

Jacamars (Aves, Galbulidae) as selective agents of mimicry in neotropical butterflies

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RESUMO. Arirambas (Aves, Galbulidae) como agentes seletivos do mimetismo em borboletas neotropicais. Arirambas, também conhecidos no Brasil como bicos-de-agulha e jacamars, têm sido considerados por muitos autores atuais como exemplos clássicos de agentes seletivos do mimetismo em borboletas neotropicais. Neste estudo são fornecidas evidências de que estas aves podem ser mesmo consideradas importantes agentes seletivos do mimetismo Batesiano, mas não do mimetismo Mülleriano, o tipo mais comum de mimetismo entre borboletas neotropicais.

PALAVRAS-CHAVES: *Galbula ruficauda*, bico-de-agulha, ariramba-da-mata, mimetismo Batesiano e Mülleriano.

KEY-WORDS: *Galbula ruficauda*, jacamars, Batesian and Müllerian mimicry.

The question of which predator feed upon butterflies, especially on the mimetic species, has been raised many times since Bates (1862) and Müller (1879) first described the two most classical forms of mimicry, based on their observations on neotropical butterflies. Mimicry was by then the most important application of natural selection theory (Fisher 1930), whose opponents argued that birds, then believed to be the most important predators of butterflies, in fact did not feed on these insects. While direct observations of bird predation on butterflies were still rare, early evolutionary biologists used beak marks, found on the wings of living butterflies, as evidence to support predation by birds. Poulton (1887, 1890) and Marshall (1902, 1908) observed that species presumed to be unpalatable usually bore beak marks more frequently than palatable species and hypothesised that butterflies had been captured, tasted, and released by birds. This hypothesis was afterwards confirmed by Carpenter (1921, 1933, 1937, 1941, 1942), who analysed a large number of both wild and museum specimens. These naturalists were also aware that unpalatable butterflies usually have tough wings that help them to resist sampling by birds (see also DeVries 2003). Nowadays, most authors agree that birds are the main butterfly predators. However, which species are involved, especially in the case of the Neotropical region, where mimicry phenomenon seems to have reached its most diverse and eye-catching forms, remains poorly documented. One exception, however, are the jacamars.

First indication that jacamars constitute important selective agents of mimicry come from reports of field naturalists who observed that wild birds selectively attack palatable butterflies, but usually avoid on sight the unpalatable and mimetic species such as *Heliconius* and Ithomiinae butterflies (Belt 1874; Skutch 1937, 1963; Sherry 1983; Chai 1986). Afterwards, experiments designed to investigate the advantage of mimicry in nature also showed that jacamar

beak marks, easily identified by their long, slender, forceps-like bill impressions, were commonly found on the wings of *Heliconius* butterflies with altered color patterns (Benson 1972) or introduced in sites where they were not mimetic (Mallet and Barton 1989). In both studies the larger occurrence of beak marks obtained on non-mimetic morphs relative to their mimetic controls were taken as evidence for the advantage of mimicry. More recently, caged jacamars were utilised in several experiments on butterfly palatability and mimicry by Chai (1986, 1988, 1990, 1996). As a consequence of all these studies, jacamars are now considered a classical example of selective agent of mimicry in neotropical butterflies (e.g. Chai 1986, 1988, 1990, 1996; Brown 1988; Melo-Junior 2001; Tobias *et al.* 2002). This assertion, however, should be viewed with caution.

Classical kinds of mimicry include Batesian mimicry, when a palatable species, usually referred as the "mimic", resembles the color patterns and other traits of one or more unpalatable, chemically defended "models" (Bates 1862), and Müllerian mimicry, when two or more unpalatable, chemically defended species converge on color patterns (Müller 1879). Such distinctions between the two kinds of mimicry have not been considered with regard to jacamars. This note suggests that jacamars could be in fact important selective agents of Batesian mimicry, but not Müllerian mimicry, the most common type of mimicry among neotropical butterflies (Chai 1986, Brown 1988, Pinheiro 1996, 2003).

With few exceptions (e.g. Melo-Junior 2001), most data obtained on jacamars' diet (reviewed in Pinheiro *et al.* 2003), as well as field observations and experiments on mimicry cited above were conducted with the rufous-tailed jacamar (*Galbula ruficauda*), one of the most common and widespread species among the Galbulidae (Sick 1997). Evidence that this jacamar does not fit the role expected for a Müllerian mimicry selective agent is the fact that attacks by these birds on Müllerian mimics rarely result in death or

severe damage to sampled individuals. Following on sight these birds on different occasions in central, western and northern Brazil it was possible to record 19 attacks by this jacamar on the following Müllerian mimics (information on the mimetic relationships among butterflies is given in Brown 1988, 1992; Pinheiro 1996, 1997, 2003): *Heliconius erato* or *H. melpomene* (Heliconiinae; two species so similar that do not allow identification in flight; n= 5); *H. sara* (n= 4), which mimics *H. wallacei* in north Brazil; *H. ethilla* (n= 2), *Mechanitis polymnia* (Ithomiinae; n= 1), and *Tithorea harmonia* (Ithomiinae; n= 1), all mimics in the “Tiger” mimicry ring; *Dircenna dero* (Ithomiinae; n= 1) and other “black & transparent” Ithomiinae (also not identified in flight to species; n= 3); *Parides anchises* (Papilionidae, Troidini; n= 2), which mimics *P. neophilus*. In all cases captured butterflies were released alive and could still fly after been handled and taste-rejected by birds.

Conversely, evidence that rufous-tailed jacamar is truly a Batesian mimicry selective agent come from observations that, although at a low rate, the birds keep on sampling mimetic butterflies, in spite of previous experience with an unpalatable species and/its Müllerian mimics. Examples include a bird that attacked *Heliconius ethilla* twice, in the same sequence of observations in which this butterfly and several other Müllerian mimics of the same mimicry complex were previously sight-rejected by the same bird. Other bird was observed to reject on sight several *Lycorea cleobaea* and *Mechanitis polymnia*, but afterwards attacked *Tithorea harmonia* (all from the “Tiger” ring). Another jacamar hunting insects very close to a large aggregation of the “black & transparent” Ithomiinae was observed to reject on sight several *Thyridia psidii*, *Ithomia agnosia*, and *Dircenna dero*, but suddenly attacked one of them (not identified). One possible explanation for these attacks is that more profitable food items became temporarily scarce, and the birds were using those relatively unpalatable butterflies as alternative food supply (Nonacs 1985, Luedman *et al.* 1981). However, all butterflies were afterwards taste-rejected by birds. The other possibility is that birds were just sampling mimetic butterflies, probably in search of Batesian mimics.

Sampling on mimetic species has been considered by many authors as the result of two antagonistic selective forces acting on predators: pressure to sample potential prey for palatable items, such as Batesian mimics, and pressure to decrease sampling and reduce the risk of poisoning by models or Müllerian mimics (Huheey 1976; Turner 1984, 1987; Nonacs 1985, Chai 1986). A tendency of the *Galbula ruficauda* to sample mimetic butterflies was also observed by Chai (1986) who attributed such behavior to the jacamars’ great ability to taste and reject unpalatable butterflies without ingesting them, making sampling less dangerous and encouraging the bird to try mimetic butterflies. It is possible, therefore, that jacamars are truly Batesian mimic hunters.

On the other hand, the evolution of Müllerian mimicry is thought to evolve in butterflies to enhance their unpalatability defences, especially (1) by reinforcing an avoidance image on the predators, and (2) by enabling that less butterflies need to be sampled until predators learn to avoid them on sight (Müller 1879, Fisher 1930). It is thus more reasonable to conceive the evolution of this kind of mimicry in response to the selective pressure of predators

that are also efficient hunters, like tyrant-flycatchers (Pinheiro and Martins 1992; Pinheiro 1996, 2003). I hope that future studies on jacamars include other species less investigated and be able to evaluate better the role of these birds as selective agents of mimicry.

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