# Why do the ithomiines (Lepidoptera, Nymphalidae) aggregate? Notes on a butterfly pocket in central Brazil

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ABSTRACT. Why do the ithomiines (Lepidoptera, Nymphalidae) aggregate? Notes on a butterfly pocket in central Brazil. This study provides information on the species composition and the number of butterflies in different phases of an ithomiine aggregation during the 2004 dry season in central Brazil, and tests some hypotheses concerning the pocket formation. The results obtained suggest that ithomiine pockets constitute primarily an adaptation of butterflies to the adverse climatic conditions of the dry season, such as high temperatures and low air relative humidity, rather than the occurrence of large concentrations of adult food resources (flowers visited for nectar were not found in the pocket site) or defense against visually hunting predators (contrary to the prediction tested, the frequency of butterflies bearing birds beak marks on the wings significantly increased along the period of pocket formation, especially in the case of *Mechanitis polymnia*, the most abundant species in the pocket). Other hypotheses concerning the pocket formation are also discussed.

KEYWORDS. Beak marks; insectivorous birds; ithomiine pockets; Müllerian mimicry.

RESUMO. Por que os Ithomiinae (Lepidoptera, Nymphalidae) se agregam? Observações sobre um bolsão de borboletas no Brasil central. Este trabalho apresenta dados sobre a composição de espécies e o número de indivíduos encontrados em diferentes fases de formação de um bolsão de Ithomiinae investigado na estação seca de 2004 em uma floresta de galeria do Brasil central, e testa algumas hipóteses relacionadas à formação do bolsão. Os resultados obtidos sugerem que o bolsão constitui primariamente uma adaptação das borboletas às condições adversas da estação seca, tais como altas temperaturas e baixa umidade relativa do ar, e não como conseqüência de grande concentração de recursos alimentares dos adultos (flores visitadas para obtenção de néctar não foram encontradas na área do bolsão), ou simples defesa contra predadores visualmente orientados (contrariamente à predição testada, a freqüência de borboletas apresentando marcas de bicadas de aves sobre as asas aumentou significativamente ao longo do período de formação do bolsão, especialmente no caso de *Mechanitis polymnia*, a borboleta mais abundante). Outras hipóteses relacionadas à formação do bolsão são também discutidas.

PALAVRAS-CHAVE. Aves insetívoras; bolsão de Ithomiinae; marcas de bicadas; mimetismo Mülleriano.

The ithomiines are forest inhabitants widely distributed over the neotropical region. Most species utilize pyrrolizidine alkaloids as defensive chemicals against predators (Brown *et al*. 1991), show aposematic coloration and participate as models or Müllerian mimics in several mimicry rings (Bates 1862; Brown 1988; Pinheiro 1996, 2007; Becaloni 1997; Willmott & Mallet 2004). The ability of these butterflies to form large aggregations – also known as ithomiine pockets – has long been observed by field naturalists (DeVries 1987), but few attempts have been made to investigate such behavior.

Ithomiine pockets in central Brazil are seen only during the dry season (June-October) and, as in many other parts where these insects occur, usually in shady sites within the gallery forest and close to water courses. These traits suggest that ithomiine butterflies are sensitive to the high temperatures and low air relative humidity that dominate the central Brazil dry season and may actively look for sites where such characteristics remain less extreme during this phase. The aggregations, therefore, could be viewed just as a consequence of many butterflies looking for and concentrating at such forest spots (hypothesis 1). However, several different hypotheses not mutually exclusive have been put forward to explain the aggregating behavior.

The possibility that multi species aggregations in insects and other animals is associated to the occurrence of large concentrations of food resources in some sites (hypothesis 2) has been advanced by several authors (Bradbury 1981; Bradbury & Gibson 1983; Beehler & Foster 1988; Brown 1992). Adult ithomiines usually visit many different flowers to obtain nectar and pyrrolizidine alkaloids (Brown 1985, 1987; Brown *et al*. 1991; Trigo *et al*. 1996). In many cases, it is possible to observe many individuals belonging to different species on a single, very attractive plant, but studies relating the spatial abundance of plants visited for pollen or larval host plants (constituted mainly by Solanaceae and Apocynaceae; see Drummond & Brown 1987; Freitas 1993) and the formation of Ithomiine pockets remain scarce.

Given that gregariousness in both larvae and adult butterflies evolved mainly in aposematic and chemically defended species (Fisher 1930; Sillén-Tullberg 1988; Clark & Faeth 1997) it is possible that the aggregation itself may enhance protection from insectivorous birds (hypothesis 3) in several different ways. The aggregation of aposematic butterflies obviously increases the strength of the warning signal, allowing predators more readily associate the butterflies color pattern and unpalatability, and making the pattern more memorable, avoiding the need of future attacks on butterflies (Gagliardo & Gilford 1993; Mappes & Alatalo 1997; Riipi *et al*. 2001; Beatty *et al*. 2005). It is possible therefore to predict that butterflies should be more attacked by birds at initial phases of the aggregation (when local insectivorous birds are still learning to associate butterfly chemical defenses and color patterns, and the pocket population size is small), and less attacked at the final phase (when birds probably already learned to avoid the butterflies on sight and the aggregation reaches is maximum population numbers).

Other hypothesis concerning the pocket formation is furnished by Haber (1978), who suggested that Ithomiine pockets constitute mating displays or leks (hypothesis 4). According to this author the aggregation is initiated by a few males sitting on leaves and exposing the androconial hairs to release a pheromone derived from the pyrrolizidine alkaloids. The pheromone attracts both males and females of their own species, as well as other ithomiine species inhabiting the same place. However, we have some doubts whether such mating aggregations do correspond to true dry season aggregations or another kind of aggregation exhibited by ithomiines.

This study reports some data on the species composition and abundance of butterflies in different phases of an ithomiine pocket at Parque Estadual da Serra de Caldas Novas (PESCAN, GO) in the 2004 dry season. The predictions that ithomiine pockets occur in sites with highest relative humidity and lowest air temperatures in the gallery forest (hypothesis 1), or sites with large concentrations of adult food resources (hypothesis 2), and whether or not beak mark frequencies decrease along the period of pocket formation (hypothesis 3) are tested.

## MATERIALS AND METHODS

Field work was conducted at the Parque Estadual da Serra de Caldas Novas (PESCAN), Goiás State, Brazil (17º 46' S; 40º 39' W). The park is dominated by different physiognomies of cerrado vegetation, containing also a gallery forest along the Cascatinha stream where an ithomiine pocket distributed over a 0.5 ha was investigated.

A mark-release-recapture census was conducted for two consecutive days each month (6 h/day; 36 h total sampling time) in August (5$^{th}$ and 6$^{th}$), September (8$^{th}$ and 9$^{th}$) and October (16$^{th}$ and 17$^{th}$) 2004. Butterflies were captured with entomological nets and individually marked with a number on the underside of the forewings with permanent black ink, felt-tipped Sharpie pen. For each capture event the species, sex, and the presence of birds' beak marks were recorded. Beak marks included both beak impressions and tears. To avoid mistakes only the impressions where a birds' beak shape or part of it was clearly delineated on the wing, and tears trespassing at least one major butterfly wing vein were considered (Benson 1972). Population sizes were estimated for each species and sex by the Lincoln-Bailey method (see Southwood 1971). Air temperature and relative humidity measures were taken on different day times in three locations in the study site corresponding to the aggregation center, the border and outside the aggregation, a few meters away along the gallery forest. During butterfly sampling and on five additional days in August (from 7$^{th}$ to 11$^{th}$) we tried to observe and quantify events of courtship or mating among butterflies, the species and frequency of flower visitation by butterflies, as well as oviposition by females.

## RESULTS

A total of 554 individual butterflies in 12 species were captured, marked and released inside the ithomiine pocket in the three sampling periods conducted in August, September and October 2004 (Table 1). Recaptures between different sampling periods were obtained only in September when 8 males (8,9 %) and 9 females (10,5 %) of *Mechanitis polymnia* and 1 male (14,3 %) and 4 females (30,8 %) of *Dircenna dero* marked in August were found. Two species, *Placidina euryanassa* and *Mcclungia cymo,* were found only in October and probably did not participate in the pocket. Except in the case of species poorly represented, such as *Mechanitis lysimnia*, *Placidina euryanassa,* and *Mcclungia cymo*, the sex ratios obtained on the number of marked butterflies did not differ from unity in all other species (Table 1).

The total number of butterflies in the pocket (all species pooled) and the estimated number of males and females *Mechanitis polymnia* - the most abundant species in the pocket – are shown in Figure 1. In both cases an increasing number of butterflies were observed from the beginning of the pocket formation probably in early July (on 25$^{th}$ July a small group of butterflies in the Cascatinha trail was observed by the park field guides) through August and September, when the total population size reached a peak of 2.281 ± 1.045 butterflies. Population numbers probably remained high in early October, but on 12$^{th}$ a strong rainfall was observed in the park region, marking the end of the dry season and leading to the pocket dissolution. By this time few ithomiines were found in the

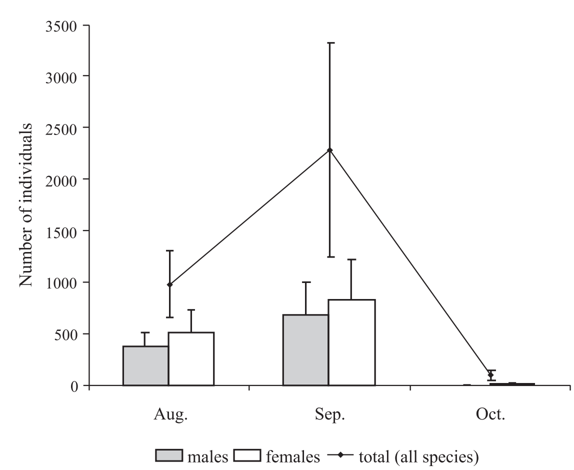


Fig. 1. Estimated number and standard errors of males and females *Mechanitis polymnia* and the total number of butterflies (all species and sexes pooled) during pocket formation (Aug. and Sep.) and just after the pocket dissolution (Oct.) at Parque Estadual da Serra de Caldas Novas (GO) in the 2004 dry season.

pocket site and *Aeria elara* became the most abundant species.

Data concerning air temperature and relative humidity at different day times in three sites corresponding to (1) the aggregation center, (2) the border and (3) outside the aggregation are shown in Figure 2. The lowest air temperatures and highest relative humidity estimates were obtained at the pocket center, while an inverse situation was found outside the aggregation. With few exceptions, data involving the pocket border were clearly intermediate between the center and outside the pocket.

As a general trend butterflies bearing birds' beak marks were relatively rare or absent in several species poorly represented in the pocket, such as many butterflies exhibiting a predominantly "transparent" wing (usually mixed with black stripes and varying portions of white, orange, or yellow) such as *Dircenna dero* (4,6%, n = 65), *Heterosais edessa* (3,2%, n = 31), *Pseudoscada acilla* (5,9%, n = 17) and *Hypoleria sarepta* (9,1%, n = 11), as well as in the small and predominantly pale green *Aeria elara* (2,4%, n = 41), but common in butterflies of the tiger mimicry ring (predominantly black, yellow, white, and orange) such as *Mechanitis polymnia* (30,2%, n = 367), *Mechanitis lysimnia* (33%, n = 3), and *Tithorea harmonia* (25%, n = 8). Comparisons involving the frequency of *Mechanitis polymnia* butterflies bearing beak marks showed no differences between sexes (2 x 2 Contingency Table test with Yates' correction, 1 d.f.: $X^2_{adj.} = 3.803$, $P > 0.05$), but differed significantly between months (August and September; $X^2_{adj.} = 9.19$, $P < 0.01$ for males; $X^2_{adj.} = 8.85$, $P < 0.01$ for females; see Figure 3), showing that beak mark frequencies significantly increased along the period of pocket formation, when butterfly population densities also increased (from 886 ± 261 in August to 1.574 ± 569 butterflies in September).

Events related to feeding by adult butterflies were never observed (in fact, we did not notice a single flower such as many Asteraceae, Verbenaceae, Compositae and many others usually visited by adult ithomines; Vasconcellos-Neto 1980; Freitas 1993; Trigo *et al*. 1996) in the pocket site. Yet, courtship or mating, and oviposition by females were also not observed during the butterfly sampling days and on five additional visits to the study site in August.

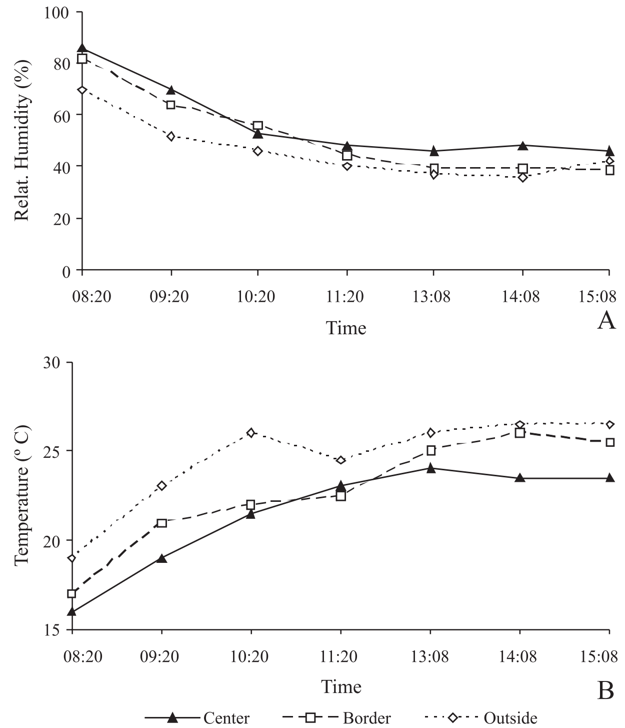


Fig. 2. (A) Relative humidity and (B) air temperature at different day times in three forest sites corresponding to the center, the border and just outside the ithomiine pocket at Parque Estadual da Serra de Caldas Novas (GO) in the 2004 dry season.

## DISCUSSION

Although some butterflies like *Placidina euryanassa* and *Mcclungia cymo* were observed only after the period of pocket formation in October (Table 1), it is possible that these, and virtually all ithomiines, participate in dry season aggregations of this kind. Vasconcellos-Neto (1980) states that *Aeria olena* do not participate in ithomiinae pockets, but P. C. Motta (pers. comm.) found evidence that this butterfly also form aggregations. Several other ithomiines commonly found in

Table I. Species and number of butterflies captured and marked in the ithomiine pocket at Parque Estadual da Serra de Caldas Novas (GO) from August to October 2004. M= males; F= females. The total number of males and females are compared ($X^2$ test; 1 d. f.) to a 1:1 sex proportion.

| SPECIES AND SUBSPECIES | AUG. | | SEP. | | OCT. | | TOTAL | | $X^2$ test |
|---|---|---|---|---|---|---|---|---|---|
| | M | F | M | F | M | F | M | F | *P* |
| *Mechanitis polymnia casabranca* Haensch, 1905 | 90 | 86 | 84 | 97 | 1 | 9 | 175 | 192 | *P*>0.05 |
| *Dircenna dero dero* (Hübner, 1823) | 7 | 13 | 20 | 22 | 1 | 2 | 28 | 37 | *P*>0.05 |
| *Aeria elara elarina* (Oberthür, 1879) | 3 | 5 | 2 | 7 | 10 | 14 | 15 | 26 | *P*>0.05 |
| *Heterosais edessa* (Hewitson, [1855]) | 1 | 1 | 13 | 16 | - | - | 14 | 17 | *P*>0.05 |
| *Pseudoscada acilla quadrifasciata* Talbot, 1928 | 6 | 7 | 2 | 2 | - | - | 8 | 9 | *P*>0.05 |
| *Hypoleria sarepta goiana* d'Almeida, 1951 | 4 | 2 | 1 | 4 | - | - | 5 | 6 | *P*>0.05 |
| *Tithorea harmonia pseudethra* Butler, 1873 | 2 | 2 | 1 | 3 | - | - | 3 | 5 | *P*>0.05 |
| *Ithomia agnosia agnosia* (Hewitson, [1855]) | - | - | 3 | 2 | - | - | 3 | 2 | *P*>0.05 |
| *Hypoleria lavinia consimilis* Talbot, 1928 | 1 | - | 1 | 2 | - | - | 2 | 2 | *P*>0.05 |
| *Mechanitis lysimnia lysimnia* (Fabricius, 1793) | 1 | - | 2 | - | - | - | 3 | - | - |
| *Placidina euryanassa* (Felder & Felder, 1860) | - | - | - | - | 1 | - | 1 | - | - |
| *Mcclungia cymo salonina* (Hewitson, 1855) | - | - | - | - | 1 | - | 1 | - | - |
| TOTAL | 115 | 116 | 130 | 155 | 13 | 25 | 258 | 296 | Σ554 |

central Brazil (Emery *et al*. 2006) not observed at PESCAN in 2004 were also found in other ithomiine pockets in southeastern Brazil (Vasconcellos-Neto 1980) or in previous years at PESCAN (the best example is *Hypothyris ninonia daeta*, by far the most abundant butterfly in the 2003 dry season, when *Mechanitis polymnia*, the most abundant butterfly in 2004, was absent). This also suggests that ithomiine population dynamics change a lot in different years.

Most evidence obtained in this study indicates that ithomiine pockets primarily occur as an adaptation of butterflies to adverse climatic conditions of the dry season (hypothesis 1), rather than large concentrations of adult food resources (hypothesis 2), or defense against insectivorous birds (hypothesis 3). In addition to the fact that ithomiine pockets occur only during the dry season, in shady conditions and often close to water courses, this study showed that pockets are centered in sites with highest relative humidity and lowest air temperatures in the gallery forest, and that the first rainfall after a long dry season may determine the pocket dissolution. Haber (1978) and Vasconcellos-Neto (1980) also observed a strong reduction in population numbers after a strong rainfall in their respective study sites, but the former attributed such reduction to butterfly mortality whereas the latter attributed it to dispersal, a conclusion that we also agree. To our view the fact that rainfall may determine the pocket dissolution constitutes strong evidence that climatic factors, especially relative humidity, are responsible for the pocket assemblage. Further evidence that pocket formation is associated to low relative humidity comes from observations by Freitas (1996) who reports that in coastal forests of eastern Brazil that receive rainfall all year round ithomiine pockets were never observed along a six year study period.

As a matter of fact the pocket investigated seemed more similar to a climatic jail imposed on butterflies – and lots of potential predators spying around - than a place for feeding, ovipositing or mate finding. This obviously does not imply that such behaviors do not occur in ithomiine pockets in general. Vasconcellos-Neto & Brown (1982) observed not only many instances of mating among butterflies in different ithomiine pockets, but also the occurrence of several hybrids between *Mechanitis polymnia casabranca* and *Mechanitis lysimnia lysimnia*. According to these authors, the occurrence of hybrids is common in dense, dry season populations of these butterflies. Vasconcellos-Neto (1980) also observed many flowers visited by butterflies, as well as many larval host plants inside a pocket containing more than 20.000 butterflies and 23 species in southeastern Brazil. However, the fact that feeding, ovipositing and mating were not observed in the pocket investigated suggests that these factors do not play a fundamental role in determining the pocket assemblage. This, however, deserves further investigation.

Whether ithomiine pockets work as a defensive strategy of butterflies against insectivorous birds should be viewed with caution. The results obtained on beak mark frequencies showed that sampling of butterflies by birds is intense - at least among the butterflies in the tiger mimicry ring - and tends to increase along the aggregation period. Previous hypothesis concerning the advantage of gregarious over isolated

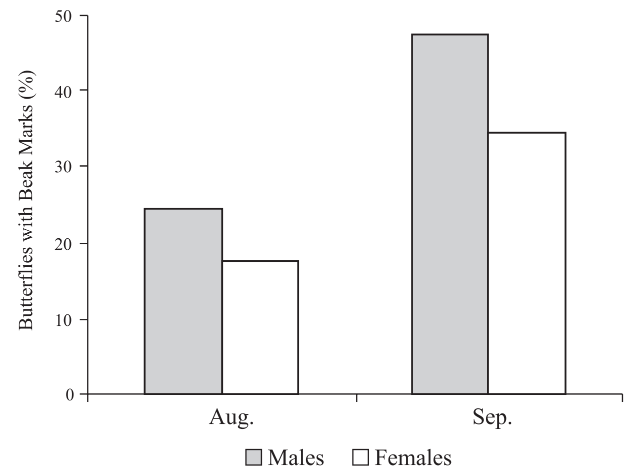


Fig. 3. Frequency (%) of *Mechanitis polymnia* butterflies bearing birds' beak marks (impressions and tears) in different phases of an ithomiine pocket at Parque Estadual da Serra de Caldas Novas (GO) in the 2004 dry season.

aposematic prey (Gagliardo & Gilford 1993; Mappes & Alatalo 1997; Riipi *et al*. 2001; Beatty *et al*. 2005) led us to predict that sampling by predators should decrease along the period of pocket formation, but the results obtained on birds' beak marks did not corroborate such prediction. A relatively high frequency of beak marks at the initial phase of the aggregation (August 2008) might be expected not only as a consequence of the learning process of local predators, but also by the fact that *M. polymnia* butterflies are very vagile (some butterflies were observed to travel almost two km in less than 24 h interval; Vasconcellos-Neto, pers. comm.; see also DeVries 1987), and individuals were probably exposed to many different predators before reaching the pocket site. However, the fact that beak marks increased along the period of pocket formation (from August to September 2008) indicate that most butterflies were attacked inside the pocket site. In fact, several birds already identified as true butterfly predators such as the *Galbula ruficauda* (Benson 1972; Pinheiro *et al*. 2003; Langham 2006; but see Pinheiro 2004), *Tyrannus melancholicus* (Pinheiro 1996, 2003), *Megarynchus pitangua* and several other tyrant-flycatchers (Cook *et al*. 1976) were observed on different occasions in the pocket site. A motmot (probably *Momotus momota*, see Marden 1992) was observed to attack and capture a *Mechanitis polymnia* (the bird flew away with the butterfly). Brown & Vasconcellos-Neto (1976) also observed a tanager (*Pipraeidea melanonota*, Thraupidae) attacking and consuming many *Mechanitis polymnia* in a butterfly pocket in southeastern Brazil. Attacks by insectivorous birds on aposematic butterflies were also observed in the overwintering colonies of monarch butterfly in Mexico (Fink *et al*. 1983; Brower & Calvert 1985; Brower 1988), which probably constitutes the largest assemblage of aposematic butterflies in the world. It seems therefore that aggregations of aposematic butterflies usually attract the attention of a large number of potential predators. Although Riipi *et al*. (2001) found that multiple benefits of gregariousness cover detectability costs in aposematic prey, it is possible that the ithomiine pocket investigated attracted not only the attention of local predators, but of many other insectivorous birds living in the neighborhood or just passing close to the pocket, producing an increasing number of beak marks along the whole period of pocket formation, as observed in this study. Future studies involving true mortality rates in gregarious and isolated aposematic prey will help to elucidate whether gregariousness helps to protect aposematic butterflies from visually hunting enemies.

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