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Large-sized insects show stronger seasonality than small-sized ones: a case study of fruit-feeding butterflies

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Animal species have a restricted period during the year when conditions for development are optimal, and this is known as the temporal window. Duration of the temporal window can vary among species, although the causes of variation are still poorly understood. In the present study, examining butterflies, we assume that the temporal window duration is correlated with the seasonal period of flight (termed seasonality). To understand how species characteristics are correlated with this, we examine whether there is a relationship between body size and length of flight period of fruit-feeding butterflies in forest fragments, and whether these two parameters have a phylogenetic signal. Using wing size as a measure of body size and the period of adult flight as a measure of seasonality, we found significant positive correlations between body size and seasonality among subfamilies but not within subfamilies. We also found a clear phylogenetic signal in size but not in seasonality. The results obtained suggest the existence of a trade-off between insect size and seasonality, with size limiting flight period length. The relationship between body size and seasonality and the synchrony with their resources may be one factor explaining the vulnerability of large insects to forest fragmentation. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, ••, ••–••.

ADDITIONAL KEYWORDS: circular analyses – conservation – fragmentation – nymphalidae – phenology – temporal variation.

INTRODUCTION

Seasonality is an important and relatively well studied aspect of insect biology (Wolda, 1988). Even in localities with little seasonal climatic variation, seasonal fluctuations of arthropods have been reported (Ebert, 1969; Richards & Windsor, 2007). Such seasonality in insects could be explained by several different factors. The physical conditions, for example, have a non-uniform distribution during the year, and insects could emerge when temperature and humidity are favourable to activities such as flight, courting, mating or oviposition (Torres-Vila & Rodríguez-Molina, 2002). Natural enemies also affect insect seasonality. For example, recent studies have suggested that herbivorous insects avoid emerging simultaneously with their parasitoids (Morais, Diniz & Silva, 1999; Barbosa & Caldas, 2007). Finally, the seasonal variation in resource availability is extremely important, and insect activity should be synchronized with both larval and adult resources because asynchrony with these resources has a deleterious effect on their fitness (Lawrence, Mattson & Haack, 1997; Torres-Vila *et al*., 2005; Hamer *et al*., 2006; Kursar *et al*., 2006; van Asch & Visser, 2007).

Even if some resources are available during all the year (e.g. leaves), the quality of these resources varies over time. In most environments, there is a restricted period in the year when conditions are most favourable, called the 'temporal window' (*sensu* Hunter & Lechowicz, 1992). For herbivorous insects, this period is characterized by an optimal combination of physical conditions, enemy-free space, and

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*Corresponding author. E-mail: biodbr@yahoo.com.br resource availability. Thus, any asynchrony with this phenological window can have severe negative consequences on herbivore fitness (Begon & Parker, 1986; Torres-Vila & Rodríguez-Molina, 2002; Visser & Both, 2005; van Asch & Visser, 2007). Consequently, evolutionary pressures that synchronize insect emergence with these windows are expected to occur. Because larger insects need to allocate more nitrogen per egg (García-Barros, 2006), and require more resources to complete their life cycle, it is reasonable to surmise that larger insects may appear in shorter periods comparative to smaller ones. For butterflies, this period is the flight period of adults.

In the Atlantic Forest, the production of new leaves occurs in restricted periods. This resource has higher levels of nitrogen, sugar, and other nutrients than old leaves (Morellato *et al*., 2000), which may result in differences in larval performance through the year (Schroeder, 1986). In addition, the availability of adult resources (e.g. decaying fruits) is not evenly distributed through out the year (Morellato *et al*., 2000). The objective of the present study is to test whether there is a relationship between body size and flight period of adult butterflies in a fragmented landscape in the Brazilian Atlantic Forest. In the present study, we assume that the duration of the temporal window is correlated with the flight period of the adults (hereafter called seasonality). We used fruit-feeding butterflies (*sensu* Freitas & Brown, 2004) as a model group of insects because of their easy sampling, well resolved taxonomy, sensitivity to habitat disturbance, and positive correlation with total butterfly diversity (Brown & Freitas, 2000; Horner-Devine *et al*., 2003; Brown, 2005).

MATERIAL AND METHODS

Study site

Field work was carried out in São Luiz do Paraitinga county, São Paulo State, Southeastern Brazil (23°20' S, 45°20' W). The average altitude is 740 m and the relief is composed of a complex landscape with rolling hills, steep escarpments, and narrow deep valleys (MME 1983). The climate is humid with an annual mean temperature of 20 °C (monthly minimum 12 °C, maximum 27 °C) and mean annual rainfall of 1340 mm (MME 1983).

The original vegetation was primarily dense humid forest (MME 1983); however, the process of forest fragmentation had drastically changed the land cover in the region (Petrone, 1959; Dean, 1997). Currently, a large part of the native vegetation has been removed, with small patches of disturbed forest scattered in a matrix of ranching areas and abandoned pastures with some areas of non-native *Eucalyptus* plantations.

Study group

Among the several insect groups that can be used as ecological models, butterflies are ideal for study. They are relatively large, conspicuous, easy to sample, and have a well known taxonomy. Accordingly, butterflies are among the most studied insects. Butterflies offer great potential insights into patterns of diversity and conservation of insects and their habitats (DeVries, 1987; Brown, 1991; DeVries, Murray & Lande, 1997; Bonebrake *et al*., 2010).

Tropical butterflies fall naturally into two adult feeding guilds (DeVries, 1987). The first guild (i.e. those adult butterflies that feed primarily on flower nectar) includes most species in the six known butterfly families. The second guild (i.e. those whose adults gain virtually all of their nutritional requirements by feeding on rotting fruits or plant sap) is represented mainly by species in the subfamilies Biblidinae, Charaxinae, Morphinae, Satyrinae, and the tribe Coeini (Nymphalinae).

Sampling methods

Ten forest fragments were selected for sampling butterflies from June 2004 to May 2005. Sampling was conducted *sensu* Ribeiro *et al*. (2008, 2010), where each fragment received five portable traps baited with a mixture of banana and sugar cane juice fermented for 48 h. In each month, the traps remained open in the field for 8 days and were visited at 48-h intervals. The traps were located along a linear transect, 30 m apart from each other.

Statisitical analysis

To test the relationship between body size and seasonality, we used the length of the mean vector (r) as a measure of seasonality (Zar, 1999), which ranges between 0 and 1 and describes the temporal pattern of occurrence of the species throughout the year. Values close to 0 indicate that the probability of occurrence is the same in every day of the year (or any other unit of time) and values close to 1 indicate that all butterflies occur in the same day of the year. The length of the mean vector was calculated with PAST software (Hammer, Harper & Ryan, 2001). We used forewing length as a body size measure (Miller, 1977), and $\log_{10}$ transformed the data afterwards. The correlation between wingspan and weight is more than 0.8 in fruit-feeding butterflies (Shahabuddin & Ponte, 2005), making this a robust method for measuring the size of these

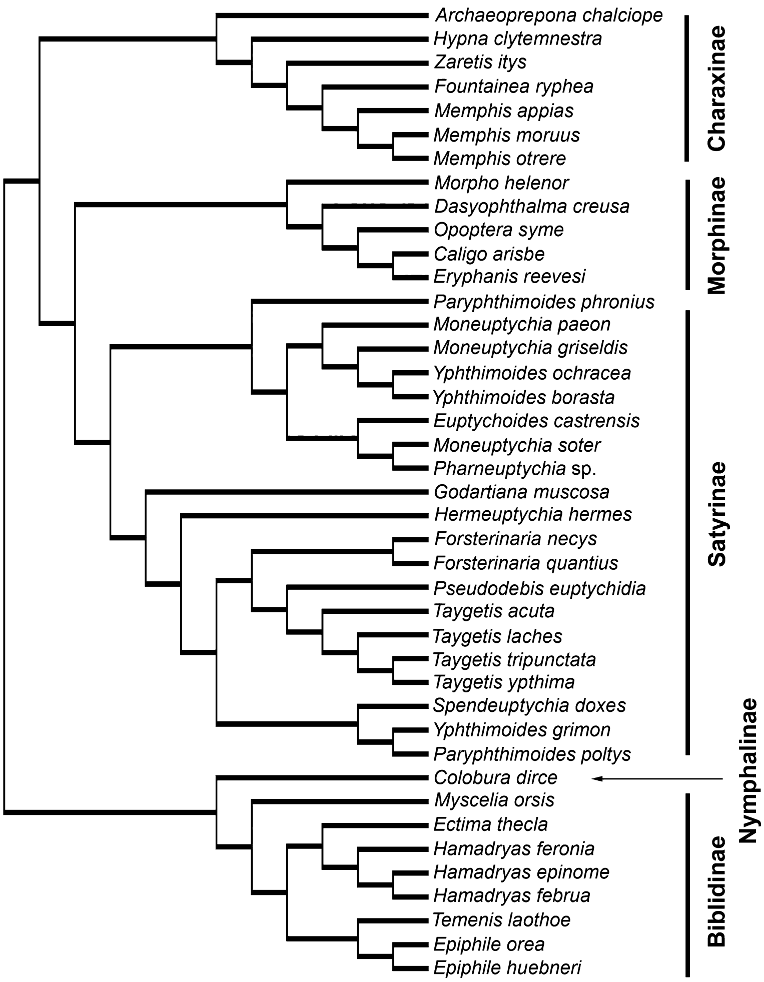

Figure 1. Cladogram of all sampled species in the present study, *sensu* Wahlberg *et al.* (2009).

insects. We used two taxonomic levels to test the correlation between body size and seasonality: (1) subfamilies in the Satyroid lineage of Nymphalidae ('among subfamilies') and (2) species of the most speciose subfamilies (Satyrinae, Morphinae, Charaxinae, and Biblidinae) ('within subfamilies') (butterfly taxonomy *sensu* Lamas, 2004). For the first level, we calculated the average body length and length of the mean vector (*r*) of each subfamily and analyzed the size of subfamilies together and separated by species. At the second level ('within subfamilies'), we calculated $\log_{10}$ of average size in all species that had at least 15 individuals captured, and the length of the mean vector (*r*). The relationship between body size and (*r*) was analyzed through a simple linear regression.

We produced a cladogram of all sampled species based on the results of Wahlberg *et al.* (2009) and on unpublished information provided by Dr Niklas Wahlberg (Fig. 1). We used MESQUITE software (Maddison & Maddison, 2001) to test whether there was a phylogenetic signal in both seasonality and size. Characters were coded as discrete states and ordered on the basis of the minimum model of evolution (see Supporting information, Table S1). We randomized the character states 300 times and optimized them on the cladogram to test whether the observed character states differed from random.

RESULTS

In total, 6488 individuals of 73 butterfly species were captured, belonging to all taxonomic groups of fruit-feeding Nymphalidae: Satyrinae, Morphinae, Charaxinae, Biblidinae, and the tribe Coeini (Nymphalinae).

We found a significant positive correlation between body size and seasonality for subfamilies in the Satyroid lineage in both approaches, using subfamilies

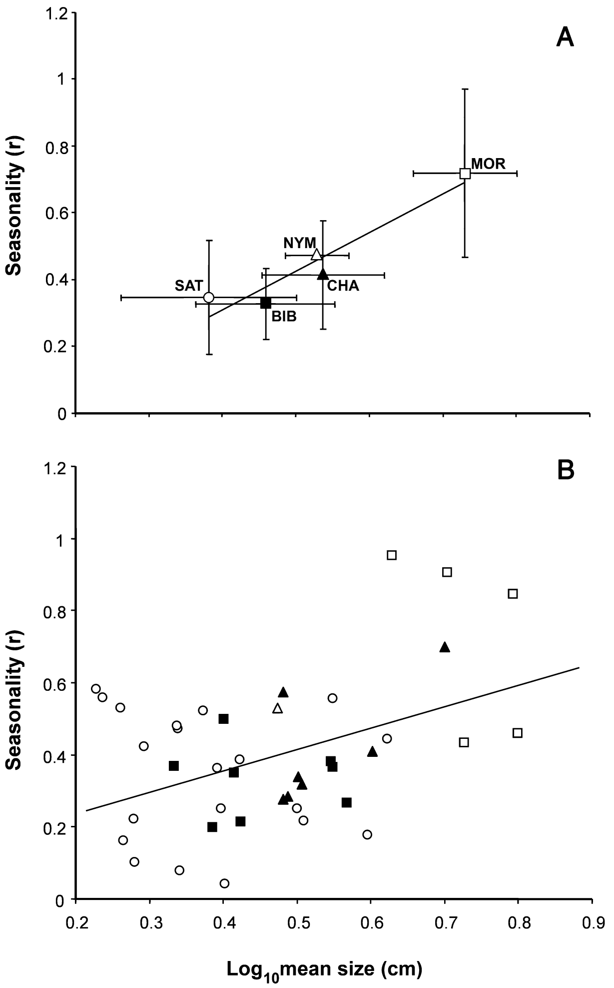

Figure 2. Linear regression between seasonality and mean size of fruit feeding butterflies among Nymphalidae subfamilies: A, subfamilies approach. B, species approach. The seasonality (*y*-axis) is the length of the mean vector (*r*). Mean rrror bars represent the mean ± SD of size. BIB, Biblidinae; CHA, Charaxinae; MOR, Morphinae; NYM, Nymphalinae; SAT, Satyrinae.

($y = 1.1543x - 0.1525$, $R^2 = 0.901$, $P = 0.009$, $N = 5$) (Fig. 2A) and species ($y = 0.553x + 0.1415$, $R^2 = 0.166$, $P = 0.008$, $N = 41$) (Fig. 2B) as unities. By contrast, there was no significant correlation between body size and seasonality in the within subfamilies level (Satyrinae: $y = -1.0986x + 1.5683$, $R^2 = -0.073$, $P = 0.745$, $N = 20$; Morphinae: $y = -1.0986x + 1.5683$, $R^2 = 0.307$, $P = 0.693$, $N = 5$; Biblidinae: $y = -0.0025x + 0.3281$, $R^2 = -0.002$, $P = 0.995$, $N = 7$), except for a marginally nonsignificant relation in Charaxinae ($y = 1.7781x - 0.5854$, $R^2 = 0.707$, $P = 0.07$, $N = 7$) (Fig. 3).

There was a phylogenetic signal in size (observed steps = 14, $P = 0.003$) but not in seasonality (observed steps = 25, $P = 0.76$).

DISCUSSION

One possible explanation for the reported positive correlation between size and seasonality found at the 'among subfamilies' level is the presence of a trade-off between being large and the inability to occur more frequently throughout the year. Subfamilies with larger species demand higher resource levels than subfamilies where smaller species dominate. This may imply an environmental constraint forcing large species to occur in a narrow period when optimal resources are available. In this way, the asynchrony with resources would be more harmful in larger fruit-feeding butterflies than in smaller ones, resulting in heavier evolutionary pressures to enhance synchrony in the subfamilies with larger butterflies. This dependency on superior resources may imply in higher susceptibility to habitat disturbance, as found by Shahabuddin & Ponte (2005) and Uehara-Prado, Brown & Freitas (2007) in fragmented landscapes. Additionally, the degree of larval host plant specialization between small versus large butterfly species is similar, and most species in the study area are specialists and usually restricted to specific plant genera or species (Beccaloni *et al.*, 2008). The suggestion that the degree of specialization could imply in a narrow phenological window is not supported by the studied assemblage. This suggests that large-sized butterflies are possibly more affected by changes in environmental conditions, and more vulnerable to local extinctions from climate change, deforestation, and habitat fragmentation. We could not disregard that other factors, particularly the abundance of natural enemies, which could affect the flight period of butterflies as well as impact on the immature stages (Barbosa & Caldas, 2007). However, these potential interactions need to be explored further through future research.

The absence of a clear relationship between body size and seasonality at the 'within subfamilies' level may be a result of the low variation in size among extant species. Size is a phylogenetic constraint of subfamilies, and the low variation may obscure any potential relationship at this level.

In fragmented landscapes investigated in the present study, it is well known that the fragmentation process changes the abiotic and biotic conditions including vegetation structure and composition (Saunders, Hobbs & Margules, 1991; Tabarelli, Mantovani & Peres, 1999). Herbivores and their hosts could use different environmental cues to control their phenological behaviour (van Asch & Visser, 2007). Despite photoperiod being usually the major environmental signal in insect life-history adaptation (Masaki, 1972; Musolin & Numata, 2003; Burke *et al.*, 2005), some herbivores also use humidity as a phenological trigger, with host plants using photoperiod

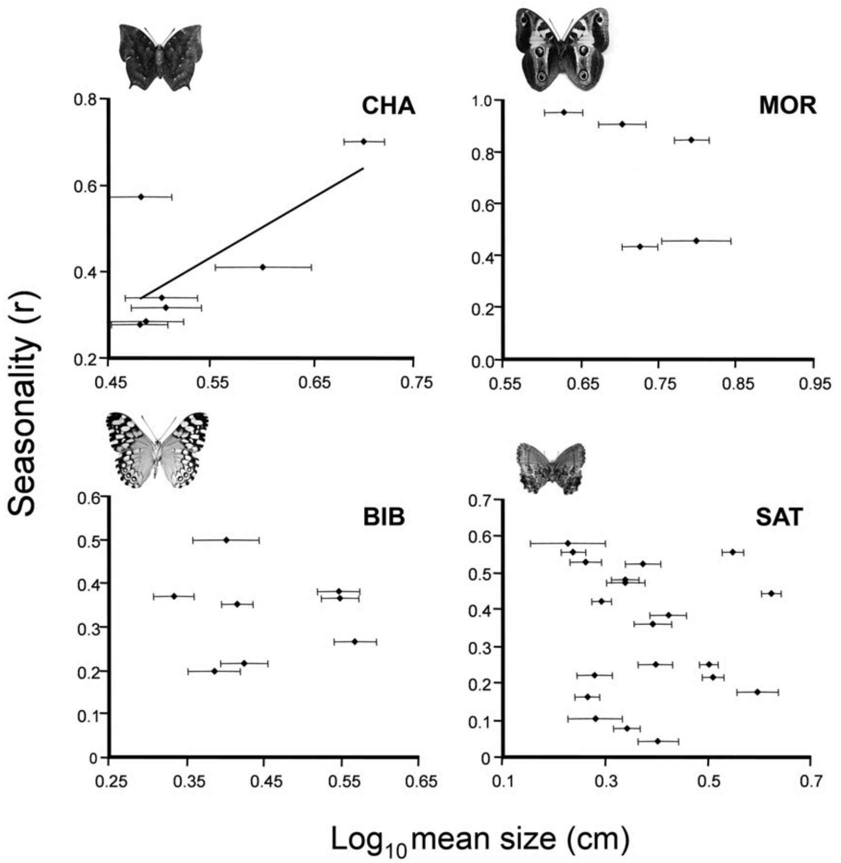

Figure 3. Linear regression between seasonality and mean size of fruit feeding butterflies within Nymphalidae subfamilies. The seasonality (*y*-axis) is the length of the mean vector (*r*). Error bars represent the mean ± SD of size. BIB, Biblidinae; CHA, Charaxinae; MOR, Morphinae; SAT, Satyrinae.

(Sloan, Zimmerman & Sabat, 2006). These two characteristics are strongly correlated in undisturbed habitats; however, the fragmentation process consistently affects the humidity of forests and has no influence on photoperiod. Consequently, the fragmentation process could break the synchrony between those factors. This loss of synchrony can be extremely harmful for herbivores because forest fragmentation represents a rapid ecological process that vulnerable herbivores may be slow to re-synchronize their life cycle against.

The same process that occurs in large fruit-feeding butterflies may occur in other large size insects. Rainio & Niemelä (2003) stated that large carabid beetles are more affected by habitat disturbance than smaller ones because of their poor dispersal ability and the high level of habitat specialization. However, Ishitani, Kotze & Niemelä (2003) found that small carabid beetles are more affected by urbanization than medium-sized ones. In this case, it was suggested that smaller beetles are more specialized, and habitat specialization and dispersal ability could be correlated in different ways with body size in different habitats. These results indicate that body size in carabid beetles is indicative of other biological traits that are correlated with extinction risk. Gibbs & Stanton (2002), studying carrion beetles (Coleoptera: Silphidae) in an urban–rural gradient forest, found positive correlations between body size, habitat specialization and extinction proneness. Nichols *et al.* (2007) reviewed studies with dung-burying beetles in tropical forests (Coleoptera: Scarabaeidae: Scarabaeinae) and demonstrated that habitat disturbance in high levels affects large beetles. Most studies of different families have suggested that the vulnerability of large beetles is correlated with habitat specialization and low dispersal abilities; however, the narrow temporal window could be another important trait leading to this vulnerability. This is a poorly studied topic in beetles and needs further investigation and clarification.

Large species are known to be more vulnerable to anthropogenic disturbance, such as habitat fragmentation, because they reproduce more slowly, requires more energy and resources, and have larger home ranges than small species (Tscharntke *et al*., 2002). However, the results obtained in the present study suggest that a narrow phenological window may be an important characteristic in the vulnerability scenario when considering an insect's life cycle. These results are important for understanding how to optimize insect species conservation in anthropogenic habitats. In light of the impact of global climate change and continued habitat fragmentation on insect phenology, species persistence, especially in tropical regions, is of concern (Deutsch *et al*., 2008; Dingenmanse & Kalkman, 2008; Kurz *et al*., 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean size (cm) and seasonal concentration (*r*) of fruit-feeding butterflies collected in São Luiz do Paraitinga, SP, Brazil. Data are shown by mean (left) and category (right) used in the analysis of the phylogenetic signal trace. Species are ranked by decreasing size in each subfamily.