, but perched as low as 3 m to obtain nectar from balsa flowers (Ochroma pyramidale). Twice in July 2000 and once in August 2002, we saw 1-4 individuals probing in blossoms of large Erythrina trees. Cultivated fruits eaten by this species in the Chapare included tangerines, papayas and bananas. On three occasions, Olive Oropendolas were observed in mixed flocks with Yellow-billed and Crested Oropendolas, usually in flowering balsa trees. However, it was more frequently found in monospecific flocks, through all seasons. We observed this oropendola up to 900 m a.s.l.

Around El Puente, in July 2004, a male was seen displaying (with deep bows) and singing in a *Ceiba samauna* tree, followed by 3–4 females that sometimes carried fibers. However, on two occasions, the male was attacked and chased by Yellow-billed Oropendolas (both sexes) that had started a nesting colony in the same tree, and no further breeding activity was observed there. Two or three males were singing and displaying around Villa Tunari in July 2005, but did not attract nest building females.

We found three nesting colonies. At Chocolatal, at the end of August 2001, at least six Olive Oropendolas were found attending nests in a Socratea palm emerging above the general canopy, and hidden from view. At least one male was regularly singing at the site, and two females were observed arriving with nest material (dry fibers) in their bills. Tape recordings from this site included begging calls, indicating the presence of nestlings. In the the same area, at the end of November 2002, five individuals were seen attending a small colony, again in a Socratea palm, which was standing at the edge of a large, recently cut clearing. There, we observed one short intraspecific antagonistic encounter between two birds.

By far the largest nesting colony was found in Cruce Avispas, at the bottom of a steep-sided valley (500 m a.s.l.) near agricultural fields and plantations. It was built on an emergent "almendro" tree (a leguminous species, probably Dypterix sp.), about 35 m in height. This tree grew on sloping terrain near a stream, and the nests were entirely inaccessible to us. We had observed nesting colonies at this tree in the years 2001 and 2002. On 18 October 2004 we estimated a minimum of 60 nests for this colony, built in two separate clusters in opposite branches. One cluster was closer to the canopy, the other at mid-height. From a distance both clusters contained similar numbers of nests, but fewer females visited the lower one, which might have more inactive or abandoned nests. In the same tree there were three nests of an active nesting colony of Crested Oropendolas, built between the clusters, in a branch above the stream.

The nests of both species were easy to separate, as those of the Crested Oropendola had an elongated pyriform shape, and were more neatly woven, typical characteristics of this species' nests, from Venezuela to northern Argentina (Schäfer 1957, pers. observ.). The nests of Olive Oropendolas were more cylindrical, built of coarser fibres, and thickly clustered. At least four female Olive Oropendolas were still nest building on 18 October 2004, while many others were incubating or feeding chicks. Some nests were apparently inactive. One male Olive Oropendola was seen at each cluster, displaying and singing to incoming females. Males did not participate in nesting activities. However, both sexes of this oropendola attacked a pair of Giant Cowbirds (Molothrus oryzivorus) that landed in one nest cluster.

In July 2005, no nesting activity by oropendolas was detected in this tree, perhaps because of adverse weather conditions (see below). A flock of Yellow-rumped Caciques was seen once displaying in the topmost branches.

Yellow-billed Oropendola. The Yellow-billed Oropendola was the only form of the Russet-backed Oropendola complex seen in the Chapare. As described by Jaramillo & Burke (1999), all individuals had pale bills (ivory yellow to pale salmon), and most of them had yellow frontal patches. Sexes were readily recognized by size; museum specimens from Bolivia and Peru gave a mean body mass (\pm SD) of 436.5 \pm 28.7 g for males (n = 4), and 210.5 \pm 12.8 g (n = 4) for females. The size dimorphism score was 2.07.

The Yellow-billed Oropendola was the most abundant oropendola in our study sites. A roost on a river island near Villa Tunari attracted about 120 individuals in late July 2005. This oropendola was particularly abundant in plantations and secondary forest, always traveling in flocks, mixed and monospecific. It foraged mostly on trees, often probing and gaping in rotten wood, epiphytes and moss. At Cruce Avispas in August this species was often observed inspecting dead leaf clusters. Occasionally, foraging individuals descended to the ground, usually near tree cover. Stomach contents from museum specimens include insects, fruits and seeds. Large flocks of this oropendola were observed taking nectar from the huge flowers of balsa, one of the most abundant trees in secondary forest. It was also seen visiting the red blossoms of Erythrina sp. (local name: "gallito rojo") in mid-August, and the brush-shaped, orange inflorescences of a Combretum vine in July. We also saw this oropendola eating bananas and papayas. And, as it is the case for all Chapare oropendolas, local people reported it to be destructive to fruit crops, particularly oranges and tangerines (the main harvest of which is May to June).

Foraging flocks were observed regularly, and through all seasons, up to 1500 m with a

maximum altitudinal record of 1940 m. The regular upper limit in Bolivia is given as 1400 m (Hennessey et al. 2003, see also MacLeod et al. 2005). However, nesting colonies of Yellow-billed Oropendolas in the Chapare were only found up to around 700 m. While systematic nest searches may reveal a somewhat wider altitudinal breeding distribution, our data suggest that upper elevations may be visited predominantly for the purpose of foraging.

Active nesting colonies were studied in July and October 2004, and again in July 2005. In the 2004 season, most nests were still unfinished in July, and many of these were already inactive by October. Part of the inactive October nests could have been successful, as some females were feeding recently fledged chicks. The 2004 egg-laying season probably extended past October, because we detected Yellow-billed Oropendolas starting new colonies in that month. In July 2005, a period when an unusual number of successive cold fronts affected the Chapare, nest building was clearly delayed. Female Yellow-billed Oropendolas did not even visit the colonies during cool, rainy weather. The breeding season of this oropendola started after the production peak of cultivated citrics (May-June), and before the insect flush that emerges around October (pers. observ.). We have no data on what months the breeding season ends. In Panama and Costa Rica other species of oropendolas stop breeding during the months of maximum daily rainfall (R. Fraga pers. observ.), and this may occur in the Chapare.

Nesting trees were somewhat isolated, usually located in clearings in secondary forest, plantations and large gardens. A great number of Yellow-billed Oropendolas nested within villages and towns (Villa Tunari, Chimoré, Puerto Aurora, etc.). Most nest trees were small to mid-sized (8–15 m high). Identified colony trees included native species like

Cecropia sp., Erythrina sp., Ceiba samauma, and exotic species like Asiatic bamboos (Phyllostachis sp.) and African oil palms (Elaeis guineensis). Nine of 15 colonies occupied native peach palms or "tembes" (Bactris gasipaes). This palm has been cultivated since Precolombian times by many Amazonian tribes (Cavalcante 1996), and was a main crop for the Yuracaré in the Chapare (Sánchez 2002). Peach palms of the "native" cultivars have trunks densely covered with sharp, stiff spines, which may deter climbing predators like monkeys and squirrels; modern cultivars can be spineless. We saw two nesting colonies in spineless palms near settlements.

We did not find Yellow-billed Oropendolas nesting in mixed colonies with other oropendolas, and only one mixed colony with Yellow-rumped Caciques was observed in July 2004. This colony occupied a 15-m tall Ceiba samauma; in July 2004, the top branches had active nests of Yellow-rumped Caciques, built around a large wasp nest. Most cacique nests had chicks. Three female oropendolas were starting their nests in a lower branch 8 m below the cacique colony. Agonistic interactions between both species were not detected at this site. However, in October 2004, wandering post-breeding groups of Yellowrumped Caciques (with fledglings) were persistently attacked by nesting Yellow-billed Oropendolas, of both sexes, around three other colonies.

Two colonies observed around El Puente had four and three active nests in July 2004, respectively, that increased to 10 and 12 nests in October 2004. In total, the 15 colonies had from 3 to 14 nests, but some nests were inactive at the largest colonies. The number of active nests per colony in 2004 was three to nine nests, with a mean and SD of 6.7 ± 1.8 nests. Within colonies, the nests were rather well spaced, and never clustered; in the peach palms, only one nest was built at the end of each frond. Colonies often spread to two or

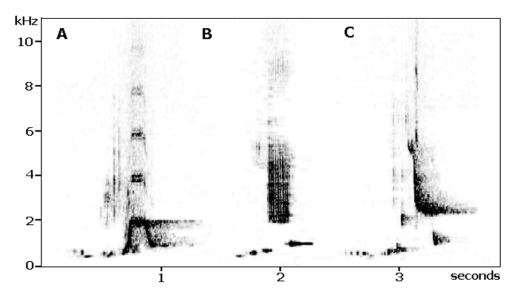


FIG. 2. Three songs of male Yellow-billed Oropendolas at nesting colonies in Chapare (left to right): Hotel El Puente (17 July 2004), Cruce Avispas (18 October 2004), and Hotel El Puente (21 July 2005). Recordings by Rosendo M. Fraga.

three palms, leaving several fronds unoccu-

Three fallen nests from Hotel El Puente, and three more in the collection of the Museo Kempf Mercado, had a mean length of 110 cm, and were woven of rather coarse material. Items in the fabric included strips of palm leaves, strips and pieces of banana leaves, coarse roots up to 3 mm in diameter, and finer and more resistant roots used to attach the structure. At El Puente, female oropendolas collected fibers from native (e.g., Socratea exhorriza) and cultivated (Elaeis guineensis) palms. Nests were lined with large dry leaves, including those of bamboos. The clutch size remains unknown, but it is probably one or two eggs. Two of the museum nests contained one egg or chick when collected, but we observed females feeding two fledglings.

As in other oropendolas, only females built nests, incubated eggs and fed chicks. Females building nests were sometimes escorted by singing and displaying males, but those feeding chicks traveled alone, or in small groups of females. Males displayed with deep bows and wing-shaking, while singing, not only in the colony trees, but also in nearby trees. Songs of males from the Chapare (n = 18, from 17 colonies) lasted 0.66 to 1.51 s, usually started with low pitched notes, and peaked in volume in the last or the penultimate note. Otherwise songs were variable (B. Hennessey *in* Jaramillo & Burke 1999, Mayer 2000), even within localities (Fig. 2). Displaying males observed continuously for 15+ min often switched to different song types.

The number of males displaying in or around active colonies was one to four. In one colony at Villa Tunari observed during 3 h, a single male displayed in succession to five nest-building females. However, during a similar observation period at a second colony, two males were singing from the same branch to three nest-building females, regularly alternating in displays and songs, suggesting some

sort of cooperation. Their songs were considerably different.

A certain number of females were still feeding semidependent juveniles in July 2005, almost at the start of the current breeding season. Judging by size, plumage and the lack of rictal flanges those chicks were not recently fledged. Sexual size dimorphism in fledged chicks was clearly visible, and male chicks were larger than their mothers.

DISCUSSION

Our data on foraging habits of Olive Oropendolas generally agree and supplement the meagre published information. Henriques et al. (2003) also categorized the species in Amazonian Brazil as monospecific flock-forming. Our nesting data agree with the information reported by Rodríguez-Ferraro (2006) from Venezuela, and by Oren & Parker (1997) from Brazil. The species nests in large, even emergent trees, and its nests are often clustered. Rodríguez-Ferraro (2006) also reported mixed colonies with other colonial icterids. Olive Oropendolas have not been reported as hosts of Giant Cowbirds (Jaramillo & Burke 1999), but our observations suggest that it is perhaps parasitized.

Our current information on the natural history and behavior of Olive Oropendolas may not be extensive, but still contrasts with the poverty of data available for the Pará Oropendola (*P. bifasciatus*). Both Olive and Para oropendolas are often treated as conspecific (Haffer 1974, Remsen *et al.* 2006). Only minimal information on one nesting colony has been published for Pará Oropendolas (Snethlage 1935), and details of its behavior, including the song, have not been published (Hardy *et al.* 1998). Our data lays the basis for future comparisons between both forms.

The Russet-backed Oropendola complex comprises seven mostly allopatric populations, all with distinctive differences in coloration (Jaramillo & Burke 1999). Jaramillo & Burke (1999) provisionally treated all the six pale-billed, montane forms of the complex as a separate species from the black-billed, nominate lowland form *Psarocolius angustifrons.* The montane forms occur up to 2500 m a.s.l. from the Coastal Cordillera of Venezuela (form *oleagineus*), and along the Andes down to central Bolivia (form *alfredi*).

Our behavioral and natural history data on alfredi can be compared with information available for the lowland form angustifrons (mostly Robinson 1986, 1988, 1997), and the montane form oleagineus from Venezuela (Schäfer 1957). Although placed among the montane forms by its pale bill color, some characters of alfredi suggest a closer relationship with the lowland form angustifrons, notably the similar tail pattern (Jaramillo & Burke 1999) and the small DNA sequence divergence (Price & Lanyon 2004a, 2004b).

The angustifrons form breeds in riparian habitats in western Amazonia, from southeastern Colombia to Peru and western Brazil (Jaramillo & Burke 1999), but extends its breeding range up to 750 m a.s.l. in the Cordillera Oriental of Colombia (Salaman et al. 2000). Our data suggest a similar altitudinal breeding range for the Chapare alfredi population. Robinson (1986, 1988, 1997) studied the behavior and nesting ecology of a small angustifrons population (30 to 35 individuals) around an oxbow lake in Amazonian Peru. Colony sizes at his site were apparently similar to those of alfredi, but a colony of 28 nests was also reported. In addition, F. G. Stiles (pers. com.) observed a colony of 25 angustifrons nests in Colombia. Both alfredi and angustifrons use mid-sized trees (albeit of different species) for nesting, and the nests were similar, cylindrical bag-shaped structures woven with rather coarse materials. Nests of angustifrons were also spaced and not clustered. In contrast with alfredi, angustifrons often nested in mixed colonies with Yellow-rumped

Caciques. However, some angustifrons males attacked neighboring nesting caciques and killed their chicks (Robinson 1997). Robinson (1986) suspected the mating system of angustifrons to be a harem-defense polygyny. Our data for alfredi suggest a lower level of simultaneous polygyny, because colonies were never as large, and often visited by more than one male.

Giant Cowbirds visited 88 times the Peruvian colonies of angustifrons, and cowbird chicks were regularly reared by this oropendola (Robinson 1986). By contrast, we never observed Giant Cowbirds visiting colonies of Yellow-billed Oropendolas in Bolivia, and no Giant Cowbird chicks were detected among the dozens of juveniles provisioned by females of this oropendola in 2004 and 2005. Giant Cowbirds were not rare in the Chapare, with groups seen on stretches of gravel on the Villa Tunari-Cochabamba road, and along the Río Espíritu Santo. Although Jaramillo & Burke (1999) state that Giant Cowbirds may parasitize Yellow-billed Oropendolas, they provide no details (dates, localities), or mention a literature reference. In the extensive compilation of Schönwetter (1983), a putative record of such parasitism from Bolivia is discussed, but dismissed as a case of doubtful egg identification.

Many behavioral traits of our Bolivian alfredi population also occur in the montane oleagineus population (Schäfer 1957), like the use of mid-sized, non-emergent trees for nesting, the well-spaced nests built with coarse fibers, and the small colony sizes (2–20 nests, with a mean of 10.6 nests). One to three dominant males frequented each oleagineus colony (Schäfer 1957), and the mating system was suspected to be sequential polygyny. Mixed colonies with Yellow-rumped Caciques and Crested Oropendolas were far more common in oleaginous than in alfredi. Parasitism by Giant Cowbirds was not reported by Schäfer. As in our study, females starting the first nests of

the season were sometimes followed by semidependent juveniles. According to Schäfer, the postfledging period of parental care lasts up to eight months.

Most characters related to nesting and colony structure are shared by the three forms, excepting the large colony sizes sometimes reported for the lowland *angustifrons*. Although each of the compared forms has a slightly different set of behavioral characters, we conclude that our *alfredi* population shared more behavioral traits with the montane form of the Russet-backed Oropendola complex.

Recent field data has been obtained in the contact zone between a montane form (neglectus) of the Russet-backed Oropendola complex and the lowland form angustifrons in the Cordillera Oriental of Colombia (Salaman et al. 2002). Their data suggest that both forms behaved as good biological species, with a minimum percentage (less than 1%) of intermediate individuals. Similar field studies in the contact zone of alfredi and angustifrons are needed.

ACKNOWLEDGMENTS

K. Cockle commented on an earlier draft of the MS. R. Fraga thanks T. Nornberg for good companionship in the field, and for digital photos of important colonies; thanks also to E. Brunetto for help with the map, and to J. Balderrama and O. Maillard for information on sites. He is also grateful to the curators of the ornithological collections mentioned in the text. Collections in the US were visited thanks to grants from Fundación Antorchas (Argentina), the American Museum of Natural History, and a Robert O. Bass scholarship from the Field Museum, Chicago. S. Kreft would like to thank Fundación Amigos de la Naturaleza (FAN Bolivia) for scientific as well as logistical support. He is also grateful to his agreeable field companions M. Herrera, J. C. Montero, M. Scholze, C. Sierra and J. Weber. Thanks also to S. Herzog for providing initial key information. Special thanks for scientific advice go to H. Ellenberg. S.K received partial funding by the Graduate Grant Program of the City of Hamburg/German Academic Exchange Service and by the German Society of Tropical Ornithology. We both thank M. Blendinger for advice and field support.

REFERENCES

- Cavalcante, P. B. 1996. Frutas comestíveis da Amazônia. Museu Paraense E. Goeldi, Belem, Brazil.
- Haffer, J. 1974. Avian speciation in tropical South America, with a systematic survey of the toucans (Ramphastidae) and jacamars (Galbulidae). Pub. Nuttall Ornithol. Club No. 11, Cambridge, Massachusetts.
- Hardy, J. W., G. B. Reynard & T. Taylor. 1998. Voices of the troupials, blackbirds and their allies. Family Icteridae. Two cassette tapes with texts. ARA Records, Gainesville, Florida.
- Hellmayr, C. E. 1937. Catalogue of the birds of the Americas and the adjacent islands. Vol. 12. Field Museum of Natural History, Chicago, Illinois.
- Henkel, R. 1995. Coca (Erythroxylum coca) cultivation, cocaine production, and biodiversity loss in the Chapare region of Bolivia. Pp. 551–560 in Churchill, S. P., H. Balslev, E. Forero, & J. L. Luteyn (eds.). Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden, New York, New York.
- Hennessey, A. B., S. K. Herzog, & F. Sagot 2003. Lista anotada de las aves de Bolivia. 5^{ta} ed.. Asociación Armonía/BirdLife International, Santa Cruz de la Sierra, Bolivia.
- Henriques, L. M. P., J. M. Wunderle, & M. R. Willig. 2003. Birds of the Tapajos Forest, Brazilian Amazon: a preliminary assessment. Ornitol. Neotrop. 14: 307–338.
- Ibisch, P. L. 1996. Neotropische Epiphytendiversität – das Beispiel Bolivien. Martina Galunder – Verlag, Wiehl, Germany.
- Ibisch, P. L., S. G. Beck, B. Gerkmann, & A. Carretero 2003. Ecoregiones y ecosistemas. Pp. 47–88 in Ibisch, P. L., & G. Mérida (eds.).

- Biodiversidad: La riqueza de Bolivia. Estado de conocimiento y conservación. Ministerio de Desarrollo Sostenible y Planificación/Editorial FAN, Santa Cruz de la Sierra, Bolivia.
- Jaramillo, A., & P. Burke. 1999. New World blackbirds. The Icterids. A. & C. Black Publishers, London, UK.
- MacLeod, R., S. E. Ewing, S. K. Herzog, R. Bryce, K. L. Evans, & A. MacCormick. 2005. First ornithological inventory and conservation assessment for the yungas forests of the Cordilleras Cocapata and Mosetenes, Cochabamba, Bolivia. Bird Conserv. Int. 15: 361–382.
- Mayer, S. 2000. Birds of Bolivia 2.0. Sounds and photographs. CD-ROM, Bird Songs International, Westernieland, The Netherlands.
- Mueller, R., S. G. Beck, & R. Lara. 2002. Vegetación potencial de los bosques de Yungas en Bolivia, basado en datos climáticos. Ecol. Bolivia 37: 5–14.
- Oren, D. C., & T. A. Parker III. 1997. Avifauna of the Tapajos National Park and vicinity, Amazonian Brazil. Ornithol. Monogr. 48: 493–525.
- Price, J. J., & S. M. Lanyon. 2004a. A robust phylogeny of the oropendolas: polyphyly revealed by mitochondrial sequence data. Auk 119: 335–348.
- Price, J. J., & S. M. Lanyon. 2004b. Patterns of song evolution and sexual selection in the oropendolas and caciques. Behav. Ecol. 15:485–497.
- Remsen, J. V., Jr., A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, J. M. C. da Silva, D. F. Stotz, & K. J. Zimmer. 2006. A classification of the bird species of South America. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.html (Accessed 5 November 2006).
- Robinson, S. K. 1986. The evolution of social behavior and mating systems in the
- blackbirds (Icterinae). Pp. 175–200 in Rubinstein, D. I., & R. W. Wrangham (eds.). Ecological aspects of social evolution. Princeton Univ. Press, Princeton, New Jersey.
- Robinson, S. K. 1988. Foraging ecology and host relationship of Giant Cowbirds in southeastern Peru. Wilson Bull. 100: 224–235.
- Robinson, S. K. 1997. Birds of a Peruvian oxbow lake. Ornithol. Monogr. 48: 613–639.

- Rodríguez-Ferraro, A. 2006. Notes on the behavior of the Olive Oropendola (*Psarocolius yuracares*) during the breeding season. Ornitol. Neotrop. 17: 57–62.
- Salaman, P. G. W., F. G. Stiles, C. I. Bohórquez, M. Álvarez-R., A. M. Umaña, T. M. Donegan, & A. M. Cuervo. 2002. New and noteworthy bird records from the Andean east slope of Colombia. Caldasia 24: 157–189.
- Sánchez, W. 2002. Chonta y tembe: sistema de
- paisajes, ocupación del territorio e intercambio de los Yuracaré. Bol. INIAN-Museo 6 (29): 1–18.
- Schäfer, E. 1957. Les conotos. Étude comparative de *Psarocolius angustifrons* et *Psarocolius decumanus*. Bonn. Zool. Beitr. 5: 1–151.
- Schönwetter, M. 1983. Handbuch der oologie. Lieferung 34. Akademie-Verlag, Berlin, Germany.
- Snethlage, E. 1935. Beiträge zur Brutbiologie brasilianischer Vögel. J. Ornithol. 83: 534–562.