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BUTTERFLY PREDATORS IN THE NEOTROPICS: WHICH BIRDS ARE INVOLVED?

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ABSTRACT. Butterflies have evolved a variety of defensive traits against visually hunting predators, especially insectivorous and omnivorous birds. However, few bird species that attack and feed on butterflies in the Neotropical region are known. Here we present a list of 36 species belonging to 15 bird families observed to attack butterflies in different sites of Central and South America. In addition to comments on the birds involved, we also indicate which bird families are expected to reveal new butterfly predators.

Additional key words: escape tactics, insectivorous birds, mimicry, protective coloration, unpalatability

Butterflies have evolved a variety of defensive traits to avoid predation by birds. These include: defensive chemicals (Brower 1984), aposematic and cryptic coloration (Poulton 1890), Batesian and Müllerian mimicry (Bates 1862, Müller 1879), fast and unpredictable flight, weak/fragile wings that allow escape by tearing when pecked by birds (Pinheiro et al. 2016). Recent evidence indicates that palatable butterflies also use bright colors to advertise difficulty of capture to birds, and may also evolve mimetic interactions with similar (escape Müllerian mimicry) or less evasive species (escape Batesian mimicry), analogous to unpalatable butterflies and their Müllerian and Batesian mimics (reviewed in Pinheiro & Freitas 2014).

Although some evidence suggests that lizards are also involved (Boyden 1976, Ehrlich & Ehrlich 1982, Odendaal et al. 1987) the high frequency of beak marks found on the wings of live butterflies (Benson 1972, Brower 1984, Pinheiro et al. 2014) indicates that birds are likely the most important butterfly predators and, therefore, the selective agents involved in the evolution of most defensive traits listed above (Brower 1984). Despite the importance placed on adaptive coloration as a deterrent to avian predation, few birds are known to prey on butterflies, especially in the neotropics, which contains the highest diversity of both butterflies (Heppner 1991) and birds (Del Hoyo et al. 1992–2010) on Earth. Bates himself did not witness a single bird attack on aposematic and mimetic butterflies in the eleven years he stayed in the Amazon (Bates 1862). More than 150 years later, all we know about butterfly predators in this region is restricted to a jacamar (Benson 1972; Chai 1986, 1990; Pinheiro & Campos 2013), a tanager (Brown & Vasconcellos-Neto 1976), two tyrant-flycatchers (Pinheiro 1996, 2003, 2011), an ani (Burger & Gochfeld 2001) and a few other birds (Brower 1984). In consequence, many defensive traits of butterflies remain uninvestigated. Furthermore, defensive traits have been investigated mostly with caged birds that do not attack butterflies under natural conditions, sometimes with the implicit assumption that natural predators would behave in a similar fashion. Here we present a list of birds observed to attack butterflies in the neotropics. To our knowledge, this is the first list of butterfly predators ever produced for this region.

MATERIAL AND METHODS

The majority of our list of butterfly predators is based on our own field observations of interactions between butterflies and birds taken at different sites and occasions in South America. In addition, we included some reports of bird attacks on butterflies observed in Central America, and bird species utilized or observed in palatability and mimicry experiments conducted in the eastern Amazon and Central America. References on bird stomach contents and studies that report bird attacks on Lepidoptera were excluded, as they did not distinguish whether individuals attacked or consumed were butterflies (Papilionoidea), skippers (Hesperioidea) or moths (in many cases authors do not even indicate whether lepidopterans were larvae, pupae or adult individuals). Information on the butterflies attacked by birds and the location of observations are given in Table 1.

RESULTS AND DISCUSSION

Our observations combined with data from the literature document butterfly predation by 36 bird

species of 15 families (Table 1). We believe, however, that many additional unobserved birds are involved, especially among the Galbulidae, Tyrannidae, and Thraupidae.

Galbulidae, Tyrannidae, and Thraupidae

Galbulidae contains 18 species (Remsen et al. 2016) including the Rufous-tailed Jacamar (*Galbula ruficauda* Cuvier), regarded as the most specialized butterfly predator in the Neotropics and utilized in several feeding and mimicry experiments with butterflies (Benson 1972; Chai 1986, 1990; Pinheiro & Campos 2013). Preliminary observations on wild Paradise Jacamar (*Galbula dea* Linnaeus) showed that this bird also feeds on a variety of butterflies. Similar to Rufous-tailed Jacamar, the Paradise Jacamar usually perches with the bill pointed upwards while moving the head in all directions, monitoring the space around, then performing a sudden and fast sally, sometimes in acrobatic loops, after flying insects like bees, dragonflies, and butterflies. Additional observations on the feeding behavior of this and other Galbulidae, which remain virtually uninvestigated, would certainly reveal many butterfly predators.

Tyrannidae is the largest Neotropical bird family (418 species; Remsen et al. 2016), most of them insectivorous (Ridgely & Tudor 2009). Wide ranging tyrant-flycatchers like the Boat-billed Flycatcher (*Megarynchus pitangua* Linnaeus), the Great Kiskadee (*Pitangus sulphuratus* Linnaeus), the Tropical Kingbird (*Tyrannus melancholicus* Vieillot), the Streaked Flycatcher (*Myiodynastes maculatus* Müller), and the Rusty-margined Flycatcher (*Myiozetetes cayennensis* Linnaeus) occur in almost all vegetation strata in wetlands and terrestrial habitats of Central and South America (Cintra 1997, 2014; Ridgely & Tudor 2009), and attack a variety of Papilionidae, Nymphalidae, and Pieridae butterflies (Cook et al. 1969; Pinheiro 1996, 2003; 2011). This is also the case for the Cliff Flycatcher (*Hirundinea ferruginea* Gmelin) (Pinheiro 2003) and many other tyrant-flycatchers sometimes observed to attack butterflies like the Grey Monjita (*Xolmis cinereus* Vieillot), the White-throated Kingbird (*Tyrannus albogularis* Burmeister), the Long-tailed Flycatcher (*Colonia colonus* Vieillot), the Short-crested Flycatcher (*Myiarchus ferox* Gmelin), and the Drab Water-Tyrant (*Ochthornis littoralis* Pelzeln). Given the large number of species in this family we suspect that many other species could be involved in predation on butterflies.

Thraupidae is a bird family restricted to the Western Hemisphere that contains 329 species (Remsen et al. 2016) and reaches maximum diversity in the tropics. These birds are usually referred to as exclusively frugivores (Ridgely & Tudor 2009), but attacks on wild butterflies have been observed in many species like the Silver-beaked Tanager (*Ramphocelus carbo* Pallas), the Blue-gray Tanager (*Tangara episcopus* Linnaeus), which occur in most of the Brazilian Amazon, and White-lined Tanager (*Tachyphonus rufus* Boddaert), also utilized in palatability experiments with butterflies (Brower 1984). Fawn-breasted Tanager (*Pipraeidea melanonota* Swainson) has been observed to feed on chemically defended Ithomiini (Nymphalidae) that form large aggregations in the dry season in southeastern Brazil (Brown & Vasconcellos-Neto 1976). According to Brown & Vasconcellos-Neto the birds consume only the abdominal contents, which contain low quantities of defensive chemicals, and reject most of the body afterwards. Summer Tanager (*Piranga rubra*, now in the Cardinalidae) breeds in North America, but overwinters in South America where it feeds on fruits (Dunn & Alderfer 2014) and insects like butterflies, termites and wasps. Such a diverse collection of examples strongly suggests that other birds in this large family also feed on butterflies.

Ground-based bird predators

In contrast to jacamars and many other birds, which are able to catch both flying and resting butterflies, the Sunbittern (*Eurypyga helias* Pallas), the Collared Plover (*Charadrius collaris* Vieillot), and the Smooth-billed Ani (*Crotophaga ani* Linnaeus) feed mostly on puddling butterflies, especially males that perch on the ground to obtain salt and other minerals (Molleman 2010). Puddling aggregations occur on humid soil, sometimes as large butterfly carpets containing several species of Pieridae, Papilionidae, and Nymphalidae that cluster by color similarity (Tyler et al. 1994). Burger & Gochfeld (2001) observed that predation by Smooth-billed Ani on these butterflies can be intense. In addition, many other birds like the Rufous-tailed Jacamar, the Drab Water-Tyrant (*Ochthornis littoralis* Pelzeln) (R.A.A. Plácido, pers. comm.) and other tyrant-flycatchers occasionally feed on puddling butterflies.

Additional groups with new records

With few exceptions, most other birds cited in Table 1 constitute new records of butterfly predators. The Amazonian Motmot (*Momotus momota* Linnaeus) and the Rufous-capped Motmot (*Baryphthengus ruficapillus* Vieillot) are widely distributed over the neotropics (Hilty 2003). Foraging in these species involves a short, fast jump from the ground to obtain small fruits, butterflies and other insects perched on herbaceous plants. Amazonian Motmot attacks both palatable and chemically defended butterflies like several Ithomiini. Carla M. Penz (pers. comm.) observed this bird unsuccessfully attacking a group of flying *Opsiphanes* in

Panama. Rufous-capped Motmot is less common, and occurs as solitary individuals or in pairs in humid and wet lowland forests from middle to upper story. They hunt by a sudden sally to catch butterflies and other insects on foliage, limbs or trunks, and follow army ants (Hilty & Brown 1986).

The Black Nunbird (*Monasa atra* Boddaert) occurs in the understory of the Amazon *terra-firme* forest and its congeneric, the Black-fronted Nunbird (*Monasa nigrifrons* Spix) is a resident species in *varzea* and secondary forests. They catch crickets, cockroaches, spiders, and several butterfly species that perch on branches and trunks. One of us (RC) observed this bird following troops of squirrel monkeys (*Saimiri sciureus* Linnaeus), which dislodge butterflies and many arthropods that are afterwards detected and attacked.

The Laughing Falcon (*Herpetotheres cachinnans* Linnaeus) is able to catch the large *Morpho* butterflies. R. Hill (pers. comm..) observed this bird repeatedly attacking *Morpho* sp. on the wing. According to him the Falcon flew out and flew very swiftly taking the butterfly out of the air. Then it returned to high exposed perch and clipped wings off before consuming the butterfly.

The Plain-brown Woodcreeper (*Dendrocincla fuliginosa* Vieillot) occurs from Honduras to Ecuador, east of the Andes to southern Bolivia, Brazilian Amazonia, and northeastern Brazil (Hilty 2003). This bird is a mixed-species flock follower in the understory of *terra-firme* forest (Willis 1972). It usually perches low in saplings and shrubs before jumping to catch escaping arthropods, including butterflies, which are flushed from vegetation by the passing wave of birds. Sometimes they climb up trees to forage on butterflies and insects hidden in the bark. Given the relatively large number of woodcreepers (51 species; Remsen et al. 2016) and the fact that most are insectivores, we also expect to find other butterfly predators among them.

The Red-eyed Vireo (*Vireo olivaceus* Linnaeus) occurs all over Brazil, and the southern population is an austral migrant to Amazonia (van Perlo 2009). This bird often searches for food at the forest edge, in woodlands, shrubby clearings, and in the canopy of tall trees in cities. Although they feed mostly on larvae, they also attack, with sudden sallies, small Lycaenidae and Riodinidae perched on branches and leaf surfaces. Also in the *Vireo* family, the Rufous-browed Peppershrike (*Cyclarhis gujanensis* Gmelin) is a solitary, territorial, and widely distributed bird occurring from Mexico to Argentina. Its foraging behavior is similar to Red-eyed Vireo, often staying in foliage, but prefers the sub-canopy, concentrating activities mostly in primary forests, and follow mixed-species flocks at the forest border (Hilty 2003).

The Southern House Wren (*Troglodytes musculus* Naumann) is a small resident bird occurring over the Americas to Tierra del Fuego (Hilty 2003). This species is uncommon in natural habitats but is very abundant in urban areas and gardens. This is a very active wren, usually seen foraging from the ground to the canopy on all sorts of arthropods, including small insects and butterflies like Riodinidae and Lycaenidae, which they catch everywhere, including on the ground, shrubs, tree leaf surfaces and trunks.

The Pale-breasted Thrush (*Turdus leucomelas* Vieillot) is also very abundant in cities. It feeds mostly on the ground by hopping to find insects. Early in the morning and late in the afternoon it perches at low heights or in small trees, and sometimes attacks flying butterflies. The Cocoa Thrush (*Turdus fumigatus* Lichtenstein) is an uncommon, resident species that dwells in forest sites near water, occurring as solitary individuals or in pairs. Its range includes Trinidad, Guianas, Venezuela, eastern Colombia, Brazil, and eastern Bolivia (Cintra 2014). This species forages on the ground, and performs a sudden run after organisms and will also flip leaves with its bill, catching its prey by surprise. The Yellow-rumped Cacique (*Cacicus cela* Linnaeus) is a common, gregarious, and widespread bird, occurring solitarily, in pairs or in loose flocks in natural forest and urban areas. This cacique occurs from western Panama to Bolivia, Brazilian Amazonia, the Guianas, and to the east coast of Brazil (Hilty 2003). This bird breeds in colonies with many nests like hanging pouches in the canopy of tall trees, sometimes associated with Crested Oropendola (*Psarocolius decumanus* Pallas) breeding colonies. It forages in groups and away from the colony and brings all sorts of arthropods to its nests, including many lepidopteran larvae and adults. In contrast, the Solitary Black Cacique (*Procacicus solitarius* Vieillot) is a very uncommon, territorial, and solitary bird, and somewhat overlaps its geographical distribution with Yellow-rumped Cacique. It constructs a solitary nest, similar in shape to the Yellow-rumped Cacique, at forest edge in aquatic environments (Cintra 2014). It also feeds on a variety of large arthropods, including butterflies, which it catches by quickly jumping on them just after take-off.

Although relatively small, the list of predators provided here illustrates the variety of insectivorous and omnivorous birds whose species composition and abundance vary in different Neotropical communities, and are likely the major selective agents shaping butterfly defensive traits. We strongly encourage future investigations on bird feeding behavior and the role it has played as a selective agent on butterfly traits.

TABLE 1. Bird species observed to attack butterflies in the Neotropical region. Butterfly families are: Nym = Nymphalidae, Pap = Papilionidae, Pie = Pieridae, Lyc = Lycaenidae, Rio = Riodinidae, Hes = Hesperiidae. Brazilian states: AC = Acre, AM = Amazonas, DF = Distrito Federal, MT = Mato Grosso, PA = Pará, RO = Roraima, SP = São Paulo, TO = Tocantins. The bird taxonomic order followed SACC classification (Remsen et al. 2016). * = moth painted to resemble different mimetic morphs.

Family	Bird Species	Butterflies Attacked	Sites / References
Eurypygidae	*Eurypyga helias* (Sunbittern)	Nym + Pie (several species)	(Novo Airão, AM, 2009; RC)
Charadriidae	*Charadrius collaris* (Collared Plover)	Pie (several species)	(Porto Velho, RO, 1986; RC)
Cuculidae	*Crotophaga ani* (Smooth-billed Ani)	Nym + Pap + Pie (several species) Pie (several species)	Burger & Gochfeld (2001) (Iranduba, AM, 2015; RC)
	Piaya cayana (Squirrel Cuckoo)	*Hyalophora promethea* (Drury)*	Cook et al. (1969)
Momotidae	*Momotus momota* (Amazonian Motmot)	Ithomiini (Nym) (several species) Nym (several species) *Opsiphanes* sp. (Nym)	Pinheiro et al. (2008) (Manaus, AM, 2016; RC) (Gamboa, Panamá, 1994;
	Baryphthengus ruficapillus (Rufous-capped Motmot)	*Phoebis* sp. (Pie)	(Rio Tocantins, TO, 1997; CEGP)
Galbulidae	*Galbula ruficauda* (Rufous-tailed Jacamar)	*Heliconius* sp. (Nym) *Eueides isabella* Stoll (Nym) Nym + Pap + Pie (several species) *Morpho* sp. (Nym)	Benson (1972) Pinheiro & Campos (2013) Chai (1986, 1990) (many sites; RC, CEGP)
	Galbula dea (Paradise Jacamar)	Nym + Pap + Pie (several species)	(Manaus, AM, 2014; RC)
Bucconidae	*Monasa atra* (Black Nunbird)	Nym + Pie (several species)	(Manaus, AM, 2013; RC) (Carajás, PA, 1995; CEGP)
	Monasa nigrifrons (Black-fronted Nunbird)	*Heliopetes* sp. (Hes)	
Falconidae	*Herpetotheres cachinnans* (Laughing Falcon)	*Morpho* sp. (Nym)	(Guanacaste, C. Rica, 2014; RH)
Furnariidae	*Dendrocincla fuliginosa* (Plain-brown Woodcreeper)	*Hyalophora promethea* (Drury)*	Cook et al. (1969)
Tyrannidae	*Hirundinea ferrugínea* (Cliff Flycatcher)	Nym (several species) Nym + Pap (several species)	Pinheiro & Martins (1992) Pinheiro (2003)
	Xolmis cinereus (Grey Monjita)	Pie (several species)	(Brasilia, DF, 1982; RC)
	Colonia colonus (Long-tailed Flycatcher)	*Parides* sp. (Pap)	(Carajás, PA, 1995; CEGP)
	Myiozetetes cayennensis (Rusty-margined Flycatcher)	Nym + Pie + Pap (several species)	(many sites; RC)
	Pitangus sulphuratus (Great Kiskadee)	Nym + Pie + Pap (several species) Nym + Pie (several species) *Hyalophora promethea* (Drury)*	(Carajás, PA, 1995; CEGP) (Manaus, AM; RC) Cook et al. (1969)

TABLE 1. CONTINUED

Family	Bird Species	Butterflies Attacked	Sites / References
Tyrannidae	*Myiodynastes maculates* (Streaked Flycatcher)	*Heliconius* sp. (Nym)	(Carajás, PA, 1995; CEGP)
	Megarynchus pitangua (Boat-billed Flycatcher)	*Mechanitis polymnia* Linnaeus (Nym) *Heliconius ethilla* Godart (Nym) Nym + Pie (several species) *Hyalophora promethea* (Drury)*	(Brasília, DF, 2000; CEGP) (Campinas, SP, 1984; CEGP) (Manaus, AM, 2004; RC) Cook et al. (1969)
	Tyrannus albogularis (White-throated Kingbird)	Nym (several species)	(Santarém, PA, 1999-2001; RC)
	Tyrannus melancholicus (Tropical Kingbird)	Nym (several species) Nym + Pap + Pie (several species) *Hyalophora promethea* (Drury)*	Pinheiro & Martins (1992) Pinheiro (1996); (many sites; RC) Cook et al. (1969)
	Ochthornis littoralis (Drab Water-Tyrant)	*Marpesia* spp. (Nym)	(Mâncio Lima, AC, 2016; RAAP)
	Myiarchus ferox (Short-crested Flycatcher)	Pie (several species)	(Poconé, MT, 1984; RC)
	Myiarchus sp.	*Temenis laothoe* ssp. (Nym)	(Carajás, PA, 1995; CEGP)
Vireonidae	*Cyclarhis gujanensis* (Rufous-browed Peppershrike)	Lyc + Rio (several species) *Hyalophora promethea* (Drury)*	(Santarém, PA, 1999-2001; RC) Cook et al. (1969)
	Vireo olivaceus (Red-eyed Vireo)	Lyc + Rio + Hes (several species)	(Poconé, MT, 1983; RC)
Troglodytidae	*Troglodytes musculus* (Southern House Wren)	Lyc + Rio (several species)	(many sites; RC; CEGP)
Turdidae	*Turdus leucomelas* (Pale-breasted Thrush)	Pie (several species)	(Manaus, AM, 2012; RC)
	Turdus fumigatus (Cocoa Thrush)	*Hyalophora promethea* (Drury)*	Cook et al. (1969)
Thraupidae	*Tachyphonus rufus* (White-lined Tanager)	Nym + Pap (several species) Nym + Pap + Pie (several species) *Hyalophora promethea* (Drury)*	Brower (1984) (Santarém, PA, 2000; RC) Cook et al. (1969)
	Rhamphocelus carbo (Silver-beaked Tanager)	Nym + Pap (several species)	Brower (1984); (many sites; RC)
	Pipraeidea melanonota (Fawn-breasted Tanager)	Ithomiini (Nym) (several species)	Brown & Vasconcellos-Neto (1976)
	Tangara episcopus (Blue-gray Tanager)	Pie (several species)	(Manaus, AM, 2011; RC)
Cardinalidae	*Piranga rubra* (migrant) (Summer Tanager)	Nym (several species)	(Manaus, AM, 2015; RC)
Icteridae	*Cacicus cela* (Yellow-rumped Cacique)	Pie (several species)	(Tefé, AM, 2003; RC)
	Procacicus solitarius (Solitary Black Cacique)	Pie (several species)	(Poconé, MT, 1983; RC)

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