# PHYLOGENY AND BEHAVIORAL EVOLUTION IN THE FAMILY ICTERIDAE

**Rosendo M. Fraga**

CICYTTP-Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET),
España y Materi, (3105) Diamante, Entre Ríos, Argentina.
*E-mail*: chfraga@yahoo.com

**Resumen. – Filogenia y evolución de la conducta en los ictéridos. –** Se discute la evolución de algunas características de la conducta de los tordos de la familia Icteridae a la luz de la nueva filogenia basada en secuencias del ADN. El nido tejido péndulo se encuentra solo en dos linajes o clados principales de la familia, los caciques mas oropéndolas (*Cacicus* y *Psarocolius*), y en el género *Icterus*. Resulta difícil deducir si este tipo de nido es una característica ancestral a ambos linajes (plesiomorfía) o un caso de convergencia. La construcción de nidos principalmente por el macho se conoce solamente en el género sudamericano *Chrysomus*. La cría cooperativa es registrada principalmente en el linaje de los quiscalinos sudamericanos, donde ha sido reportada para 13 especies. La hipótesis de que la cría cooperativa fuese una característica ancestral en este linaje resulta posible, primero por su frecuencia inusual en el mismo, y además por encontrarse en el género *Macroagelaius*, ubicado en una posición basal en este clado. El parasitismo de cría evolucionó una sola vez en la familia, probablemente en formas ancestrales norteamericanas de *Molothrus*. Sin negar un rol al medio ambiente en moldear la conducta de los ictéridos, los nuevos datos moleculares permiten también reconocer un importante componente filogenético en la evolución de la misma.

**Abstract. –** The evolution of selected behavioral characteristics in the family Icteridae is discussed in the light of the new DNA phylogeny. The woven pensile nest is found in only two of the main icterid clades, the caciques plus oropendolas (*Cacicus* and *Psarocolius*), and in the genus *Icterus*. It is difficult to assert if this nest type represents an ancestral character to both lineages, or a case of convergence. Nest building mostly by males is only known in the South American genus *Chrysomus*. Cooperative breeding is found mostly in the South American quiscaline clade, with reports for 13 species. The hypothesis that cooperative breeding is an ancestral trait in this clade is supported by its unusual frequency in the group, and also because it is found in the genus *Macroagelaius*, placed in a basal position in the lineage. Brood parasitism evolved only once in the family, probably in ancestral North American cowbirds. Withouth denying a role for environment in shaping icterid behavior, the new molecular data supports the idea of an important phylogenetic component in behavioral evolution. *Accepted 6 October 2007.*

**Key words**: Icteridae, DNA phylogeny, behavioral evolution, nest characteristics, cooperative breeding, brood parasitism.

## INTRODUCTION

The family Icteridae comprises about 110 species, found only in the Americas, from Alaska to Tierra del Fuego. It is one of the most intensively studied of the avian families, particularly in the areas of ecology and behavior. Many important overviews of behavioral evolution in icterids have been published (Lack 1968, Orians 1980, 1985a, 1985b; Robinson 1986). Lack's review (1968) concentrated mostly on Nearctic icterids, as informa-

tion on basic natural history for most Neotropical species was scant. This situation is steadily improving, and in this review I will concentrate mostly on Netropical icterids.

Studies on behavioral evolution rely mostly in comparisons between related species, therefore requiring a reasonable phylogeny. The older evolutionary studies on icterid behavior suffered from the lack of a solid phylogenetic background. Traditional phylogeny was mainly based on morphological and plumage characters (e.g., Beecher 1950), and those characters often show convergent evolution in birds. More recently a molecular phylogeny of the Icteridae was built by S. Lanyon and coworkers (e.g., Lanyon & Omland 1999, Johnson & Lanyon 1999), first based on mitochondrial DNA, and posteriorly also on nuclear DNA. Most species in the family (about 90%) have been sequenced, and the phylogeny has been enlarged and refined in successive papers (e.g., Cadena *et al.* 2004, Price & Lanyon 2004a).

Some recent behavioral studies on icterids have used the new phylogeny to reconstruct evolutionary trends or patterns, like male poligyny (Searcy *et al.* 1999, Webster 1999) or song (Price & Lanyon 2004b). Here I will use the new phylogeny to discuss the evolution of other behavorial traits in the family Icteridae. The role of phylogeny in behavioral evolution was somewhat controversial in the older comparative studies. Some authors minimized its role (e.g., Robinson 1986), but others (e.g. Orians 1985b) recognized the existence of conservative, phylogenetic components in the behavior of icterids. My results are used to revaluate the role of phylogeny in shaping the behavioral evolution of icterids.

## METHODS

I deliberately selected behavioral traits which I have studied or researched in the field in the last 34 years (e.g., Fraga 1972, Fraga & Kreft

2006). Besides my own data, other behavioral information was obtained from the general literature (e.g., Jaramillo & Burke 1999) or from published and unpublished field studies. As I am currently involved in writing the family account of the Icteridae for the Handbook of the Birds of the World (Fraga in prep.), I have accumulated an important amount of information for the group.

Behavioral evolution was interpreted with the DNA phylogenetic trees. However, not all the icterid species have been sequenced or incorporated in the new phylogenetic trees. There are two main reasons for this incomplete coverage. First, the authors of the DNA phylogeny based their research on the taxonomic list of Sibley & Monroe (1990). This list, with 97 recognized icterid species, is somewhat outdated. Jaramillo & Burke (1999) recognized 103 species. Second, several icterid species endemic to Brazil, Colombia and Cuba have not been sequenced and incorporated in the molecular tree. In this review I discuss three additional icterid species, endemic to Brazil and Colombia, and not found in the molecular trees.

## RESULTS AND DISCUSSION

The DNA phylogenetic tree for the entire family (Lanyon & Omland 1999) is presented in Fig. 1. For this review the family is conveniently subdivided into five main clades or lineages: caciques and oropendolas (*Psarocolius*, *Cacicus* and related genera), orioles (*Icterus*), meadowlarks and allies (*Sturnella* and related genera), North American quiscalines (*Quiscalus*, *Euphagus* and related genera), and the South American quiscalines (a complex group with about 10 genera). Both quiscaline lineages are distantly related, but otherwise the molecular methods have not yet resolved the relationships between the main icterid clades.

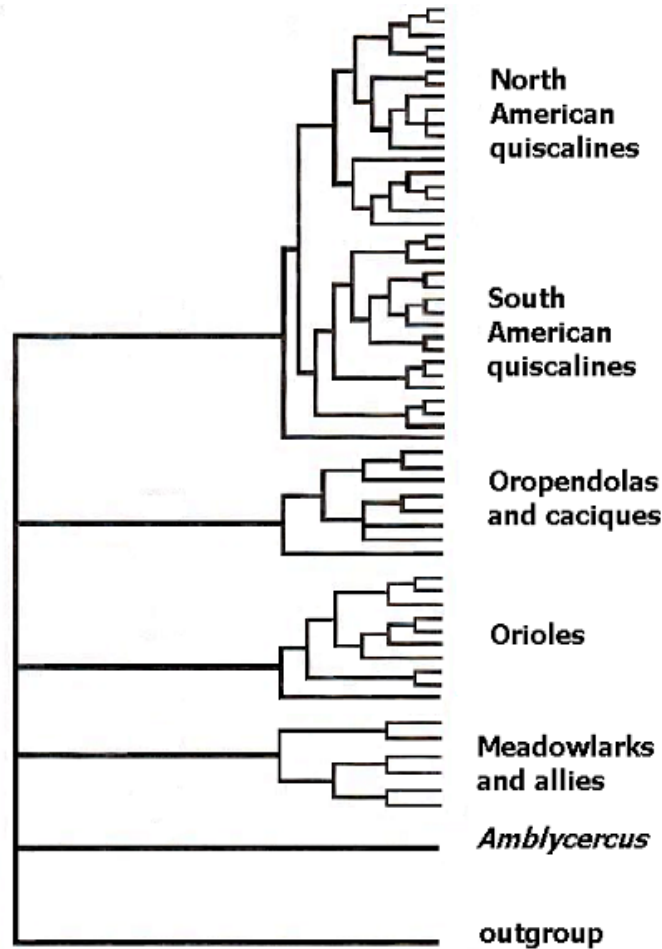The molecular tree agrees with the traditional taxonomy in recognizing the mono-

FIG. 1. The DNA phylogenetic tree of the family Icteridae, showing the main lineages or clades (modified from Lanyon & Omland 1999).

phyly of some species-rich genera (e.g., orioles *Icterus*, oropendolas *Psarocolius*). On the other hand, the traditional marsh blackbird genus *Agelaius* results in a composite of North and South American lineages (Lanyon 1994). A nomenclaturial solution for the poliphyletic *Agelaius* has been proposed (Lowther *et al.* 2004) and is followed here. A nomenclaturial solution for the equally poliphyletic and species-rich genus *Cacicus* awaits further information (Fraga 2005a).

*Icterid nests, particularly woven pensile nests.* In some passerine families, notably the Furnariidae in the Neotropics, the nest structure and nest building behavior may reflect phylogenetic relatedness (Zyskowski & Prum 1999). One good example in the Icteridae is the misnamed Yellow-billed Cacique (*Amblycercus holosericeus*). Because of its external morphology and skulking habits, *Amblycercus* was often included in the genus *Cacicus* (e.g., Fjeldså & Krabbe 1990). Skutch (1954) rejected this

view because its nest is an open cup, supported upon branches and vines in dense vegetation, therefore quite unlikely the nest of any other cacique. The DNA data show this icterid to conform an isolated lineage by itself, not closely related to the true caciques and oropendolas (Fig. 1). This result is also supported by a distinctive skeletal anatomy (Webster 2003).

Icterids are one of the two passerine families that weave pensile nests, the other family being the Ploceine weavers (Ploceinae) of Asia and Africa (Collias & Collias 1964, Lack 1968). Nest weaving is a complex behavior, involving a careful selection of fibrous materials, a series of movements for interlacing the material into a resistant fabric, and the firm attachment of the structure to a branch or leaf. Detailed studies of weaving behavior in icterids are available for female Crested Oropendolas (*Psarocolius decumanus*) (Schafer 1957, Drury 1962). Although nest weaving skills are affected by experience (Schafer 1957, Drury 1962), weaving behavior probably involves a strong genetic component. The overall rarity of this type of nesting behavior in birds makes this trait particularly useful for a phylogenetic analysis.

Within the icterids, woven pensile nests are found only in two main clades, the orioles (*Icterus*), and the cacique plus oropendola clade (fig. 1). *A priori*, this shared nest type may reflect a common ancestry for both lineages (technically a plesiomorphy). The nests of the oriole clade are, however, far more heterogeneous than those of caciques and oropendolas.

Some oriole species like Scott's Oriole (*I. parisorum*) may built semipensile nests, attached to lateral branches or other vegetation (Flood 2002). The structures woven by many smaller orioles are just shallow bags, quite unlike the elongated bags of caciques and oropendolas. Only some of the larger orioles weave elongated pendant nests that closely resemble the structures of caciques and oropendolas (Howell & Webb 1995). Lastly, different troupial populations show a remarkable graduation in nesting habits, from conventional nest weaving to almost obligate nest piracy (Lindell & Bosque 1999); in this case, the use of other birds'nests is a derived character. The many types of nests found in the orioles would suggest that the weaving of pensile nests has evolved independently in the oriole and the cacique-oropendola clades.

In the last lineage all nests are pendant elongate bags. The nests of *Psarocolius* oropendolas are relatively uniform in shape and materials (e.g., Fraga & Kreft 2007), but those of caciques (*Cacicus*) vary in size, shape and materials, probably reflecting the polyphyly of this group. The Golden-winged Cacique (*C. chrysopterus*) weave nests mostly with dark fungal fibers (Chatellenaz & Ferraro 2000, pers. observ.). This trait is found in other smaller caciques and may reflect phylogenetic relatedness.

*Roles of both sexes in nest building.* All the possible combinations of male and female roles occur among icterids. The most widespread role combination is nest building only by the female. This situation characterizes the oropendolas and caciques, most if not all the orioles (*Icterus*), and also the meadowlarks (*Sturnella*). This combination occurs in monogamous and polygynous species. Among the quiscalines there are further role combinations. In the parasitic cowbirds (*Molothrus*) neither males or females build nests. Nest building only by females occurs in most quiscaline species, either in the North or South American clades. Nest building by both sexes occurs in some quiscalines, notably in the genus *Dives* (Skutch 1954). A somewhat transitional stage is found in many quiscaline species, in which males gather nesting material that is rarely placed in the nest site. In some species, this non-functional behavior
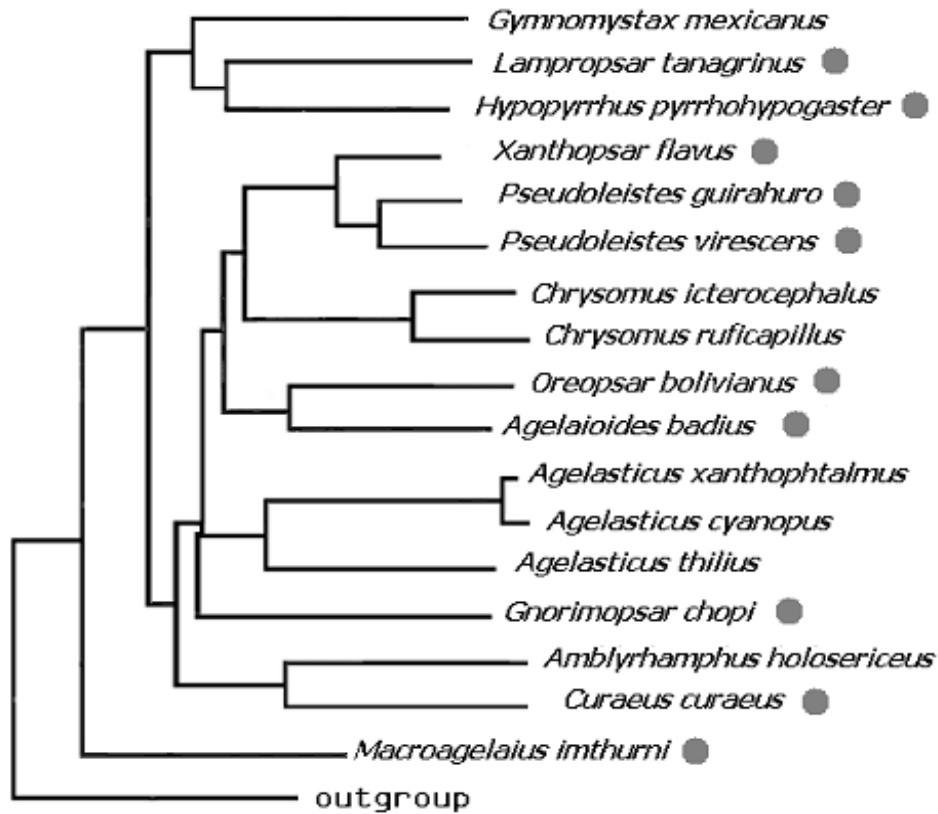
FIG. 2. The DNA phylogenetic tree of the South American quiscalines (modified from Cadena *et al.* 2004) showing with gray circles the species with reports of cooperative breeding.

seems to be a mating display (Orians & Christman 1968). Lastly, the most unusual role combination is nest building mostly by the male. It has been reported only in two South American quiscalines, the Yellow-hooded and Chestnut-capped Blackbirds (*Chrysomus icterocephalus* and *C. ruficapillus*) (Lowther *et al.* 2004), which, according to the DNA data are sister species (Fig. 2). This represents a remarkable coincidence of behavioral and molecular data.

*Phylogeny and polygyny.* Searcy *et al.* (1999) and Webster (1999) discussed the role of phylogeny and the marsh environment in the evolution of male polygyny in Nearctic species of *Agelaius*, notably the Red-winged Blackbird (*A. phoeniceus*). Their models were not very predictive for the equivalent species of the South American quiscaline clade, which are mostly monogamous (Orians 1980, Fraga 2005b). The role of phylogeny in the evolution and maintenance of polygyny in *Agelaius* cannot be strong, as Caribbean species in the genus are marsh-nesting but monogamous (Withingham *et al.* 1996). Besides, different populations of Red-winged Blackbirds differ in their degree of polygyny, as measured by male harem size (Beletsky 1996). Other icterid genera contain monogamous and polygynous

65

TABLE 1. Life zones, altitudinal ranges (m) and main habitats of cooperative breeding icterids of the South American quiscaline clade.

| Species | Life zones | Altitude range (m) | Main habitats |
|---|---|---|---|
| Tepui-Mountain-Grackle (*Macroagelaius imthurni*) | Tropical to subtropical | 500–2000 | Wet montane forest |
| Colombian Mountain-Grackle (*Macroagelaius subalaris*) | Subtropical to temperate | 1900–3100 | Wet montane forest |
| Velvet-fronted Grackle (*Lampropsar tanagrinus*) | Tropical | 0–500 | Flooded forest and savanna |
| Red-bellied Grackle (*Hypopyrrhus pyrrohypogaster*) | Subtropical to temperate | 1200–2700 | Wet montane forest |
| Grayish Baywing (*Agelaioides badius*) | Subtropical to temperate | 0–3200 | Mesic to dry open woodland |
| Pale Baywing (*Agelaioides fringillarius*) | Tropical | 150–900 | Dry open woodland |
| Bolivian Blackbird (*Oreopsar bolivianus*) | Temperate | 2400–3200 | Dry woodland, scrub |
| Chopi Blackbird (*Gnorimopsar chopi*) | Tropical to subtropical | 0–1200 | Mesic woodland, savanna |
| Saffron-cowled Blackbird (*Xanthopsar flavus*) | Subtropical to temperate | 0–1000 | Wet grassland, marshes |
| Yellow-rumped Marshbird (*Pseudoleistes guirahuro*) | Tropical to subtropical | 0–1200 | Wet grassland, marshes |
| Brown-and-yellow Marshbird (*Pseudoleistes virescens*) | Subtropical to temperate | 0–500 | Wet grassland, marshes |
| Austral Blackbird (*Curaeus curaeus*) | Temperate | 0–2000 | Mesic to wet forest edge |
| Forbes' Blackbird (*Curaeus forbesi*) | Tropical | 200–900 | Mesic forest edge |

species, like *Quiscalus*. The oropendolas (*Psarocolius*) constitute the only large icterid genus containing exclusively polygynous species.

*Cooperative breeding in icterids.* Cooperative breeding involves the participation of individuals (helpers) other than a mated pair in the feeding and care of the young (Brown 1987). This definition stresses the helperís role in chick feeding, but helpers may perform other parental duties like nest building, feeding of the breeding female, incubation, nest guarding, and mobbing of chick predators. Cooperative breeding in icterids was first reported for Grayish Baywings (*Agelaioides badius*) (Fraga 1972) and, since then, it has been found in 13 species of South American quiscalines (Fraga 1972, 1986; Orians *et al.* 1977a, 1977b; Studer & Vielliard 1988, Ochoa & Cuervo Maya 1998, Azpiroz 2000, Cadena *et al.* 2002, Hilty 2003, Fraga & Di Giacomo 2004, Fraga 2005b) (Table 1). Other three species have been added to Table 1. J. Tobias (pers. com) has seen cooperative breeding in Velvet-fronted Grackles (*Lampropsar tanagrinus*) in Bolivia. The Pale Baywing (*Agelaioides fringillarius*) was a regular cooperative breeder at six nests I studied at Minas Gerais, Brazil (R. Fraga, unpubl.). This endemic Brazilian taxon is regarded as a separate species by Jaramillo & Burke (1999) and by the official checklist of Brazilian birds (CBRO 2006), an opinion in which I concur. Lastly, Chopi Blackbirds (*Gnorimopsar chopi*) had helpers at three nests with chicks I found in Corrientes (Argentina) and Paraguay (R. Fraga unpubl.).

The data confirms the suspicions of Orians *et al.* (1977b) that cooperative breeding is particularly frequent among South American icterids. Among North American icterids, helping behavior has been reported with some frequency only in the Bobolink (*Dolychonix oryzivorus*) (Beason & Trout 1984). Outside the Bobolink, all known cooperative breeding icterids belong to the South American quiscaline clade. No members of the North American quiscaline clade are known cooperative breeders. In Figure 1 I have mapped the occurrence of cooperative breeding in the South American quiscalines that have been sequenced, using the tree presented by Cadena *et al.* (2004). Note that three species in Table 1 have not been sequenced.

Brown (1987) discussed large-scale patterns in the geographical distribution of cooperative breeding in birds, and found most cooperative breeders in the southern continents, mostly in warm to subtropical climates. In Table 1, I have summarized several environmental variables (life zones, altitudinal range, main habitat) for the cooperative breeding quiscalines of South America. Environmental data was taken from the specific publications on those species mentioned above, as well as from the main field guides (e.g., Hilty 2003) and my own observations on 10 species. Occurrences in man-made habitats (urban parks, agricultural fields, etc.) have been excluded from the table. It can be seen that cooperative breeding quiscalines occur from tropical to temperate latitudes, breed from sea level to 3200 m, and occupy almost all the main South American habitats used by icterids. However, cooperative breeding seems rare or absent in marsh-nesting South American quiscalines, even in monogamous species (Orians 1980).

Brown (1987) classified the different social systems found in cooperative breeding birds. Only few and preliminary studies on the social systems of South Americann quiscalines are available (Orians *et al.* 1977a, Fraga 1991) and much more information is needed. However, there seems to be important differences in social complexity between quiscalines, even between closely related species (Fraga 2005).

*Origin and evolution of cowbird parasitism.* Within the Icteridae, five species of cowbirds (genus

*Molothrus*) are obligate brood parasites. Parental care in the female parasites is reduced to egg formation, plus finding and depositing the eggs in the nests of appropiate hosts. Speculations on the the origin and evolution of cowbird brood parasitism can be tested with the new DNA phylogeny.

One set of hypotheses assumed that the Grayish Baywing was the ancestor of the parasitic cowbirds, and that parasitic cowbirds first evolved in South America. This hypothesis was first advanced by Hudson (1920). Hudson selected Grayish Baywings as ancestors on two main reasons: they often breed in other bird's nests, and look quite cowbird-like in their external morphology (hence their former name of Bay-winged Cowbirds). Hudson suggested that a progressive decay of the parental instincts occurred in this lineage, starting with the loss of nest building behavior. He also discovered that Screaming Cowbirds (*Molothrus rufoaxillaris*) were parasitic on Grayish Baywings and that chicks of both species were remarkably similar in plumage and voice (Hudson 1920). He reasoned that the chick resemblance was a shared ancestral character, therefore a proof of the common origin of both species. The alternative idea that chick resemblance between host and parasite was due to mimicry was rejected, on the ground that chicks of most brood parasites do not resemble host chicks, and yet receive parental care from their foster parents (Hudson 1920).

Friedmann (1929) expanded Hudson's ideas and placed them in an evolutionary frame. He presented a cowbird phylogeny in which Grayish Baywings occupied the ancestral position, giving origin to Screaming Cowbirds, the first parasitic cowbird. A behavioral unbalance between nest building and egg-laying instincts, even mediated by hormone unbalance, would have occurred during the evolution of parasitic habits in this lineage (Friedmann 1929). Although he realized that

baywings were unusual and distinctive in plumage and behavior (for instance, they do no follow grazing mammals), he accepted the view that the presence a host-like plumage in the Screaming Cowbird chick was evidence of a shared ancestry. Friedmann's views become textbook classics, and few authors (Hamilton & Orians 1965, Lack 1968) questioned its importance.

More recently Skutch (1996) elaborated an hypothesis also based on Hudson's and Friedmann's views. However, for Skutch the main factor responsible for the evolution of brood parasitism was intense competion between closely related icterids for the use of closed nests or nesting cavities. The competitors would be the Grayish Baywings and the ancestral Screaming Cowbirds. The less agressive species (Screaming Cowbirds in his view) evolved parasitism on the most sucessful competitor (the Grayish Baywings).

The traditional view of Baywings as ancestors of the parasitic cowbirds collapsed when Lanyon (1992) showed that Baywings were not closely related to the Screaming Cowbirds, or to any other parasitic cowbird. Mitochondrial DNA showed that Baywings are members of the South American quiscaline icterids, whereas *Molothrus* belongs with the North American quiscalines. In fact, many of the "unusual" behavioral traits found in Grayish Baywings by Hudson and Friedmann occur in other cooperative breeding South American icterids. The close resemblance, in plumage and voice, between Baywing and Scraming Cowbird chicks become a remarkable case of mimicry (Fraga 1979, 1986).

The DNA data shows that parasitic cowbirds are a monophyletic group, and therefore brood parasitism evolved only once in the Icteridae (Lanyon *et al.* 2000). The parasitic cowbirds are inserted within the North American quiscaline clade, even if the molecular data suggests that the Screaming Cowbird, a South

American species, is possibly the oldest extant species of parasitic cowbird. The fossil record does not contradict the idea that parasitic cowbirds first evolved in North America, because several species of extinct cowbird-like icterids are known from the Upper Pleistocene of the United States (Brodkorb 1978).

If cowbirds are of Nearctic origin, an old hypothesis on the origin of cowbird parasitism (Widmann 1907) becomes worth considering. Widmann's hypothesis was based on the foraging dependence of all extant parasitic cowbirds on grazing mammals. It is widely believed that, in pre-European times, Brown-headed Cowbirds (*M. ater*) followed the large nomadic herds of grazing bison (*Bison bison*) in the North American prairies (Lowther 1993), and still do so in some bison reserves. Cowbird dependence on such a mobile and erratic source of food could have precluded or difficulted normal nesting in a fixed site. Recently, Goguen *et al.* (2005) studied Brown-headed Cowbird behavior in a bison reserve, and found that radio-tracked cowbird females commuted a daily average of 7 km from their breeding grounds to the bison herds. This daily movement probably affected egg formation and egg deposition by the cowbird females. Ancestral cowbirds may have evolved parasitism to circumvent this constraint. As intermediate forms between parasitic and non-parasitic breeding do not occur among living icterids, most ideas on the origin of parasitism will perhaps remain untested.

## CONCLUDING REMARKS

The specific distribution of most behavioral traits discussed here, like woven pensile nests in oropendolas and brood parasitism in cowbirds, correlated well with phylogenetic relatedness as defined by DNA analysis. Such characters may be even used to support molecular phylogenies. Behavioral characters that were not found in all members of larger taxonomic categories include nest weaving in orioles and male polygyny in *Agelaius*. We do not know what makes such characters relatively unstable, and this will require new information.

Brown (1987) suggested a minimal role of phylogeny in the evolution of cooperative breeding, though he noted some exceptions in jays (Corvidae) and anis (Crotophaginae). South American quiscalines must be treated as another exception. What makes so many species of this lineage cooperative breeders in many habitats requires further study. Possibly some basic social characteristics of the group, like delayed breeding and the long term persistence of parent-offspring relationships, have an important role.

Phylogenetic conservatism exists, but seems not to exclude evolutionary changes. A few characteristics like brood parasitism in *Molothrus* may have a low probability of evolutionary reversals, at least within the average life span of icterid species and genera.

## REFERENCES

Azpiroz, A. B. 2000. Biología y conservación del Dragón (*Xanthopsar flavus*, Icteridae) en la Reserva de Biosfera Bañados del Este. Documento de trabajo No. 29. PROBIDES, Rocha, Uruguay.

Beason, R. C., & L. L. Trout. 1984. Cooperative breeding in the Bobolink. Wilson Bull. 96: 709–710.

Beecher, W. J. 1950. Convergent evolution in the

American Orioles Wilson Bull. 62: 51–86.

Beletsky, L. 1996. The Red-winged Blackbird. The biology of a strongly polygynous songbird. Academic Press, New York, New York

Brodkorb, P. 1978. Catalogue of fossil birds. Part 5, Passeriformes. Bull. Fla. State Mus. Biol. Sci. 23: 139–228.

Brown, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, New Jersey.

Cadena, C. D, C. Devenish, & N. Silva. 2002. First observations on the nesting behavior of the Colombian Mountain-Grackle (*Macroagelaius subalaris*), a probable cooperative breeder. Ornitol. Neotrop. 13: 301–305.

Cadena, C. D., A. M. Cuervo & S. M. Lanyon. 2004. Phylogenetic relationships of the Red-bellied Grackle (Icteridae: *Hypopyrrhus pyrohypogaster*) inferred from mitochondrial DNA sequence data. Condor 106: 664–670.

CBRO (Comite Brasileiro de Registros Ornitologicos). 2006. Lista das aves do Brasil. Available at http//www.cbro.org.br. Version of 15/7/2006.

Collias, N. E., & E. C. Collias. 1964. The evolution of nest building in weaverbirds (Ploceidae). Univ. Calif. Publ. Zool. 73: 1–239.

Chatellenaz, M. L., & L. I. Ferraro. 2000. Materiales vegetales y fúngicos en nidos de aves del Noreste Argentino y Paraguay. Facena 16: 103–119.

Fjeldså, J., & N. Krabbe. 1990. Birds of the High Andes. Apollo Books and Zoological Museum of the Univ. of Copenhagen, Svendborg, Denmark.

Flood, N. J. 2002. Scott's Oriole (*Icterus parisorum*). *In* Poole, A., & F. Gill (eds.). The birds of North America, No. 608. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Fraga, R. M. 1972. Cooperative breeding and a case of successive polyandry in the Baywinged Cowbird. Auk 89: 447–449.

Fraga, R. M. 1979. Differences between nestlings and fledglings of Screaming and Baywinged cowbirds. Wilson Bull. 91: 151–154.

Fraga, R. M. 1986. The Baywinged Cowbird (*Molothrus badius*) and its brood parasites: interactions, coevolution and comparative efficiency. Ph. D. diss., Univ. of California, Santa Barbara, California.

Fraga, R. M . 1991. The social system of a communal breeder, the Bay-winged Cowbird *Molothrus badius*. Ethology 89: 195–210.

Fraga, R. M. 2005a. A new generic name for the Solitary Cacique. Bull. Br. Ornithol. Club 125: 286–287.

Fraga, R. M. 2005b. Behavior, ecology and social organization of Saffron-cowled Blackbirds (*Xanthopsar flavus*). Ornitol. Neotrop. 16: 15–29.

Fraga, R. M., & A. Di Giacomo. 2004. Cooperative breeding of the Yellow-rumped Marshbird (Icteridae) in Argentina and Paraguay. Condor 106: 671–673.

Fraga, R. M , & S. Kreft. 2007. Natural history and breeding behavior of the Olive (*Psarocolius yuracares*) and Yellow-billed (*P. angustifrons alfredi*) oropendolas in the Chapare province, Bolivia. Ornitol. Neotrop. 18: 251–261.

Goguen, C. B., D. R. Curson, & N. E. Mathews. 2005. Behavioral ecology of the Brown-headed Cowbird (*Molothrus ater*) in a bison-grazed landscape in New Mexico. Ornithol. Monogr. 57: 71-83.

Hilty, S. L. 2003. Birds of Venezuela.2nd ed. Princeton Univ. Press, Princeton, New Jersey.

Howell, S. N. G., & S. Webb. 1995. A field guide to the birds of Mexico and northern Central America. Oxford Univ. Press, Oxford, UK.

Hudson, W. H. 1920. Birds of La Plata. J. M. Dent, London, UK.

Johnson, K. P., & S. M. Lanyon. 1999. Molecular systematics of the grackles and allies, and the effect of additional sequence (CYT *b* and ND2). Auk 116: 759–768.

Lanyon, S. M. 1992. Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. Science 255: 77–79.

Lanyon, S. M. 1994. Polyphyly of the blackbird genus *Agelaius* and the importance of assumptions of monophyly in comparative studies. Evolution 48: 679–693.

Lanyon, S. M., & K. E. Omland. 1999 A molecular phylogeny of the blackbirds (Icteridae): five lineages revealed by cytochrome-*B* sequence data. Auk 116: 629–639.

Lindell, C., & C. Bosque.1999.Notes on the breeding and roosting biology of Troupials (*Icterus icterus*) in Venezuela. Ornitol. Neotrop. 10: 85–

90.

Lowther, P., & W. Post. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* Poole, A., & F. Gill (eds.). The birds of North America, No. 47. The Birds of North America Inc., Philadelphia, Pennsylvania.

Lowther, P., R. M. Fraga, T. S. Schulemberg, & S. M. Lanyon. 2004. Nomenclaturial solution for a polyphyletic *Agelaius*. Bull. Br. Ornithol. Club 124: 171–177.

Ochoa, J. M., & A. Cuervo Maya. 1998. Apuntes sobre la nidificación del Cacique Candela (*Hypopyrrhus pyrohypogaster*) en el municipio de Barbosa. Bol. Soc. Antioqueña Ornitol. 9: 61–68.

Orians, G. H. 1980. Some adaptations of marsh nesting blackbirds. Princeton Univ. Press, Princeton, New Jersey.

Orians, G. H. 1985a. Blackbirds of the Americas. Univ. of Washington Press, Seattle, Washington.

Orians, G. H. 1985b. Allocation of reproductive effort by breeding blackbirds, family Icteridae. Rev. Chil. Hist. Nat. 58: 19–29.

Orians, G. H., & G. M. Christman. 1968. A comparative study of the behavior of Red-winged, Tricolored and Yellow-headed blackbirds. Univ. Calif. Pub. Zool. 84: 1–81.

Orians, G. H., L. Erckmann, & J. C. Schultz. 1977a. Nesting and other habits of the Bolivian Blackbird (*Oreopsar bolivianus*). Condor 79: 250–256.

Orians, G. H., C. E. Orians, & K. J. Orians. 1977b. Helpers at the nest in some Argentine blackbirds. Pp. 137–151 *in* Stonehouse, B., & C. Perrins (eds.). Evolutionary ecology. Macmillan Press, London, UK.

Price, J. J., & S. M. Lanyon. 2004. A robust phylogeny of the oropendolas: polyphyly revealed by mitochondrial sequence data. Auk 119: 335–348.

Price, J. J., & S. M. Lanyon. 2004. Patterns of song evolution and sexual selection in the oropendolas and caciques. Behav. Ecol. 15: 485–497

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.

Schäfer, E. 1957. Les conotos. Étude comparative de *Psarocolius angustifrons* et *Psarocolius decumanus*. Bonn. Zool. Beitr. Sonderheft: 1957: 1–151.

Searcy, W. A., K. T. Yasukawa, & S. Lanyon. 1999. Evolution of polygyny in the ancestors of Red-winged Blackbirds. Auk 116: 5–19.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, Connecticut.

Skutch, A. F. 1954. Life histories of Central American birds. Vol.ume 1. Pacific Coast Avifauna No. 31, Cooper Ornithological Society, Berkeley, California.

Skutch, A. F. 1996. Orioles, blackbirds and their kin. Univ. of Arizona Press, Tucson, Arizona.

Webster, M. S. 1999. Reconstructing the evolutionary origin of polygyny in Red-winged Blackbirds. Auk 116: 1–4.

Webster, J. D. 2003. Skeletal characters and the genera of blackbirds (Icteridae). Condor 105: 239–257.

Widmann, O. 1907. A preliminary catalog of the birds of Missouri. Trans. Acad. Sci. St. Louis 17: 1–288.

Withingham, L. A., A. R. Kirkconell, & L. M. Ratcliffe. 1996. Breeding behavior, social organization and morphology of Red-shouldered(*Agelaius assimilis*) and Tawny-shouldered (*A. humeralis*) blackbirds. Condor 98: 832–836.

Zyskowski, K., & R. O. Prum. 1999. Phylogenetic analysis of the nest architecture of Neotropical ovenbirds (Furnariidae). Auk 116: 891–911.