Journal of Tropical Ecology (2007) **23**:119–123. Copyright © 2007 Cambridge University Press
doi:10.1017/S0266467406003749 Printed in the United Kingdom

SHORT COMMUNICATION
Asynchrony in daily activity patterns of butterfly models and mimics

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(*Accepted 23 September 2006*)

KEY WORDS Atlantic Forest, Batesian mimicry, Brazil, insectivorous birds, neotropical butterflies

Bates' theory of mimicry (Bates 1862) postulates that vertebrate predators avoid attacks on chemically defended butterflies, and a profitable species, usually referred to as the mimic, can obtain protection by resembling one or more unpalatable models. The evolution of Batesian mimicry requires that predators meet, taste and learn to avoid the models before meeting the mimics. For this reason, some authors have adopted the assumption that mimic population sizes must be smaller than the models' populations (Fisher 1930, Huheey 1980, Lindström *et al.* 1997).

Mimic rarity relative to models seems to occur both in terms of species – the number of model or Müllerian mimic species is locally larger than Batesian mimics in most Neotropical butterfly mimicry complexes (or 'mimicry rings'; Chai 1986, Pinheiro 1996) – and individuals within a given ring (data on the population dynamics of many Batesian mimics remain scarce, but their rarity is well known to most butterfly collectors). We may therefore conclude that mimic rarity relative to models remains as a valid assumption for the evolution of Batesian mimicry. However, there are two mechanisms, both concerning temporal asynchronies between models and mimics, which allow that predators meet the models predominantly first, regardless of the relative frequency of models and mimics in a given Batesian mimetic complex.

The first mechanism is well known and involves asynchrony in the occurrence of models and mimics throughout the year. Huheey (1980, 1988) argues that Batesian mimics could benefit by retarding their emergence until after the appearance of its models, thus enhancing mimicry and allowing the predator to be educated before being exposed to the mimics. Examples of this kind of asynchrony are found in several temperate Batesian mimicry complexes involving moths (Rothschild 1963), stinging bumblebees or wasps and flies (Waldbauer 1988) and salamanders (Brodie 1981). The other mechanism that might lower the risk of lethal encounters with naïve predators for Batesian mimics involves asynchronies in the daily activity patterns of predators, models, and mimics, and has received surprisingly little attention by mimicry researchers. The description of such a mechanism constitutes the purpose of this study.

It is widely accepted that birds are the main selective agents of mimicry in butterflies (Brower 1984, Srygley & Ellington 1999). In the neotropics the predators involved include a large set of birds such as jacamars (Chai 1986, Langham 2004), tyrant-flycatchers (Pinheiro 1996, 2003), tanagers (Brown & Vasconcellos-Neto 1976), motmots (Marden 1992). Although bird activity patterns are poorly documented in the literature, I observed that adult, non-breeding jacamars investigated in central Brazil usually start feeding activities before sunrise and tend to feed all day long (Pinheiro *et al.* 2004). Adult tyrant-flycatchers such as the neotropical kingbird and the cliff-flycatcher also tended to feed all day long in eastern Amazon Forest (Pinheiro 1996, 2003), but tyrant-flycatchers in general and many other birds found in more open habitats in subtropical regions of the Atlantic Forest and central Brazil usually show a peak of foraging activity early in the morning, and reduce their activities during the hottest or driest periods of the day. In many cases, a second peak occurs late in the afternoon.

On the other hand, butterflies are ectotherms and their activity patterns depend on a series of morphological, behavioural, and physiological traits of these insects, as well as on their palatability to predators (Srygley & Chai 1990b). As a general trend, unpalatable butterflies fly slowly and regularly, exhibit lower body temperatures relative to palatable species (Chai & Srygley 1990), and are able to fly in different habitats – including both sunny and dark places – and day times. In contrast, palatable species fly fast and erratically – characteristics that help them

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https://doi.org/10.1017/S0266467406003749 Published online by Cambridge University Press

Table 1. Mimicry rings investigated for differences in daily activity patterns of models and mimics, including: TIGER I (large) and TIGER II (small): black, yellow, orange and white; BRY: black, red with yellow bar; BRW: black, red with white spot. M = model or Müllerian mimic, BM = Batesian mimic.

Mimicry rings/species	Family: subfamily or tribe	Kind of mimic
TIGER I		
Heliconius ethilla narcaea (Godart, 1819)	Nymphalidae: Heliconiinae	M[2,3]
Lycorea cleobaea halia (Hübner, 1823)	Nymphalidae: Danainae	M[2,3,4,5]
Consul fabius drurii (Butler, 1873)	Nymphalidae: Charaxinae	BM[1,2,3]
Dismorphia amphiona astynome (Dalman, 1823)	Pieridae: Dismorphinae	BM[1,2,5]
TIGER II		
Mechanitis polymnia casabranca (Haensch, 1905)	Nymphalidae: Ithomiinae	M[1,2,3,4]
Mechanitis lysimnia lysimnia (Fabricius, 1793)	Nymphalidae: Ithomiinae	M[2]
Tithorea harmonia pseudethra (Butler, 1873)	Nymphalidae: Ithomiinae	M*
Eresia eunice esora Hewitson, 1857	Nymphalidae: Nymphalinae	BM[3]
BRY		
Heliconius erato phyllis (Fabricius, 1775)	Nymphalidae: Heliconiinae	M[2,3,4,5]
Heliconius besckei Ménétriés, 1857	Nymphalidae: Heliconiinae	M*
Eresia lansdorfi (Godart, 1819)	Nymphalidae: Nymphalinae	BM*
BRW		
Parides anchises foetterlei (Roth. & Jordan, 1906)	Papilionidae: Troidini	M[5]
Heraclides anchisiades capys (Hübner, 1806)	Papilionidae: Papilionini	BM*

*not tested for palatability, but see references below for data on closely related species.
[1,2]tested to jacamars (Srygley & Chai 1990a,b).
[3,4]tested to tyrant-flycatchers (Pinheiro 1996, 2003).
[5]tested to many other birds (reviewed in Brower 1984)

to evade attacks by predators (Srygley & Chai 1990a) – show higher body temperatures relative to unpalatable butterflies, fly mainly in open and sunny places and are more active in the hotter parts of the day. However, direct comparisons of daily activity patterns of models and Batesian mimics remain scarce.

Unpalatable butterflies like *Heliconius*, Ithomiinae, Danainae and *Parides* species are commonly regarded as models in several neotropical mimicry rings (Table 1). Batesian mimics could thus benefit by (1) delaying their daily activities until after the appearance of their models, allowing the predator to be educated before being exposed to them, and/or (2) stopping their daily activities before the disappearance of their models late in the afternoon, when a second peak of foraging activity could be expected in some predators.

Figure 1 summarizes several examples of daily activity patterns of butterfly models and mimics which suggest that such possibilities do occur. Activity patterns were obtained by the number of 'active' butterflies (mostly flying, but also feeding, egg-laying, mating and other activities) captured and marked or just sighted along an extension of forest vegetation repeatedly surveyed from dawn to dusk. As a general trend, all models investigated started their daily activities early in the morning (06h01–08h00) and stopped in middle to late afternoon (16h01–18h00), indicating that they remain active most of the day. Conversely, all Batesian mimics were active only during the hottest part of the day (10h01–16h00), starting their daily activities later than their respective models and stopping earlier. Except in the case of *Consul fabius*, rare in the field (n = 4; but also observed only in the hotter hours of the day), comparisons involving the distributions of butterflies at distinct time intervals showed significant differences for all pairs of models and mimics (two-tailed, two-sample Kolmogorov–Smirnov test (Sokal & Rohlf 1995): *Mechanitis polymnia* and *Eresia eunice*: $D = 0.26$, $P < 0.05$; *Mechanitis lysimnia* and *Eresia eunice*: $D = 0.37$, $P < 0.05$; *Tithorea harmonia* and *Eresia eunice*: $D = 0.31$, $P < 0.05$; *Heliconius ethilla* and *Dismorphia amphiona*: $D = 0.44$, $P < 0.05$; *Lycorea cleobaea* and *Dismorphia amphiona*: $D = 0.48$, $P < 0.05$; *Heliconius erato* + *Heliconius besckey* (pooled) and *Eresia lansdorfi*: $D = 0.35$, $P < 0.01$; *Parides anchises* and *Heraclides anchisiades*: $D = 0.31$, $P < 0.05$). In contrast, comparisons between models showed no significant differences ($P > 0.05$ in all cases). Therefore, the actual risk of lethal encounters with naïve predators in nature, often estimated as a proportion of models to mimics in most theoretical models of Batesian mimicry, is certainly higher for models and lower for Batesian mimics, when compared with their simple proportions or relative frequencies within their respective mimicry rings.

Learning to avoid a given prey item is a time- and energy-consuming process that may require several trials until the predators are able to associate prey colour and other attributes to its palatability (Huheey 1980). Inside a relatively small area in the neotropics there are a variety of naïve predators that must be educated by model species. A large number of chicks recruit to bird populations

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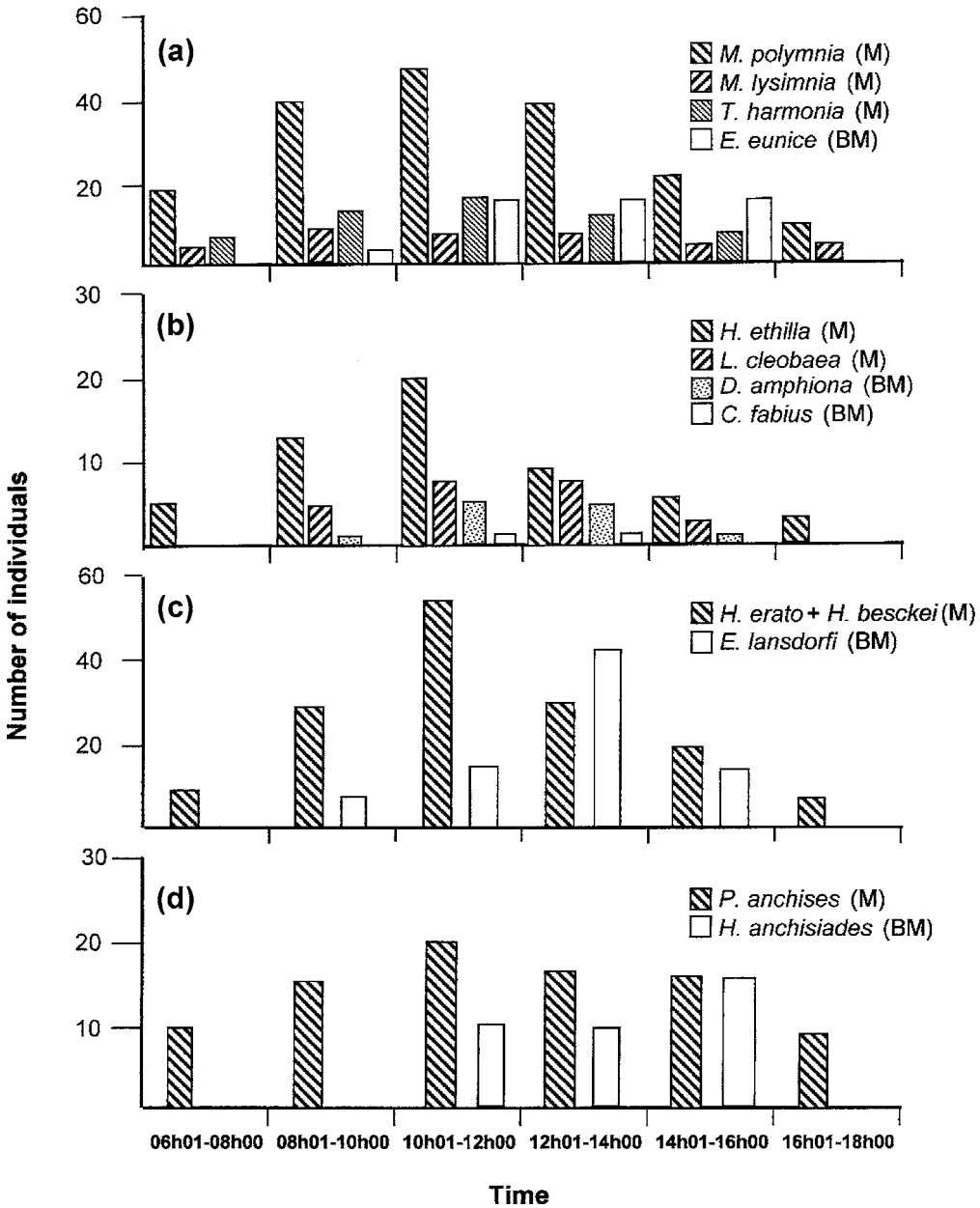


Figure 1 Activity patterns of models and mimics in four mimicry rings investigated in the Brazilian Atlantic Forest and central Brazil. Species and sites include: *Mechanitis polymnia casabranca*, *M. lysimnia lysimnia*, *Tithorea harmonia pseudethra* and *Eresia eunice esora* studied at a 300-m extension of a gallery forest along the Córrego Cascatinha at Parque Estadual de Caldas Novas, Goiás State (17°46′S; 40°39′W) (a); *Heliconius ethilla narcaea*, *Lycorea cleobaea halia*, *Consul fabius drurii* and *Dismorphia amphiona astynome* studied along a 600-m unpaved road bordered by Atlantic Forest vegetation at Ilha Grande, Rio de Janeiro State (23°50′S, 44°15′W) (b); *Heliconius erato phyllis*, *H. besckei* and *Eresia lansdorfi* studied along an 800-m unpaved road bordered by Atlantic Forest vegetation at Serra do Japi, São Paulo State (23°15′S, 46°52′W) (c); *Parides anchises foetterlei* and *Heraclides anchisiades capys* studied in a 600-m extension of a gallery forest along a tributary of the Maranhão river, central Brazil (15°30′S, 47°10′W) (d). All observations taken on sunny days (respectively in August 2004, July 2000, June 1986 and June 2004). Note that Batesian mimics may surpass the number of models at the hottest times of the day, when bird foraging activity is presumably low (c).

every year. The reproductive season, which occurs in the Atlantic Forest and central Brazil from the end of the dry season to the end of the rainy season (September to March), and is soon followed by the entry of newly fledged birds into the adult populations, may last more than 5 mo (Marini & Durães 2001). Some of the predators involved, such as many tyrant-flycatchers, consist of migratory species that may also require further education to avoid butterflies exhibiting new mimetic colour patterns. The arrival and permanence of migratory birds in the Atlantic Forest and central Brazil may also take several months (Marini & Cavalcanti 1990). Thus, the education of naïve

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predators probably takes a large part of the year and daily asynchronies in the timing of activity of models and mimics certainly help to protect the latter against many different predators.

How such asynchronies between models and mimics affect avian memory remains an open question. Although several feeding experiments have suggested that birds are able to retain avoidance learning for at least more than 1 d (Langham 2004, 2006; Lindström *et al.* 2001, Pinheiro 2003), it is possible that old, experienced birds may also forget mimetic colour patterns and turn to attack prey they have already learnt to avoid (Huheey 1988, Speed & Turner 1999). Thus, if predators do forget mimetic colour patterns, daily asynchrony of models and mimics would again operate to remind them which prey should be avoided.

Some evidence suggests that activity patterns in Batesian mimics evolved as a plesiomorphic character that butterflies retained of their groups (Table 1), rather than derived in response to mimicry. Investigations on the flight-related morphology of several Batesian mimics such as *Dismorphia amphiona*, *Consul fabius* and *Heraclides anchisiades* showed that they do not fly nor appear in shape exactly like their models, but demonstrate intermediate characteristics between palatable species within their groups and their distasteful models (Srygley 1994, 1999; Srygley & Chai 1990a). Thus, although converging on colour patterns and other characteristics of their models, Batesian mimics seem to retain some characteristics similar to their palatable sister species which are not mimetic that allow them to escape predator attacks. Efficient escape flights require high energy and can only be effective in the hotter hours of the day (Srygley & Chai 1990b). This provides a physiological explanation for the differences in daily activity patterns of butterfly models and mimics found in this study. Future studies on daily activity patterns of models and mimics will help to better elucidate this question.

ACKNOWLEDGEMENTS

I thank Keith S. Brown Jr., Regina H. F. Macedo and three anonymous reviewers for their helpful comments on the manuscript.

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