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FOLLOWING THE LEADER: HOW *HELICONIUS ETHILLA* BUTTERFLIES EXCHANGE INFORMATION ON RESOURCE LOCATIONS

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Neotropical forest-dwelling *Heliconius* butterflies exhibit different types of social behavior such as nocturnal communal roosting—aggregations at specific locations to spend the night together (Benson 1971; Turner 1971a, 1975; Young & Thomason 1975; Young & Carolan 1976; Waller & Gilbert 1982; Mallet 1986) and cooperative egg laying, where females of some species are believed to cooperate in jointly laying batches of eggs (Turner 1971b; Mallet & Jackson 1980; Reed 2003; but see Turner 1981). In addition, the ability of *Heliconius* to learn and incorporate resource locations into daily routes and broadly overlapping generations (Ehrlich & Gilbert 1973) has led some authors to propose that younger butterflies may learn resource locations by following more experienced ones (Gilbert 1975; Brown 1981; Turner 1981). However, evidence for the education of younger butterflies remains scarce.

Heliconius ethilla narcaea Godart 1819, one of the largest butterflies in the genus, is common in forest patches across southeastern Brazil. It flies faster and higher than most other *Heliconius* and home range size (3.0 ha) is three times that of sympatric *H. erato phyllis* (1 ha; Pinheiro 1987). In contrast to *H. erato* and other *Heliconius*, which cluster tightly on nocturnal communal roosts (examples in Brown 1981; Mallet 1986), *H. ethilla* rests solitarily or forms loose aggregations of few individuals (pers. obs.; see also Turner 1971a; Brown 1981). During a two year capture-recapture program conducted with *H. ethilla* in southeastern Brazil and occasional observations in other parts of country, I observed this butterfly to engage in what appear to be three kinds of pursuits in which individuals follow one another and could obtain information on resources locations, especially plants visited for pollen (Gilbert 1972; Beltrán *et al*. 2007). In this note I describe these interactions and provide information on sex and age of butterflies (including six categories based on scale loss: VF = very fresh, F = fresh, I = intermediate, IW = between intermediate and worn, W = worn, and VW = very worn butterflies; Ehrlich & Gilbert 1973) that were utilized to test the prediction that "followers" are younger than "leaders" (= first butterfly in a queue), as might be expected if following serves mainly to educate young butterflies. Three types of following behaviors could be distinguished.

(1) "Acrobatic" flights. The most spectacular and certainly the best demonstration that *H. ethilla* butterflies transmit information on food locations is found in the "acrobatic" flights. This behavior occurs in groups of 2 to 5 butterflies in a line formation, approximately 1 m apart, engaging in acrobatic flights in the forest middlestory. From time to time butterflies would dive, passing within a few centimeters of flowers of *Lantana camara* L.—the most utilized pollen plant in the study site that may elicit strong feeding responses in *Heliconius* butterflies (Andersson & Dobson 2003)—before ascending and moving on to a neighboring area or flower patch. Although butterflies did not stop to feed, flowers clearly constituted important reference points in these flights, allowing followers to learn many flower locations shown by the leader. However, on the few occasions I was able to capture part or all butterflies of a given group, often close to *L. camara* flowers, only relatively older males were found (mostly I and IW individuals; see Table 1). In groups 1–3, two or more butterflies were captured together and it was not possible to separate leaders and followers. However, on two additional occasions only a leader (an I male; group 4) and only a follower (another I male, group 5) were captured. "Acrobatic" flights were more common in mid-afternoon, when butterfly feeding is reduced. Most observations were from the end of the wet season, when populations tend to be larger.

(2) "Long distance" flights. Another kind of following behavior exhibited by *H. ethilla* consisted of "long distance" flights. These often involved two butterflies engaging in a relatively fast, straight flight through the forest middlestory, with the leader flying approximately 1m higher and 2m ahead of the follower. In an open forest near Campinas, São Paulo, it was possible to keep butterflies in sight for relatively long periods. Butterflies engaged in "long distance" flights are often difficult to sample because of the distance from the ground. However, on one occasion I succeeded in capturing the follower after the leader had just passed 5 m up overhead (an I male, group 6 in Table 1). The leader flew on for about 40 m, but suddenly returned, seemingly in search of its follower, performing circular flights close to vegetation along the same route previously taken, when I captured it (a W male). After learning to "capture the follower first" I was

TABLE 1. Social flights performed by groups of *H. ethilla* males. The number of individuals captured in each group, the group size (before capture) and the age category of participating butterflies based on wing-wear are also given (F = fresh, I = intermediate, IW = between intermediate and worn, W = worn; note the absence of VF = very fresh and VW = very worn butterflies); social role: L= leader, Fo= follower.

INTERACTION TYPE	GROUP NUMBER	N. INDIVS. CAPTURED / GROUP SIZE	WING-WEAR CATEGORIES (SOCIAL ROLE)
"ACROBATIC"	1.	3/5	[I, IW & IW]
	2.	2/3	[I & I]
	3.	2/2	[IW & IW]
	4.	1/3	[I (L)]
	5.	1/2	[I (Fo)]
"LONG DISTANCE"	6.	2/2	[I (L) & F (Fo)]
	7.	2/2	[W (L) & F (Fo)]
"PURSUING"	8.	4/4	[I (L), I (Fo), F (Fo), IV (Fo)]
	9.	1/3	[I (Fo)]
	10.	1/2	[IW (Fo)]

able to use this technique to sample a second pair of butterflies. As in the previous case, the leader came back and was captured. The butterflies were both males and the age categories of the leader and follower were W and F respectively (group 7 in Table 1). Although "long distance" flights seemed to be relatively common in *H. ethilla*, especially between mid and late afternoon, I was unable to discover the origin and the final destination of these flights and, therefore, their objective. Despite that, it appears that some sort of information is transmitted from leader to follower in these flights. It may be significant that followers were younger than leaders in both groups investigated.

(3) "Pursuing" flights. These involve 2–4 butterflies that chase the leader in a fast, erratic flight. At first glance, pursuing activities appear unrelated to the education of butterflies, as the leader seems to try to escape from its pursuers and not show them resources. This behavior suggests that *H. ethilla* interactions include non-cooperative relationships as well as cooperative. Moreover, one unusual observation suggests another capability of *H. ethilla* yet undemonstrated: that butterflies may follow each other with the aid of chemical cues in addition to vision. This possibility was suggested by an event in which all butterflies in a group were captured in sequence (group 8 in Table 1). I was walking on a forest-edge trail when a *H. ethilla* appeared 2m ahead coming from the inside forest in a very fast flight. The butterfly stopped to hover for a few seconds over the middle of the trail, approximately 1m above the ground, and turned to my direction in the trail (it was an I male). I had the butterfly in my hand when a second *H. ethilla* flew out of the forest at the same place and height, hovered for some seconds and flew towards me just as had the leader (another I male). Some seconds later a third butterfly emerged from the forest at the same spot and repeated the same movements of its two predecessors (a F male). Finally, a fourth butterfly appeared and repeated everything once again (an IV male). Because no follower had visual contact with its predecessors – each had been captured by the time the next butterfly arrived – the butterflies probably followed a chemical track to pursue the leader. My impression was that hovering at locations where predecessors changed flight directions played some role in helping the butterflies to perceive such chemicals and orient themselves. Thus, it seems possible that male butterflies use both visual and chemical signals to follow or pursue one another. On other occasions, usually away from flowers, I was in doubt whether or not butterflies were in following activities, for they were far apart, or just orienting to shared feeding routes that shorten the distance between feeding patches (Ehrlich & Gilbert 1973). It still remains to confirm and identify chemicals utilized by butterflies to follow one another, and document the advantage(s) of engaging in pursuing activities. In two additional cases of pursuing flights, only followers were caught (an I male and an IW male; groups 9 and 10 in Table 1).

These examples suggest that *H. ethilla* has evolved sophisticated forms of following behavior, uncommon in other butterfly taxa, which may be used to transmit information on the location of food resources. However, the fact that both leader and follower butterflies include several age classes (beyond VF only VW individuals were not found) suggest that whatever information may be transmitted is not necessarily addressed to younger butterflies. This larger demographic set may consist of distinct, as in the case of "long distance" flights, or same generation, as in the case of the "acrobatic" and "pursuing" flights, individuals. It seems therefore that information transmission in *Heliconius* butterflies may involve a more extensive network than that originally conceived for the simple education of young butterflies. Cooperative interactions of this kind are expected to be facilitated by relatively high levels of kinship, a possibility that has been suggested in *Heliconius* populations (Benson 1971; Turner 1981; Mallet & Singer 1987).

The fact that only males were observed to engage in following activities suggests they have evolved more developed forms of social behavior than females, which do not seem to cooperate with other females in laying eggs (females usually oviposit only 1 or 2 eggs under young leaves or tendrils of *Passiflora*; Brown 1981) and do not seem to participate in any following activity reported here. Male-restricted social behavior is also reported for *Actinote surima surima* (Shaus) 1902 (Heliconiinae) in which only males join communal roosts (Paluch *et al*. 2005). The possibility that social interactions are also restricted to males in the case of *H. ethilla* is, therefore, a real one, and should be further investigated.

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