

POPULATION BIOLOGY OF THE SAND FOREST SPECIALIST BUTTERFLY *HELICONIUS*
HERMATHENA HERMATHENA (HEWITSON) (NYMPHALIDAE: HELICONIINAE)
IN CENTRAL AMAZONIA)

RANY R. SEIXAS, SUZANE E. SANTOS & YUKARI OKADA

Laboratório de Zoologia, Programa de Ciências Naturais, Instituto de Ciências da Educação,
Univ Federal do Oeste do Pará, Santarém, PA, Brasil

AND

ANDRÉ V. L. FREITAS*

Departamento de Biologia Animal and Museu de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109,
Campinas, SP, 13083-970, Brazil; email: baku@unicamp.br (corresponding author*)

ABSTRACT. The present paper describes the population parameters and natural history of *Heliconius hermathena hermathena* (Hewitson, [1854]), a sand forest specialist nymphalid butterfly. Population biology was described based on a 14-month mark-recapture program in a site of open forest in Pará state, northern Brazil. The population was constant through the year, with no marked peaks of abundance for both sexes, with females always less abundant. The range of the population size was 70–150 individuals (with a maximum near 200 individuals). Sex ratio was male biased, with males dominating most of the time. Average residence time was of 35 days for males and 31 days for females, with a maximum of 139 days recorded for males and 129 days for females, with both sexes presenting survival curves approaching the type II survival curve. Males presented wing sizes greater than females in all months. Adults were observed visiting five species of flowers as nectar and pollen sources and establishing communal nocturnal roosting aggregations on small shrubs. Considering the fragility of the Amazonian white sand forests, understanding the population patterns of *H. h. hermathena* can help future conservation planning for these potentially threatened habitats.

Additional key words: Campina, Campinarana, Heliconiini, white sand forest

Studies of population ecology of tropical butterflies are extremely scarce in the literature (see Vlasanek et al. 2013, Vlasanek & Novotny 2015 and references therein), and besides some recent efforts, most published studies of tropical butterflies are restricted to species of Nymphalidae and Papilionidae (e.g. Ramos & Freitas 1999, Freitas et al. 2001, Uehara-Prado et al. 2005, Tufto et al. 2012, Beirão et al. 2012, Vlasanek & Novotny 2015). This general lack of data on dispersal and demography of tropical butterflies hinders our capacity to understand ecology and functioning of plant-insect systems in tropical forests and to propose adequate measures for the conservation of endangered tropical butterflies (Freitas 1996, Freitas & Marini-Filho 2011, Vlasanek et al. 2013).

For *Heliconius* Kluk (Nymphalidae) butterflies, however, the situation is different. These are by far the most studied tropical butterflies, and concerning population ecology, a relatively large literature is available, including several different species and populations from Florida to Southern Brazil (Turner 1971, Ehrlich & Gilbert 1973, Cook et al. 1976, Araujo 1980, Brown 1981, Mallet & Jackson 1980, Romanowsky et al. 1985, Quintero 1988, Gilbert 1991, Ramos & Freitas 1999, Andrade & Freitas 2005, Sobral-Souza et al. 2015 and references therein). All these studies helped

us to construct a general picture about *Heliconius* population patterns through space and time and to review the early ideas of low-density constant populations, which are typical of those populations from tropical sites (Ramos & Freitas 1999, Andrade & Freitas 2005, Sobral-Souza et al. 2015).

Nevertheless, although *Heliconius* butterflies are well known in terms of population ecology, published studies are restricted to a dozen of the approximately 40 described species in the genus (see references above), most of them in lowland tropical forest habitats (but see Fleming et al. 2005 for a study in an urban garden in Florida). In fact, most known *Heliconius* are typical of forested habitats, although some species such as *Heliconius erato* (Linnaeus) are able to persist in several different vegetation types (Araujo 1980, Ramos & Freitas 1999).

Contrary to its congeners, *Heliconius hermathena hermathena* (Hewitson) is associated with open vegetal formations, including the white-sand vegetation known locally as “Campina” or “Campinarana” (see detailed description of these habitats in Ducke & Black 1953, Anderson 1981 and Adeney et al. 2016), where the high-light, low-humidity, and often harsh conditions are restrictive for almost all other species of *Heliconius* (Brown & Benson 1977). In a detailed and extensive

study, Brown & Benson (1977) presented comprehensive information on the systematics, biogeography, natural history (including host plant and immature stages) mimicry and ecology of this peculiar species of *Heliconius*. However, in the above study, demographic data for *H. hermathena* was restricted to a limited mark-recapture session during a few days, where little population data has been recorded (see Brown & Benson 1977).

The present paper describes the population biology of *H. hermathena hermathena* (Hewitson, [1854]) in central Amazonia based on a 14-month mark-recapture program. Given the fragile situation of the Amazonian white sand forests (Adeney et al., 2016), the results provide information that could aid in future management of this butterfly species and its fragile and unprotected habitats.

STUDY SITES AND METHODS

A mark-release-recapture (MRR) study of *Heliconius hermathena hermathena* was carried out in the “Parque Zoobotânico das Faculdades Integradas do Tapajós” (02°27'38"S, 54°43'59"W; ca. 25–30 m a.s.l.) (Figs. 1A, B), in the city of Santarém, Pará, Northern Brazil. The study area is covered with a mosaic of “terra firme” (never floodable forest) and open forests in different degrees of succession. Annual rainfall reaches 2100 mm and the average annual temperature is 26°C (INMET 2016) (a climagram for the study area is presented in Fig. 2). Butterflies were marked and recaptured in a trail (1.8 km long, divided into 49 sectors varying from 40 to 100 m, Figs. 1A, B) inside the forest during 14 months, from January 7, 2012 to February 26, 2013, for a total of 107 days (approximately 4 hours/day). Butterflies were net-captured, individually numbered on the underside of both forewings with a black permanent felt-tipped pen, and released. Characteristics of each individual (wing size, point of capture, sex and food sources) were

TABLE 1. Permanence of males (n = 524) and females (n = 395) of marked *H. hermathena hermathena*. Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP (days)	Males	(%)	Females	(%)
1–20	214	40.8	172	43.5
21–40	133	25.4	112	28.4
41–60	80	15.3	68	17.2
61–80	41	7.8	26	6.6
81–100	29	5.5	8	2.0
101–120	21	4.0	5	1.3
> 120	6	1.2	4	1.0

recorded for later analysis (as in Ramos & Freitas; 1999 and Beirão et al. 2012).

The MRR data were analyzed using the Joly-Seber method for estimating population parameters (Francini 2010a, b). Males and females were analyzed separately. To estimate the number of individuals present per day, recaptured individuals were considered to be present on all previous days since the first capture (i.e. marked animals at risk, following Freitas & Ramos 2001). Time of permanence in population (i.e. minimum permanence, an indirect measure of longevity) was calculated as days elapsed between marking and last recapture (following Brussard et al. 1974). The sex ratio was calculated through the monthly means of daily proportions in number of individuals captured per day.

RESULTS

Population Dynamics. A total of 2014 individuals of *Heliconius hermathena hermathena* (1095 males and 919 females) (Figs. 1C, D) were captured between January 2012 and April 2013. The number of individuals captured per day varied from one to 53 for males (mean = 20.9; SD = 10.29; n = 107 d), and from two to 47 for females (mean = 17.2; SD = 7.84; n = 107 d). The number of individuals present per day varied from one to 96 for males (mean = 56.4; SD = 18.38; n = 107 d), and from six to 66 for females (mean = 37.7; SD = 10.78; n = 107 d). The population was constant through the year, with no marked peaks of abundance for both sexes, with females always less abundant (Fig. 3). In general, estimated population numbers were not greater than the number of individuals present per day, especially for females (Fig. 3).

TABLE 2. Number of recaptures for all marked individuals of males and females *H. hermathena hermathena*.

Number of recaptures	Males	Females
0	571	524
1	261	190
2	113	85
3	65	41
4	38	32
5	64	64
6	10	8
7	10	5
8	2	5
9	3	1
10	3	2
11	1	1
12	0	3
13	1	1

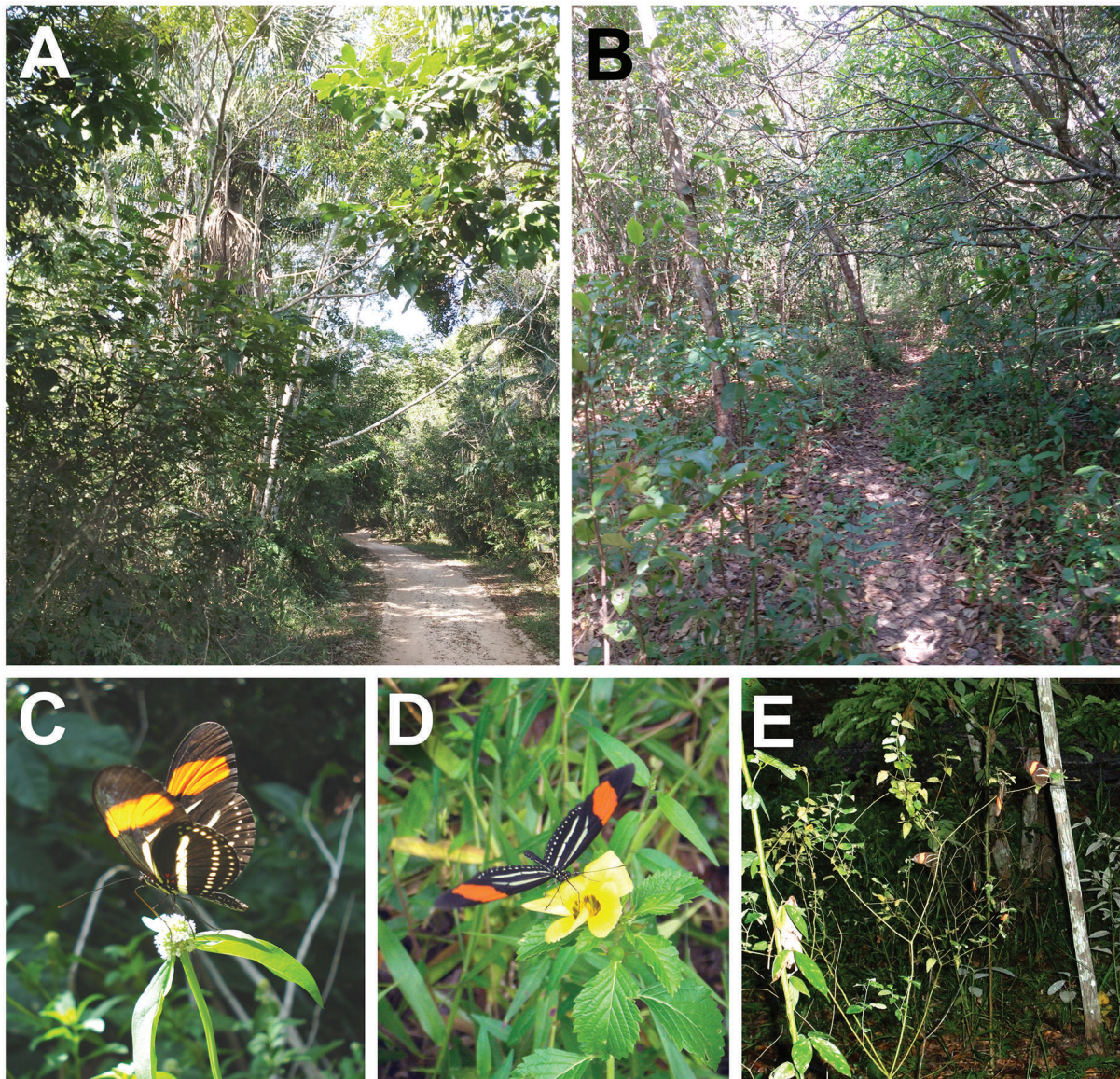


FIG. 1. **A, B.** Two views of the trails where the mark-release-recapture study of *H. hermathena hermathena* had been carried out; **C, D.** Males of *H. hermathena hermathena* visiting flowers of *Spermacoce capitata* (Rubiaceae) and *Turnera ulmifolia* (Turneraceae), respectively; **E.** A nocturnal roosting aggregation of *H. hermathena hermathena*.

Residence Time. The residence time (based on recaptured individuals) varied from two to 139 days for males (mean = 34.9 d; $n = 524$) and from two to 129 days for females (mean = 30.5 d; $n = 395$) (Table 1). Life expectancy (following Cook et al. 1967) was 50.8 days for males and 22.5 days for females. Survival curves (following Ehrlich and Gilbert 1973) are similar for both sexes (Kolmogorov - Smirnov test, $P > 0.05$, $df = 2$), approaching a type II survival curve (Fig. 4).

Sex Ratio. The sex ratio of individuals captured and marked was male biased (sex ratio of 1.2:1), with 1095

males and 919 females marked ($X^2 = 15.38$; $df = 1$; $P < 0.0001$), with males dominant in most months (Fig. 5). Both, males and females were recaptured from one to 13 times (Table 2); 524 males (47.9%) and 395 females (42.9%) were recaptured at least once, with males recaptured more than females ($X^2 = 4.78$; $DF = 1$; $P = 0.032$).

Wing Size. The forewing length ranged from 31.0 to 46.0 mm in males and from 30.0 to 45.0 mm in females. The average forewing length of males (mean = 42.1 mm, $SD = 1.74$, $n = 1094$) was greater than that of females

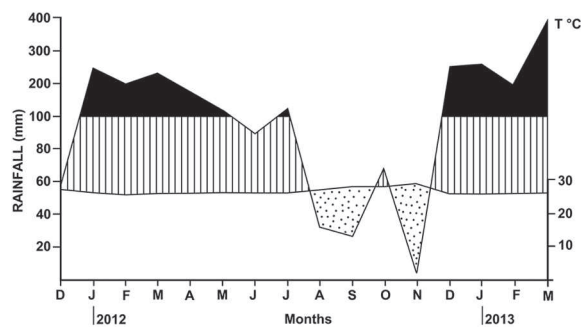


FIG. 2. Climatic diagram of the study site (see methods) during the study period (format following Walter 1985). Dotted = dry periods, hatched = humid periods, black = superhumid periods.

(mean = 41.6 mm, SD = 1.69, $n = 919$) ($t = 6.32$, $df = 2011$, $P < 0.0001$). The mean forewing length of both sexes were constant along the year (Fig. 6).

Natural history and behavior. In the study area, *H. h. hermathena* was common and easily observed throughout all the year. The adults were commonly observed near forest edges, flying from close to the ground (0.5–1 m high) to 2–3 m searching for flowers. Flower resources were not quantified but adults were observed visiting five species of flowers as nectar and pollen sources, including species in the family Costaceae (*Costus* sp.), Rubiaceae (*Spermacoce capitata* Ruiz & Pav., Fig. 1C), Turneraceae (*Turnera ulmifolia* L., Fig. 1D), Verbenaceae (*Stachytarpheta cayennensis* (Rich.)) and Vitaceae (*Cissia erosa* L. Rich.). Activity started before 0700 h in the morning and ceased around 1730 h in the afternoon; most flower visits were observed from 0800 to 1030 h in the morning, with the activity decreasing after 1200 h in the morning, when temperature became very hot in the study site and all adults moved to the shadow of the vegetation. Adults were observed establishing communal nocturnal roosting aggregations on small shrubs (Fig. 1E). The only reported host plant in the study site was *Passiflora hexagonocarpa* Barb. Rodr. (Passifloraceae).

DISCUSSION

Besides the distinct ecological requirements of *H. hermathena hermathena* compared with other studied *Heliconius*, population parameters here described are similar to those described for other species in the genus, which includes the constant populations through the year and long-lived adults with clear generation overlap (see Turner 1971, Ehrlich & Gilbert 1973, Quintero 1988, Ramos & Freitas 1999).

The male biased sex ratio reported here is a pattern usually reported for butterflies in general and for *Heliconius* in particular (Mallet & Jackson 1980, Ramos & Freitas 1999, Andrade & Freitas 2005, Herkenhoff et al. 2013, Sobral-Souza et al. 2015 and references therein). Because sex ratios are near to 1:1 in laboratory breeds, behavioral differences between sexes have been suggested as the reason for male biased sex ratios in population studies of tropical butterflies (Ehrlich & Gilbert 1973, Mallet & Jackson 1980, Ehrlich 1984, Freitas 1993, Brown et al. 1995). This is true for most nectar feeding species, where males are more easily captured along trails and forest edges where they come to visit flower resources, while females are supposedly looking for host plants inside the forest (e.g. Freitas 1993, 1996, Ramos & Freitas 1999, Francini et al. 2005). For most heliconians, which are nectar and pollen feeding, behavioral differences among sexes should be responsible for this pattern of male biased sex ratios (see above).

As described for other studied *Heliconius*, adults of *H. hermathena hermathena* live about one month on average, with some individuals living up to four months or more. These values are equivalent to those reported for previous studies with *Heliconius* in both, stable tropical (Turner 1971, Benson 1972, Ehrlich & Gilbert 1973, Quintero 1988, Ramos & Freitas 1999) or seasonal sites (Araujo 1980, Romanowsky et al. 1985, Flemming et al. 2005, Andrade & Freitas 2005). Even considering the small differences reported in previously mentioned studies, present results confirm the general pattern of long adult lifespans of species of *Heliconius* when compared to other tropical butterflies (Freitas & Ramos 1999, Uehara-Prado et al. 2005). Also in accordance with previous studies, males are more likely to be recaptured and present higher residence times than females, both possibly related to the above-mentioned behavioral differences among sexes (see Ramos & Freitas 1999 and references therein).

For tropical butterflies in general, females present greater wing sizes compared to males, a pattern reported in Pieridae (Jones 1992, Vanini et al. 1999, Ruszczyk et al. 2004), Papilionidae (Freitas & Ramos 2001, Beirão et al. 2012, Herkenhoff et al. 2013, Scalco et al. 2016), and several groups of Nymphalidae (Kemp & Jones 2001, Uehara-Prado et al. 2005, Francini et al. 2005, Tourinho & Freitas 2009, Cavanzone-Medrano et al. 2016). Conversely, in *Heliconius*, female biased sexual size dimorphism is rare; males present greater wing lengths than females (Ramos & Freitas 1999 and present study) or differences are not significant (Andrade & Freitas 2005). A notable exception is *Heliconius sara* (Fabricius) whose males are smaller

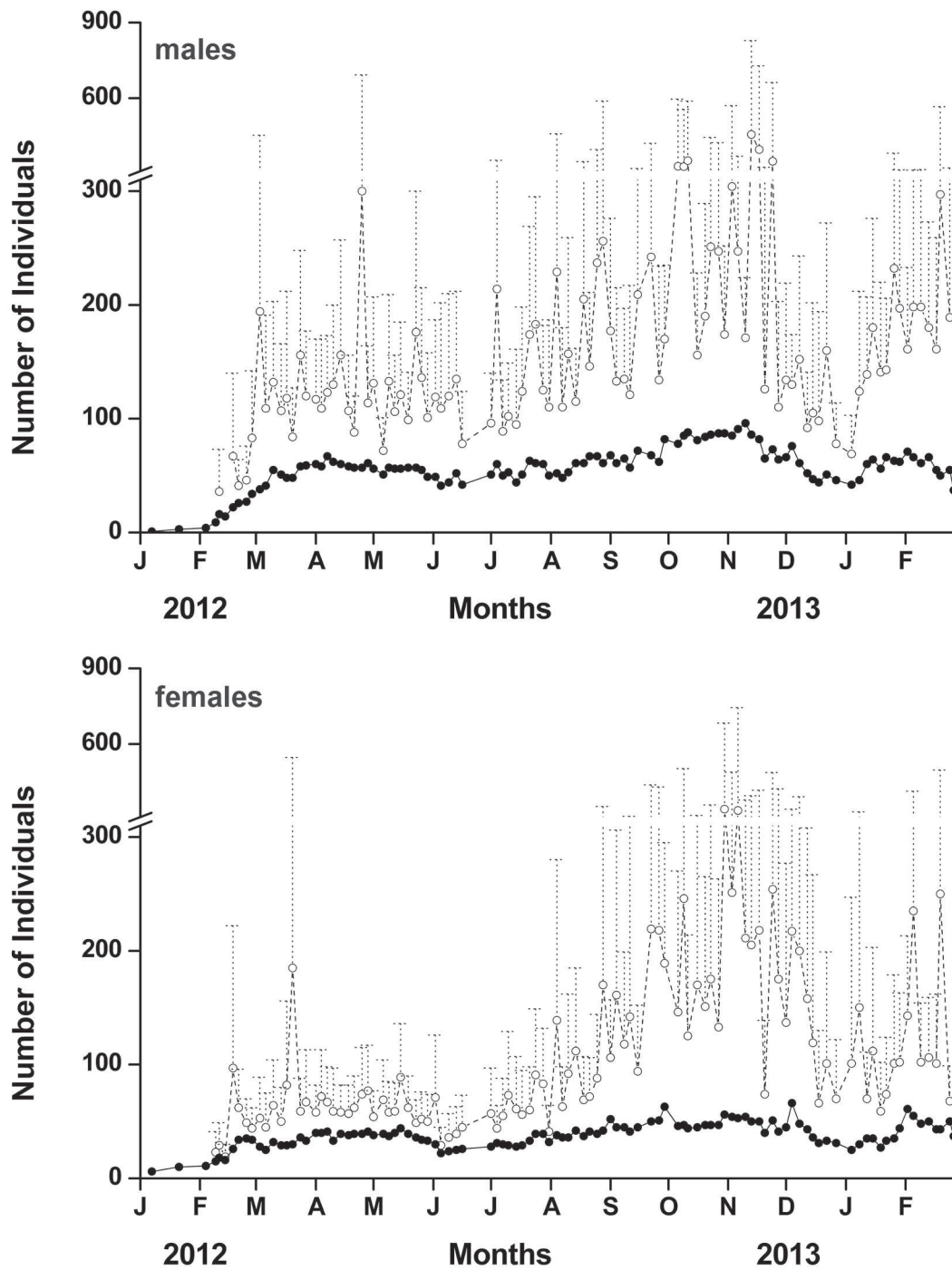


FIG. 3. Number of males (above) and females (below) of *H. hermathena hermathena* from January 2012 to February 2013 in the study site in Santarém, Pará. Solid circles = number of individuals present per day, open circles = estimated number based on Joly-Seber (bars = 1 standard error).

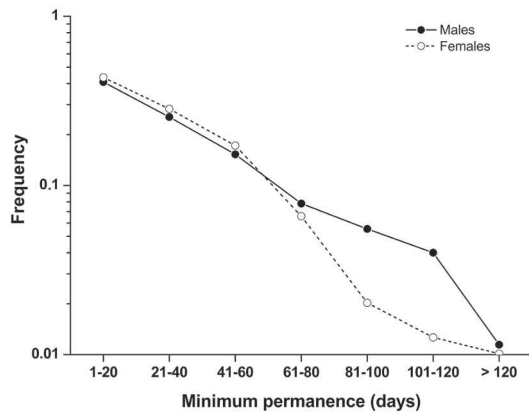


FIG. 4. Survivorship curves for *H. hermathena hermathena* males and females (following Ehrlich and Gilbert 1973). The frequencies of males and females are plotted on log scale against permanence categories (based on data presented on Table 1).

than females (and territorial advantage is associated with small sizes, see Hernandez & Benson 1998). Female-biased sexual size dimorphism is the more common pattern for insects in general (Stillwell et al. 2010) and for Lepidoptera in particular (Allen et al. 2011), and is related with larger fecundity in bigger females (Allen et al. 2011 and references therein). Although territorial behavior could partially explain this pattern (see Benson et al. 1989), the reasons for male-biased or no sexual size dimorphism in *Heliconius* are unknown and a topic to be further investigated.

Interestingly, besides the marked seasonality of the study area (with a prominent dry season), the studied population of *H. hermathena hermathena* was quite constant along the 13 months of study. This pattern is very similar to that reported in non-seasonal sites, such as for *Heliconius erato phyllis* (Fabricius) in coastal Brazilian Atlantic Forest (Ramos & Freitas 1999) and for *Heliconius ethilla* (Godart) in Costa Rica (Ehrlich & Gilbert 1973). In seasonal sites, conversely, populations of some species of *Heliconius* showed marked population fluctuations, with peaks of high densities of adults alternating with periods of extremely low population numbers. This pattern was reported in subtropical sites with a marked cold season, such as Southern Brazil (Araujo 1980, Romanowsky et al. 1985) and Florida (Fleming et al. 2005) and in seasonal forests with a marked dry season (Quintero 1988, Andrade e Freitas 2005). Conversely, *Heliconius sara apseudes* (Hübner) was reported as strongly seasonal in a stable tropical site in southeastern Brazil (Sobral-Souza et al. 2015).

Based on the present available information, four different population syndromes have been documented for *Heliconius*: 1) ecologically plastic species occurring in several different habitats, whose populations could be either, constant or seasonal, depending on the local climate—examples are *H. erato*, *H. ethilla* (Ehrlich & Gilbert 1973, Ramos & Freitas 1999, Andrade & Freitas 2005) and *Heliconius charitonia* (L.) (see Cook et al. 1976, Quintero 1988, Gilbert 1991 and Fleming et al. 2005); 2) species presenting marked seasonality independent of the climatic conditions, such as *H. sara apseudes* (Sobral-Souza et al. 2015, AVLF unpublished); 3) species from cooler montane forests, presenting marked seasonality, such as *Heliconius besckei* (Ménétriés) (AVLF unpublished) and *Heliconius nattereri* C. Felder & R. Felder (Brown Jr., K. S., pers. comm.); and 4) specialized tropical species restricted to tropical warm forests, with constant populations even in seasonal sites (such as *H. hermathena hermathena* in the present study).

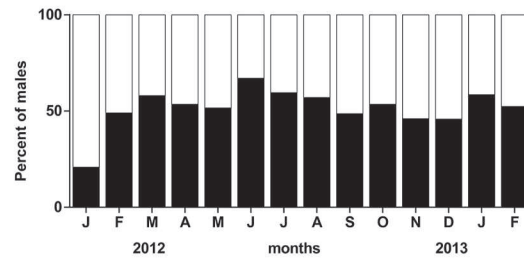


FIG. 5. Sex ratio of *H. hermathena hermathena* from January 2012 to February 2013 in the study site in Santarém, Pará. Data presented as percent of males (in black) by month (based on means of each days' captures).

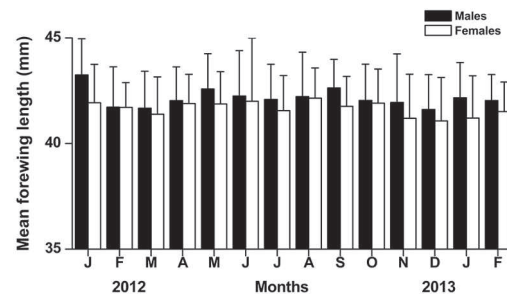


FIG. 6. Mean forewing length of males (solid bars) and females (open bars) of *H. hermathena hermathena* in the study site in Santarém, Pará, from January 2012 to February 2013 (based on monthly recruitment). Bars = monthly means, line extensions = standard deviations.

However, information about *Heliconius* population ecology is limited to very few studies focusing on a restricted subset of less than dozen of the over 40 described species in the genus. Consequently, very few species could be assigned to the above-proposed fourth category, which was for a long time considered as a model of population dynamics in *Heliconius*. The typical example is *H. ethilla*; the first studied species of *Heliconius* from a population point of view and an example of a tropical butterfly with low-density constant populations throughout time (Ehrlich & Gilbert 1973, Ehrlich 1984). Three decades later, Andrade & Freitas (2005) showed that population parameters of the same species (*H. ethilla*) in a seasonal tropical site with a marked dry period are quite distinct: the population was not constant, showing a marked peak of abundance in the rainy season and a period of extremely low population numbers during most of the dry season.

Gilbert (1991) provided demographic data for eight species of *Heliconius*, all presenting constant populations in a tropical site in Costa Rica. From these, two of them (*H. erato* and *H. charitonia*) were shown to fit in the first population syndrome when additional population data become available (see above). The remaining six species, however, are all restricted to tropical Amazonian and Central American habitats (with one also occurring in the northern tropical portion of Atlantic Forest—*Heliconius melpomene* (Linnaeus)) and could be good examples of species fitting in the fourth population syndrome (and maybe *Heliconius xanthocles* H. Bates, see Mallet & Jackson 1980).

In this sense, the present demographic data for *H. hermathena hermathena* is relevant by adding information that can help in understanding the above proposed population syndromes for the genus *Heliconius*. In addition, because *H. hermathena* is a sand forest specialist, it would be important to obtain data from other populations of this same species in different localities in the Amazonia. Finally, understanding the population patterns of this species will add information that can help in future conservation planning for these fragile and potentially threatened habitats.

ACKNOWLEDGEMENTS

We thank the “Zoológico da FIT” for allowing research in its áreas, Profa. Chieno Suemitsu for identifying the plant species used by butterflies and Dr. Larry Gilbert, Brett Seymoure and an anonymous reviewer for reading the final version of the manuscript, contributing with valuable suggestions and criticisms. AVLF thanks CNPq (grants 302585/2011-7 and 303834/2015-3), RedeLep-SISBIOTA-Brasil/CNPq (563332/2010-7), National Science Foundation (DEB-1256742), FAPESP (grants 2011/50225-3 and 2012/50260-6) and USAID (Mapping and Conserving Butterfly Biodiversity in the Brazilian Amazon).

LITERATURE CITED

- ADENEY, J. M., N. L. CHRISTENSEN, A. VICENTINI & M. COHN-HAFT. 2016. White-sand Ecosystems in Amazonia. *Biotropica* 48: 7-23.
- ALLEN, C. E., B. J. ZWAAN & P. M. BRAKEFIELD. 2011. Evolution of sexual dimorphism in the Lepidoptera. *Annu. Rev. Entomol.* 56: 445-464.
- ANDERSON, A. B. 1981. White-sand vegetation of Brazilian Amazonia. *Biotropica* 13: 199-210.
- ARAJO, A. M. 1980. Estudos genéticos e ecológicos em *Heliconius erato* (Lepidoptera, Nymphalidae). *Actas IV Congr. Latinoam. Genética* 2: 199-206.
- ANDRADE, R. B. & A. V. L. FREITAS. 2005. Population biology of two species of *Heliconius* (Nymphalidae: Heliconiinae) in a semi-deciduous forest in Southeastern Brazil. *J. Lepid. Soc.* 59: 223-228.
- BEIRÃO, M. V., F. C. CAMPOS-NETO, I. A. PIMENTA & A. V. L. FREITAS. 2012. Population biology and natural history of *Parides burchellanus* (Papilionidae: Papilioninae: Troidini), an endangered Brazilian butterfly. *Ann. Entomol. Soc. Amer.* 105:36-43.
- BENSON, W. W. 1972. Natural selection for Mullerian mimicry in *Heliconius erato* in Costa Rica. *Science* 176: 936-939.
- BENSON, W. W., C. F. B. HADDAD & M. ZIKÁN. 1989. Territorial behavior and dominance in some heliconiine butterflies (Nymphalidae). *J. Lepid. Soc.* 43: 33-49.
- BROWN JR., K. S. 1981. The biology of *Heliconius* and related genera. *Annu. Rev. Entomol.* 26: 427-456.
- BROWN JR., K. S. & W. W. BENSON. 1977. Evolution in modern Amazonian non-forest islands: *Heliconius hermathena*. *Biotropica* 9: 95-117.
- BROWN JR., K. S., C. F. KLITZKE, C. BERLINGERI & P. E. R. DOS SANTOS. 1995. Neotropical swallowtails: Chemistry of food plant relationships, population ecology, and biosystematics, pp. 405-445. In Scriber, J. M., Y. Tsubaki, & R. C. Lederhouse (eds.), *Swallowtail butterflies: their ecology and evolutionary biology*. Gainesville, Scientific Publishers, Florida.
- BRUSSARD, P. F., P. R. EHRLICH & M. C. SINGER. 1974. Adult movements and population structure in *Euphydryas editha*. *Evolution* 28: 408-415.
- CAVANZÓN-MEDRANO, L., C. POZO, Y. HÉNAUT, L. LEGAL, N. SALAS-SUÁREZ & S. MACHKOUR-M'RABET. 2016. Complex population patterns of *Eunica tatila* Herrich-Schäffer (Lepidoptera: Nymphalidae), with special emphasis on sexual dimorphism. *Neotrop. Entomol.* 45: 148-158.
- COOK, L. M., L. P. BROWER & H. J. CROZE. 1967. The accuracy of a population estimation from multiple recapture data. *J. Animal Ecol.* 36:57-60.
- COOK, L. M., E. W. THOMASON & A. M. YOUNG. 1976. Population structure, dynamics and dispersal of the tropical butterfly *Heliconius charitonus*. *J. Animal Ecol.* 45: 851-863.
- DUCKE, A. & G. A. BLACK. 1953. Phytogeographic notes on the Brazilian Amazon. *Anais Acad. Bras. Cienc.* 25: 1-46.
- EHRLICH, P. R. 1984. The structure and dynamics of butterfly populations, pp. 25-40. In Vane-Wright, R. I & P. R. Ackery (eds.), *The biology of butterflies*. Academic Press, London.
- EHRLICH, P. R. & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* 5: 69-82.
- FLEMING, T. H., D. SERRANO & J. NASSAR. 2005. Dynamics of a subtropical population of the zebra longwing butterfly *Heliconius charitonia* (Nymphalidae). *Fla. Entomol.* 88: 169-179.
- FRANCINI, R. B. 2010A. Métodos para estudar ecologia de populações de borboletas. 201pp. <http://www.archive.org/details/ParaEstudarEcologiaDePopulaesDeBorboletas> (accessed January 2017).
- FRANCINI, R. B. 2010B. CMLR_2010. Programa para estimativas populacionais (available free by the e-mail rb.francini@yahoo.com).
- FRANCINI, R. B., A. V. L. FREITAS & K. S. BROWN JR. 2005. Rediscovery of *Actinote zikani* (D'Almeida) (Nymphalidae, Heliconiinae, Acraeini): Natural history, population biology and conservation of an endangered butterfly in SE Brazil. *J. Lepid. Soc.* 59: 134-142.

- FREITAS, A. V. L. 1993. Biology and population dynamics of *Placidula euryanassa*, a relict ithomiine butterfly (Nymphalidae: Ithomiinae). *J. Lepid. Soc.* 47: 87-105.
- FREITAS, A. V. L. 1996. Population biology of *Heterosais edessa* (Nymphalidae) and its associated Atlantic Forest Ithomiinae community. *J. Lepid. Soc.* 50: 273-289.
- FREITAS, A. V. L. & R. R. RAMOS. 2001. Population biology of *Parides anchises nephalion* (Papilionidae) in a coastal site in Southeast Brazil. *Braz. J. Biol.* 61: 623-630.
- FREITAS, A. V. L. & O. J. MARINI-FILHO (eds). 2011. Plano de ação nacional para conservação dos lepidópteros ameaçados de extinção. Instituto Chico Mendes de Conservação da Biodiversidade, Brasília, DF, 124 pp.
- FREITAS, A. V. L., J. VASCONCELLOS-NETO, F. VANINI, J. R. TRIGO & K. S. BROWN JR. 2001. Population studies of *Aeria olenae* and *Tithorea harmonia* (Nymphalidae, Ithomiinae) in Southeastern Brazil. *J. Lepid. Soc.* 55: 150-157.
- GILBERT, L. E. 1991. Biodiversity of a central american *Heliconius* community: pattern, process, and problems. pp. 403-427. In Price, P. W., T. M. Lewinsohn, G. W. Fernandes & W. W. Benson (eds.), *Plant-Animal Interactions. Evolutionary Ecology in Tropical and Temperate Regions.* John Wiley & Sons, Inc., New York.
- HERKENHOFF, E. V., R. F. MONTEIRO, A. P. ÉSPERANÇO & A. V. L. FREITAS. 2013. Population biology of the endangered Fluminense swallowtail butterfly *Parides ascanius* (Papilionidae: Papilioninae: Troidini). *J. Lepid. Soc.* 67:29-34.
- HERNÁNDEZ, M. I. M. & W. W. BENSON. 1998. Small-male advantage in the territorial tropical butterfly *Heliconius sara* (Nymphalidae): a paradoxical strategy? *Anim. Behav.* 56: 533-540.
- INMET. 2016. Normas climatológicas (1961-1990). Instituto Nacional de Meteorologia, Ministério da Agricultura, Pecuária e Abastecimento. Brasília, Brasil. <http://www.inmet.gov.br/portal/index.php?r=clima/normaisClimatologicas> (accessed August 2016).
- JONES, R. E. 1992. Phenotypic variation in Australian *Eurema* species. *Aust. J. Zool.* 40: 371-383.
- KEMP, D. J. & R. E. JONES. 2001. Phenotypic plasticity in field populations of the tropical butterfly *Hypolimnas bolina* (L.) (Nymphalidae). *Biol. J. Linn. Soc.* 72: 33-45.
- MALLET, J. L. B. & D. A. JACKSON. 1980. The ecology and social behavior of the Neotropical butterfly *Heliconius xanthocles* Bates in Colombia. *Zool. J. Linn. Soc.* 70: 1-13.
- QUINTERO, H. E. 1988. Population dynamics of the butterfly *Heliconius charitonius* L. in Puerto Rico. *Caribb T. Sci.* 24: 155-160.
- RAMOS, R. R. & A. V. L. FREITAS. 1999. Population biology and wing color variation in *Heliconius erato phyllis* (Nymphalidae). *J. Lepid. Soc.* 53: 11-21.
- ROMANOWSKY, H. E., R. GUS & A. M. ARAUJO. 1985. Studies on the genetics and ecology of *Heliconius erato* (Lepid. Nymph). III. Population size, preadult mortality, adult resources and polymorphism in natural populations. *Rev. Brasil. BioI.* 45: 563-569.
- RUSZCZYK, A., P. C. MOTTA, R. L. BARROS & A. M. ARAUJO. 2004. Ecological correlates of polyphenism and gregarious roosting in the grass yellow butterfly *Eurema elathea* (Pieridae). *Braz. J. Biol.* 64: 151-164.
- SCALCO, V. W., A. B. B. DE MORAES, H. P. ROMANOWSKI & N. O. MEGA. 2016. Population dynamics of the swallowtail butterfly *Battus polystictus polystictus* (Butler) (Lepidoptera: Papilionidae) with notes on its natural history. *Neotrop. Entomol.* 45: 33-43.
- SOBRAL-SOUSA, T., R. B. FRANCINI, M. GUIMARÃES & W. W. BENSON. 2015. Short-term dynamics reveals seasonality in a subtropical *Heliconius* butterfly. *Journal of Insects* 2015 (761058): 1-5.
- STILLWELL, R. C., W. U. BLANCKENHORN, T. TEDER, G. DAVIDOWITZ & C. W. FOX. 2010. Sex Differences in phenotypic plasticity affect variation in sexual size dimorphism in Insects: From Physiology to Evolution. *Annu. Rev. Entomol.* 55: 227-245.
- TOURINHO, J. L. & A. V. L. FREITAS. 2009. Population biology of *Euptoieta hegesia* (Nymphalidae: Heliconiinae: Argynnini) in an urban area in Southeastern Brazil. *J. Res. Lepid.* 41: 40-44.
- TUFTO, J., R. LANDE, T-H. RINGSBY, S. ENGEN, B-E. SÆTHER, T. R. WALLA & P. J. DEVRIES. 2012. Estimating Brownian motion dispersal rate, longevity and population density from spatially explicit mark-recapture data on tropical butterflies. *J. Anim. Ecol.* 81:756-769.
- TURNER, J. R. G. 1971. Experiments on the demography of tropical butterflies, II. Longevity and home range behavior in *Heliconius erato*. *Biotropica* 3: 21-31.
- UEHARA-PRADO, M., K. S. BROWN JR. & A. V. L. FREITAS. 2005. Biological traits of frugivorous butterflies in a fragmented and a continuous landscape in the south Brazilian Atlantic forest. *J. Lepid. Soc.* 59: 96-106.
- VANINI, F., V. BONATO & A. V. L. FREITAS. 1999. Polyphenism and population biology of *Eurema elathea* (Pieridae) in a disturbed environment in tropical Brazil. *J. Lepid. Soc.* 53: 159-168.
- VLASANEK, P., L. SAM & V. NOVOTNY. 2013. Dispersal of butterflies in a New Guinea rainforest: using mark-recapture methods in a large, homogeneous habitat. *Ecol. Entomol.* 38: 560-569.
- VLASANEK, P. & V. NOVOTNY. 2015. Demography and mobility of three common understory butterfly species from tropical rain forest of Papua New Guinea. *Pop. Ecol.* 57: 445-455.

Submitted for publication 16 January 2017; revised and accepted 31 March 2017.