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# Stay Out (Almost) All Night: Contrasting Responses in Flight Activity Among Tropical Moth Assemblages

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## Abstract

Variations in diel activity among hyperdiverse tropical communities of moths, despite representing a key component of niche partitioning between species, have barely been studied so far. Using light trapping from dawn to sunset over a 1-year period in French Guiana, we investigated these variations within and between two families of moths (Sphingidae and Saturniidae). Our results revealed contrasting patterns in flight activity at night between Sphingidae and Saturniidae. Sphingidae reached their peak in species richness and abundance between 7:00 and 8:00 p.m., followed by a decrease around 11:00 p.m. to midnight, whereas Saturniidae were continuously present throughout the night, with a peak around midnight. In addition, we found changes in diel activity among some of the most common genera in each family, highlighting distinct behavioral, physiological, and functional traits among taxa. Given differences in flight activity at different taxonomic levels, it is strongly recommended to monitor by light trapping throughout the night to effectively sample saturniid and sphingid assemblages, even though the activity of Sphingidae sharply declines after midnight. These results improve the general natural history information of tropical moths and reinforce the need of further research on the ecological and taxonomic consequences of differences in diel activity.

## Introduction

The rates of forest degradation and loss are higher in the tropics than in almost any other ecosystem (Pimm *et al* 2001), and the resulting species extinctions may far exceed the capacity of entomologists to document insect diversity (Lawton & May 1995). We therefore face the urgent need to

gain a better understanding of insect natural history in megadiverse tropical forests, which may improve trapping methodology for ecological and biogeographical studies on insect communities (Novotny *et al* 2005, Rodriguez-Castañeda *et al* 2010). Lepidoptera, including butterflies and moths, represents a charismatic group that holds promise as an indicator of terrestrial ecosystem health and habitat

quality (Bonebrake *et al* 2010). Butterflies have long been used as ecological indicators, and specific sampling protocols have been designed to facilitate comparability and reproducibility of results and account for sampling biases (Pollard 1977, Brown & Freitas 2006, DeVries *et al* 2012). Moths, probably because of their nocturnal activity, have received comparatively less attention from a methodological standpoint, despite being more diverse within communities and easier to sample in large numbers due to their attraction to light.

Monitoring moths by light trapping is a widely used technique (Kitching *et al* 2000, Brehm *et al* 2003 and references therein), which has often been automated (Intachat & Woiwod 1999, Merckx & Slade 2014) to allow better standardization and operability. Alternatively, manual light trap—where the operator manually collects moths on a white sheet—is a long-used technique that has proven highly effective for documenting insect diversity. The main advantages of this technique include (i) attraction of multiple taxa at high density, (ii) manual selection of focal taxa, (iii) preservation of specimen integrity (large species and/or other insects often cause damage to smaller, more fragile species in automated light traps), and (iv) the observation of behavioral features of species (e.g., resting and defensive posture, time of activity). One disadvantage is the need for the operator(s) to stay active all night to account for variation in flight activity time among taxa (Janzen 1984).

Foraging, mate seeking, and finding host plants are the main drivers of moth flight activity (Beck & Linsenmair 2006), and associated traits are under strong selection through abiotic and biotic factors. In addition, differences in timing of arrival to traps might also reflect differences in moth diel activity (Janzen 1984). When the purpose of a study is to sample an entire moth assemblage, the relative abundance of species might be distorted by differences in both the attraction to light and the flight activity. Field entomologists, although aware that certain species can only be successfully captured at a given time of the night, still lack a comprehensive background in natural history for focal insect taxa. So far, little quantitative data on moth flight activity are available in tropical environments (Janzen 1984, but see Beck & Linsenmair 2006), and to our knowledge, no study has been conducted in the Amazon basin.

We present data from whole-night sampling carried out periodically over 1 year in French Guiana. The aim of this study is to determine the variation in diel activity within and between two macro-moth families (Sphingidae and Saturniidae) by means of light trapping and to consider time of arrival at light of each moth as an indicator of its activity time. Because time represents a primary axis of species ecological niche by which moths can partition resources, we expected to

find variations in flight activity at different taxonomic levels. We also explore the extent to which duration of sampling at night affects the observed species richness for our two focal groups to provide practical field information on optimal implementation of manual light trapping.

## Material and Methods

The study was conducted at the Combi Research Center in French Guiana (Sinnamary, altitude of 48 m asl, 5°18'24.73" N, 52°55'26.37" W). The area encompasses contrasting vegetation types from pristine to secondary lowland tropical forests, low-impact logging, and plantation experiments. The climate during the study period was within the mean range in precipitation compared to the last 30-year dataset available for this site (annual precipitation=2974 mm). We used one standard light trapping procedure consisting of two 125-W mercury vapor bulbs powered by a portable generator with a white sheet used as a reflector installed on each side. All specimens of Saturniidae and Sphingidae were sampled throughout one entire night (from 6:30 p.m. to 6:00 a.m.) each month over an 11-month period between November 2010 and September 2011 (with one exception in March 2011 due to a generator problem). Light traps were set up at the same location each month, covering a pristine *terra firme* clay forest. All moths were sampled by hand as soon as they arrived to the sheet, injected with ammonia and then stored and dried in labeled paper envelopes. We immediately noted species identification, arrival time, and sex for all specimens. Each individual was identified to species by FB and added to French Guiana databases of CIRAD, SEAG, and Labex CEBA institutions (Online Supplementary Resource S3).

## Data analysis

We used the accumulated abundance of each species collected per hour of light trapping during the 10 months of monitoring, from 6:00 p.m. to 6:00 a.m. (named t1 to t12). We analyzed differences in the number of species and individuals between families by nonparametric Mann-Whitney tests and estimated their kernel density. Our null hypothesis was that the distribution of the number of species (or individuals) throughout the night was identical between Saturniidae and Sphingidae. We analyzed the variation in flight activity both among and within genera with a nonparametric Kruskal-Wallis rank sum test. We excluded subfamilies where only one genus was sampled and then graphically computed the distribution of each species ordered by their median time of appearance at light within a given genus. To explore how

the duration of light trapping might influence species richness, we used a species accumulation curve that represents the rate of new species arrival with increasing sampling effort (i.e., number of hours of collection). Analyses were not separated by sex due to the low sample sizes of females (less than 10% of specimens; see Janzen 1984, Kitching & Cadiou 2000, Brehm 2002 for similar rates).

## Results

Overall, we sampled 394 individual moths representing 118 species from eight subfamilies of Saturniidae and Sphingidae (Online Supplementary Resource S3). We found significant differences in flight activity between Sphingidae and Saturniidae for both the number of individuals and species (Fig 1). Sphingidae reached their peak in species richness and abundance between 7:00 and 8:00 p.m., followed by a decrease around 11:00 p.m. to

midnight (i.e., 6 h past sunset). The highest density of sphingids was sampled during the first half of the night (t2–t5). In contrast, Saturniidae were continuously present throughout the night (from t2 to t9), although the peak of both species richness and abundance occurred around midnight (t6). The species accumulation curve confirmed that new moth species were attracted until 4:00 a.m. (t9), subsequently reaching a plateau (Online Supplementary Resource S1). At the genus level (Fig 2), our results showed significant contrasts in flight activity among genera in four of the six subfamilies (Ceratocampinae, Hemileucinae, Macroglossinae, and Sphinginae). Some saturniid genera showed broader variations of arrival time such as *Citheronia*, *Othorene* and *Adeloneivaia* (Ceratocampinae), *Hylesia*, and *Automeris* and *Automerina* (Hemileucinae). Also, the sphingid genera *Xylophanes*, *Pachylia*, *Isognathus*, and *Callionima* (Macroglossinae) exhibited relatively wide variation in flight activity. In contrast, Arsenurinae and Smerinthinae did not differ in the timing of flight activity among gen-

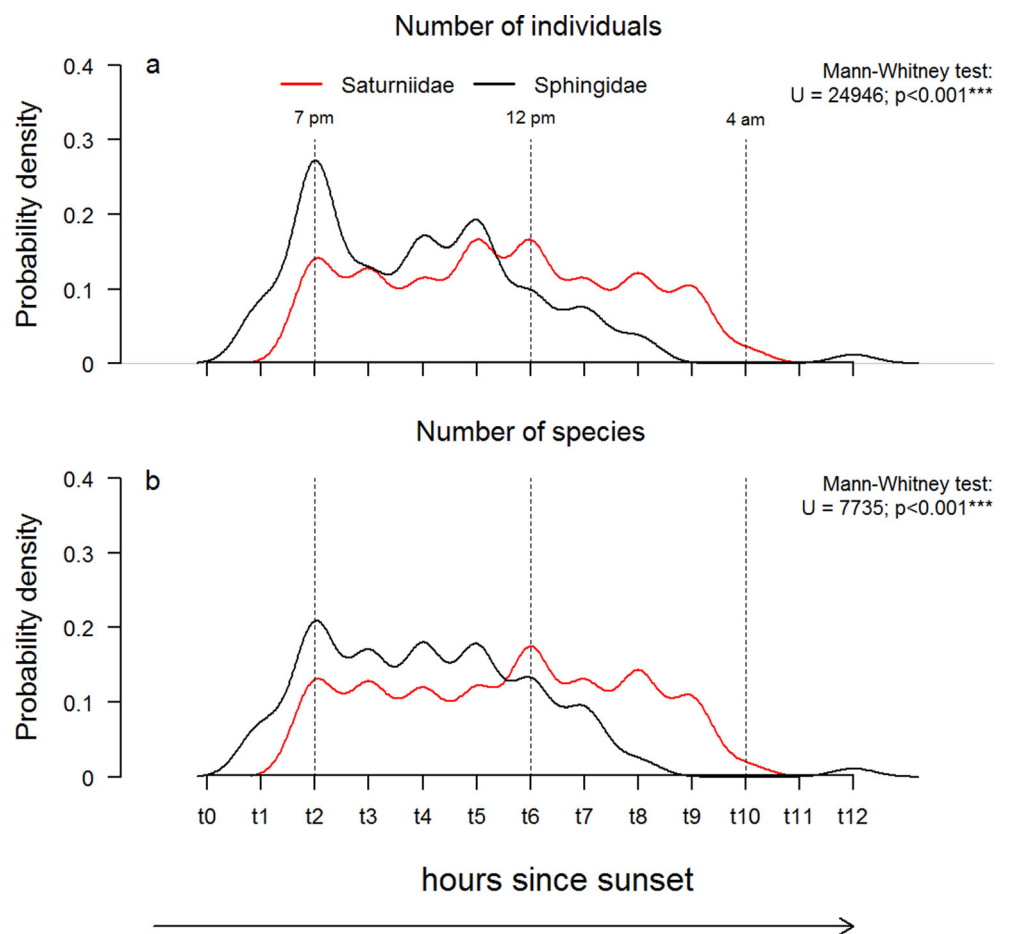


Fig 1 Relative number of individuals (a) and species (b) of saturniids (red line) and sphingids (black line) as a function of the number of hours since sunset. Density curves were estimated using a Gaussian kernel and a 0.4 bandwidth. Results of the nonparametric Mann-Whitney test showed significant differences between families for both metrics.

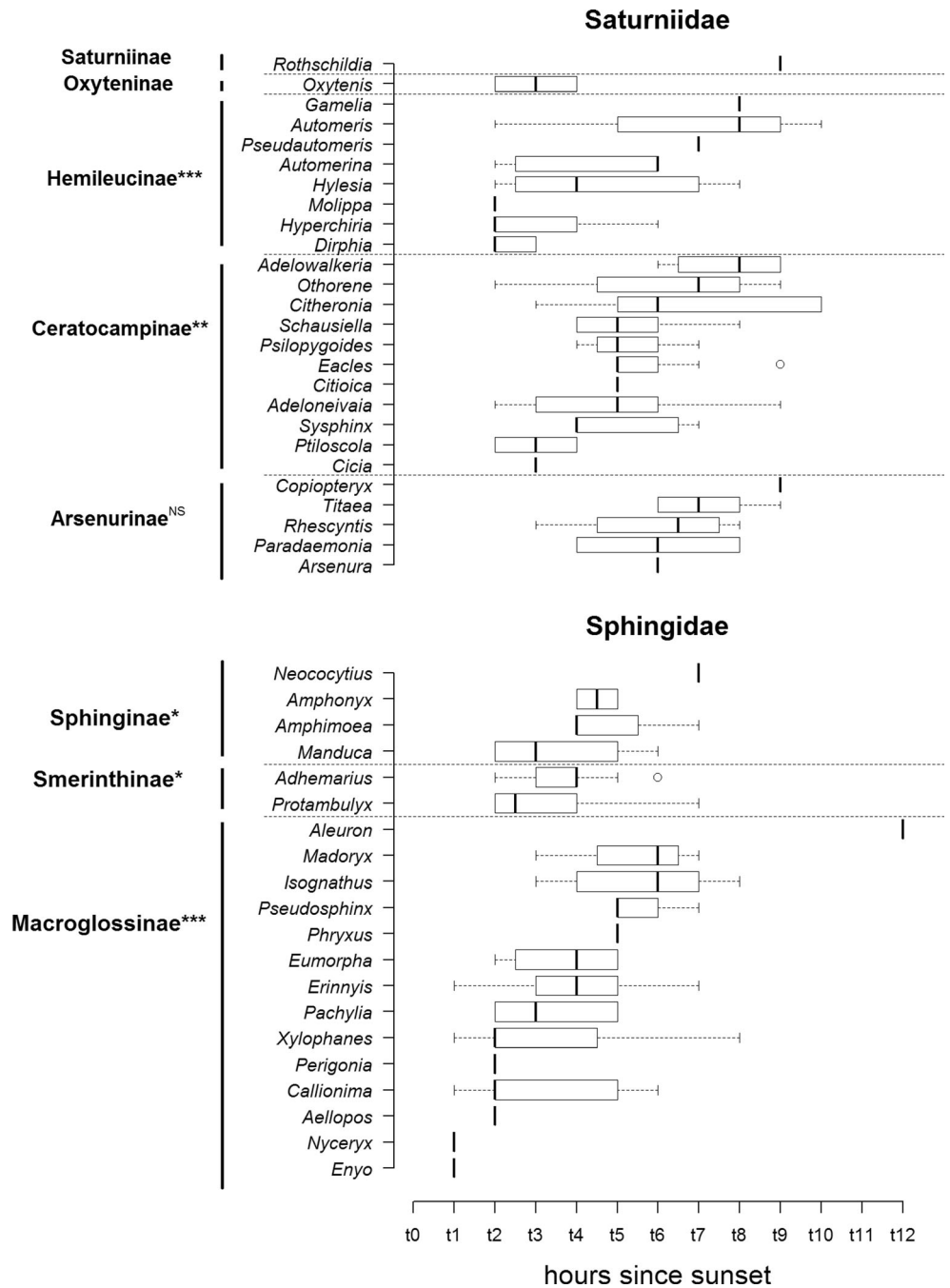


Fig 2 Differences among genus in flight arrival time. Results of nonparametric Kruskal-Wallis tests performed within the six subfamilies are shown for differences among genus for a given subfamily. *NS* non-significant, *single asterisk* significance at the 0.05 level, *double asterisks* significance at the 0.01 level, *triple asterisks* significance at the 0.001 level.

era such as *Protambulyx* and *Adhemarius*, the only two Smerinthinae in French Guiana. In Macroglossinae, flight activity was restricted within the first half of the night but also showed contrasting results among genera. At finer taxonomic level, we found striking contrasts in flight activity among species of *Automeris*, *Xylophanes*,

*Isognathus*, and *Manduca* (Fig 3), but no differences in diel activity among species of *Adeloneivaia*, *Eacles*, *Automerina*, *Hylesia*, and *Erinnyis*. Our analysis within *Automeris*, one of the most diverse and abundant genus sampled, detected highly divergent flight activities, with species only active during the early hours of night,

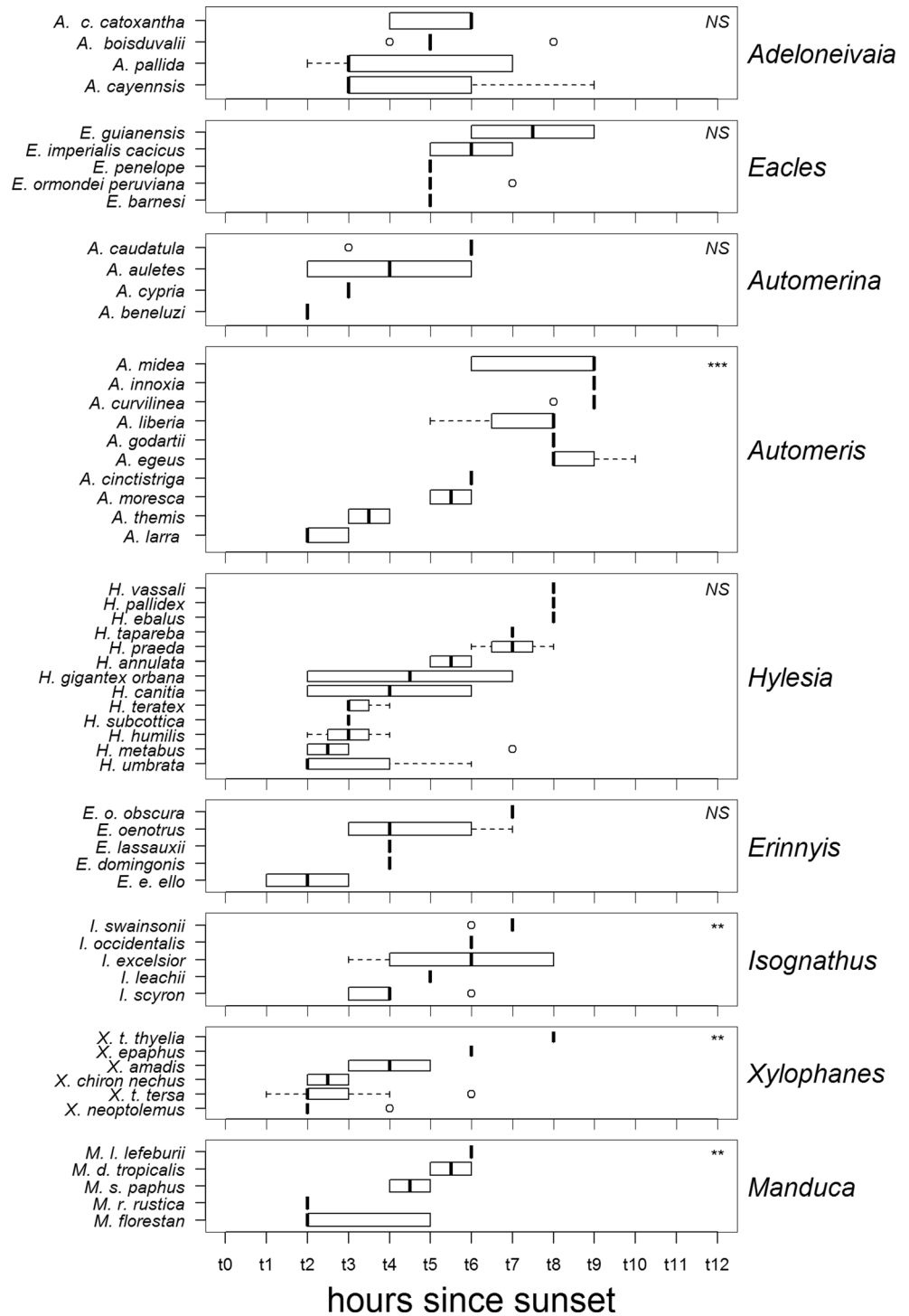


Fig 3 Within-genus differences in flight arrival time for the most abundant genus in our collection. Results of nonparametric Kruskal-Wallis tests performed within each genus are shown for differences within genus for a given subfamily. Label in the top right corner means: NS non-significant, single asterisk significance at the 0.05 level, double asterisks significance at the 0.01 level, triple asterisks significance at the 0.001 level.

e.g., *Automeris larra* (Walker, 1855) and *Automeris themis* Dognin, 1919; others distributed around midnight, e.g., *Automeris moresca* Schaus and *Automeris liberia* (Cramer, 1775); and finally, some taxa that were only observed during the second half of night, e.g., *Automeris egeus* (Cramer,

1775), *Automeris curvilinea* Schaus, 1906 and *Automeris innoxia* Schaus 1906. *Automeris*, *Manduca*, and to a lesser extent, *Hylesia* and *Automerina* clearly showed bi- or trimodality distribution in flight (see Online Supplementary Resource S2).

## Discussion

Despite the easiness of moths being attracted to artificial lights, the variations in flight activity and behavior may be so high that a complete census of moth species at night remains an elusive goal to achieve. In fact, our results showed for the first time in the Guianas that the arrival time of 46 genera of moths captured by light trapping showed significant differences between two moth families, and also, there were strong contrasts both among and within genera. For field entomologists interested in documenting the diversity of sphingid moths, the first half of the night is a critical period during which most species can be captured. In contrast, the regular arrivals during almost the entire night of new saturniid species suggest that operators should stay all night to effectively sample them. At the family level, our results are consistent with previous reports of a significant decrease in the number of specimens sampled after the first few hours of night in sphingids (Janzen 1984) and in other tropical moths (Schulze 2000, Brehm 2002). However, another study in Asia reported a greatest number of sphingid individuals distributed symmetrically around midnight (Beck & Linsenmair 2006), suggesting further complexity and disparity in these patterns when considered globally.

Contrasting patterns between these two families might occur because adult Saturniidae, exempt of functional proboscis, do not feed and therefore rely on storage of fat resources accumulated during the larval stages (but see Smerinthinae in Kitching & Cadiou 2000). We know that adult saturniids are active flyers for mating and oviposition only, while sphingids are active for mating, oviposition, and foraging for resources (Kitching & Cadiou 2000). Determinants of flight activity between families are likely related to these major life history differences. A possible explanation for sphingid moths being mostly active during the first half of the night is the decrease of temperature after sunset. Early night flight might cost less energy because the temperature is warmer. Flower-visiting sphingids may also be more active during specific phenology events such as flowering. Activity patterns of flower-visiting sphingids may also be determined by nocturnal flowering time. For instance, in the case of a temperate species, it has been shown that scent emission by flowers reached its maximum in early hours of night, therefore being the most attractive time for moths (Dotterl *et al* 2012). In addition, the inherent processes driving males to find females and females to locate suitable host plants are considered another important driver of flight activity (Beck & Linsenmair 2006). Both mating and foraging behavior related to functional attributes may therefore explain contrasting responses in flight activity between these

two families found in our study. Furthermore, representatives of the third trophic level—parasitoids and predators (Barber & Kawahara 2013)—and diseases (Janzen 1984) may also likely influence flight activity and behavior patterns as they represent conspicuous sources of caterpillar and adult mortality.

Our results revealed contrasted diel activity among taxa: some are attracted over a wide period of time, while others are active for a few hours only (Figs 2 and 3), a pattern already highlighted by Janzen (1984). For instance, species in *Automeris* were effectively sampled from 10:00 p.m. to 3:00 a.m., although most species were sampled late at light. Some species-rich genera showed a bi- or trimodal distribution of flight times (i.e., two or more peaks of distinct arrival times at night). Bimodality appeared in *Hylesia*, *Manduca*, and *Automerina* and trimodality in *Automeris* (Online Supplementary Resource S2), suggesting considerable differences in flight behavior among species in a given lineage. This pattern may be useful for field studies that seek to exhaustively sample representatives of a focal genus. Our study also showed similar and contrasting patterns in flight time within some genera (Fig 3). First, our results imply that tropical moths may have species-specific responses to light, hence influencing their behavior and flight activity. In his essay, Janzen (1984) alluded to this. He pointed out that there was species-specific variation in attraction to lights and assumed that male saturniids may have a species-specific search for pheromone plumes, which may explain divergences found in our study (e.g., *Automeris*). A great number of conditions such as competition and local climate fluctuations and anomalies may influence the search for mating (Janzen 1984). Second, some studies hypothesized that differences in flight times within sphingid genera may be due to avoidance of mating with close relatives with less time of overlapping than distantly related species (Beck & Linsenmair 2006). We might expect close relatives to share similar patterns in flight activity because functional attributes related to foraging, reproduction, and avoidance processes may be phylogenetically conserved. This is exemplified here by some convergent patterns in flight activity within species of *Hylesia*, *Eacles*, and *Automerina*. However, our study may not validate eco-evolutionary responses in diel activity for a given lineage as we only conducted sampling in one site with some very low abundance in some genera. Further, long-term survey in multiple sites over several seasons is recommended to validate these results. Moreover, we envision a phylogenetic approach among multiple moth families in which functional traits driving diel activity are related to phylogenetic relationships among taxa.

Flight activity at basic taxonomic levels as presented here produced general natural history information that contributes to our understanding of moth behavior at light traps. Our study showed contrasting patterns in flight activity between Sphingidae and Saturniidae, which underlines differentiation in behavior, physiological and functional traits among taxa. Taken together, our results strongly suggested the need to monitor lights throughout the night to effectively sample saturniid and sphingid assemblages, even though the activity of Sphingidae sharply declines after midnight. Differences found in diel activities among families, genera, and species have practical applications for entomologists' sampling in the tropics. Furthermore, we recommend the use of functional traits related to the timing of life histories such as flight behavior, foraging, reproduction, diapause, and migration to enlarge our understanding of moth assemblages.

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