Immature stages and natural history of *Yphthimoides borasta* (Nymphalidae: Euptychiina)

André Victor Lucci Freitas^{1,2,3}, Eduardo Proença Barbosa¹ and Junia Yasmin Oliveira Carreira¹

1. Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil. 2. Museu de Diversidade Biológica, Instituto de Biologia, Universidade Estadual de Campinas, SP, Brazil. 3. Corresponding author - baku@unicamp.br

Date of issue online: 3 May 2021

Electronic copies (ISSN 2575-9256) in PDF format at: http://journals.fcla.edu/troplep; https://zenodo.org; archived by the Institutional Repository at the University of Florida (IR@UF), http://ufdc.ufl.edu/ufir; DOI: 10.5281/zenodo.4721637

© The author(s). This is an open access article distributed under the Creative Commons license CC BY-NC 4.0 (https://creativecommons.org/ licenses/by-nc/4.0/).

Abstract: The present paper describes the immature stages and the natural history of *Yphthimoides borasta*. Eggs are pinkish white and round, with poorly marked hexagonal cells; the first instar is pale brown, turning dark brown with longitudinal zigzag stripes in later instars; the pupae are short, brown, without ornamentation or projections and with short, squared ocular caps. The immature stages are similar to those of other species of the genus *Yphthimoides* and to other representatives of the "*Megisto* clade". Observed sex ratio in the field is 1:1 and adults fly in the canopy, explaining the rarity of this species in inventories and museum collections in comparison with other species of *Yphthimoides*.

Resumo: O presente trabalho descreve os estágios imaturos de *Yphthimoides borasta*. Os ovos são rosa claro e esféricos, com diversas células hexagonais pouco marcadas; os primeiros ínstares são marrom-claros, passando a marrom escuro com marcas em zigue-zague longitudinais nos últimos ínstares; as pupas são curtas, marrons e sem ornamentações ou projeções, com as capas oculares curtas. Os estágios imaturos são muito similares àqueles de outras espécies do gênero *Yphthimoides* e de outros representantes do "clado *Megisto*". A razão sexual é igual a 1:1 e os adultos voam no dossel, o que pode explicar sua raridade em inventários e coleções de museus quando comparado com outras espécies de *Yphthimoides*.

Key words: Atlantic Forest, life cycle, Satyrinae, Satyrini

INTRODUCTION

Among the Neotropical Satyrini, the subtribe Euptychiina is the most species-rich, with more than 400 described species occurring from USA to Argentina, and with a single genus, Paleonympha, in east Asia (Lamas, 2004; Peña et al., 2010; Marín et al., 2011; Zacca et al., 2018). Due to a combination of: 1) a high number of similar species, 2) a taxonomy based on a relatively limited morphological characters, 3) a large number of cryptic species, and 4) a general lack of in-depth phylogenetic studies, the group became notorious as being difficult to identify and for including several non-monophyletic genera (Freitas, 2004; Seraphim et al., 2014; Marín et al., 2011, 2017; Espeland et al., 2019). In recent years, however, a large international collaborative effort is helping to achieve a better understanding of the entire group (see https://www. floridamuseum.ufl.edu/museum-voices/euptychiina). In addition to its high taxonomic diversity and continuing efforts to better understand the group, Euptychiina figures among the less studied groups of Neotropical butterflies concerning data on behavior and ecology. For example, immature stages are known for only a small fraction of all described species, and detailed descriptions are absent for some large genera, such as Caeruleuptychia Forster, 1964, Chloreuptychia Forster, 1964, and Paryphthimoides Forster, 1964, or restricted to few species in some large genera such as *Euptychia* Hübner, 1818, *Magneuptychia* Forster, 1964, *Forsterinaria* R. Gray, 1973, *Splendeuptychia* Forster, 1964, *Hermeuptychia* Forster, 1964, *Taygetis* Hübner, [1819] and *Yphthimoides* Forster, 1964 (Murray, 2001; Freitas & Peña, 2006; Cosmo *et al.*, 2014; Freitas *et al.*, 2015, 2016a,b, 2019; Freitas, 2017).

The genus *Yphthimoides* Forster, 1964 was erected to include 22 species distributed from Mexico to Argentina (Forster, 1964; see also Lamas, 2004 for a rearrangement of the genus and recent studies of Freitas *et al.* 2012 and Barbosa *et al.* 2015, 2016, 2018). In the original description, the genus was defined based on vague morphological characters of adults, including general color, size and male genitalia. Recent studies showed that the genus is non-monophyletic, based on molecular data (Espeland *et al.*, 2019; Barbosa *et al.*, in prep.) and evidence from immature stages (Freitas, 2004 and unpublished data). In contrast to most Euptychiina, which are more common in tropical forests, species of *Yphthimoides* are typical of open habitats, including dry forests, savannas, grasslands, forest edges and secondary vegetation (Brown, 1992; Freitas, 2004; Freitas *et al.*, 2012; Barbosa *et al.*, 2015, 2016, 2018).

Immature stages have been described for only three *Yphthimoides* species: *Y. cipoensis* Freitas, 2004, *Y. ordinaria* Freitas, Kaminski & Mielke, 2012 and *Y. patricia* (Hayward, 1957) (Freitas, 2004; Freitas *et al.*, 2012; Barbosa *et al.*,

2018), a very poor representation considering there are about 20 species currently assigned to this genus (Barbosa *et al.*, in prep). Accordingly, the present paper describes the immature stages and presents ecological data for *Yphthimoides borasta* (Schaus, 1902).

MATERIAL AND METHODS

Study site: Adults and immatures of *Y. borasta* were studied in montane forest in the Reserva Biológica Municipal da Serra do Japi, Jundiaí, São Paulo State, southeastern Brazil (900-1100 m; 23°13'S, 46°57'W). The area contains semi-deciduous mesophytic forest (Figs. 1A, B) and is seasonal, with a warmwet summer from October to March and a cold-dry winter from April to September (Morellato, 1992). **Sampling and rearing of immature stages**: Eggs were obtained from wild-captured females confined in plastic bags and provided with leaves of several species of grasses accepted by other Euptychiina. Larvae were reared in plastic containers cleaned daily and provided with fresh plant material every two or three days (following Freitas, 2007). Data were recorded on morphology and development time for all stages. Dry head capsules and pupal cases were retained in glass vials. Immature stages were fixed in Kahle-Dietrich solution (Triplehorn & Johnson, 2005). Voucher specimens of the immature stages and adults were deposited in the Zoological Collection of the Museu da Biodiversidade (ZUEC-AVLF), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

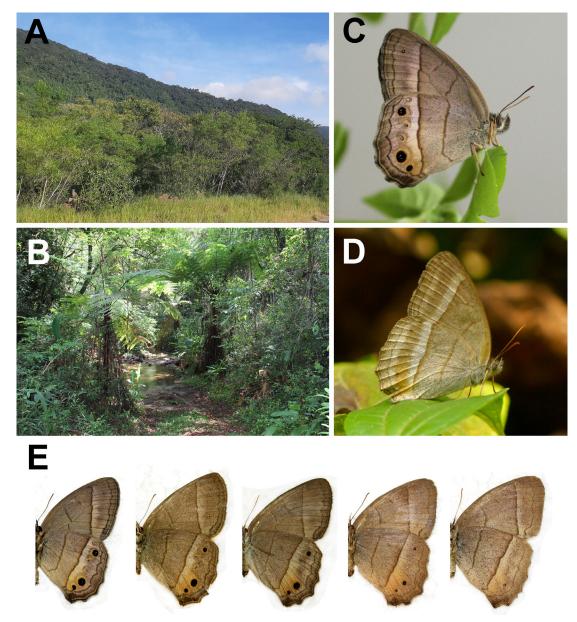


Figure 1. Habitat and adults of *Yphthimoides borasta*. **A.** General view of the habitat in Serra do Japi, Jundiaí, São Paulo. **B.** Close view of the montane forest in the same site. **C.** Extreme wet season form of a reared male from the present study. **D.** Extreme dry season form of a wild photographed male from Nova Lima, Minas Gerais, from late dry season (photo courtesy by Wolfgang Walz). **E.** Gradient of seasonal forms from wet season (December and February, the three on left) to dry season (September and August, the two on the right), all from Serra do Japi, Jundiaí, São Paulo. Leftmost is a reared male from the present study.

Morphology: Measurements were taken and general aspects of morphology were observed using a Leica®MZ7.5 stereomicroscope equipped with a micrometric scale. Egg size is presented as height and diameter, and head capsule size is the distance between the most external stemmata (as in Freitas, 2007). Terminology for early stages descriptions followed García-Barros & Martín (1995) for eggs and Stehr (1987) for larvae and pupae.

Adult ecology: Adults of Y. borasta were studied through a nine-year trap study in Serra do Japi, Jundiaí, São Paulo, Brazil. Fifty traps were placed in five transects at two heights: 25 in the understory (1.5 m above ground) and 25 in the canopy (8-18 m above ground, beneath tree crowns). Traps were installed in groups of ten per transect at alternating heights to avoid the interference of canopy traps on understory traps (following Ribeiro & Freitas, 2012). A standard mixture of mashed banana with sugar cane juice, fermented for at least 48 h, was used as attractant. The bait was placed in plastic pots with a perforated cover inside the traps, which were checked every 48 h and were replaced at each visit. All traps were kept open simultaneously in the field for consecutive periods of five days. Butterflies were sampled monthly from October 2011 to September 2020. All butterflies were marked with an individual number on the ventral surface of the hind wings and released unharmed. For further details about the methods, see Freitas et al. (2014).

RESULTS

Description of immature stages

Egg (Figs. 2A, B). Pinkish white and ellipsoid, with a poorly marked pattern of mostly hexagonal cells. Height 1.26-1.40 mm (n = 4); diameter 1.06-1.18 mm (n = 4); duration 10-12 days (mean = 11.2 days, SD = 0.68 days, n = 13). First instar (Figs. 2C, D). Head capsule width 0.80-0.86 mm (mean = 0.829 mm, SD = 0.0247 mm, n = 9); head scoli 0.07-0.08 mm (mean = 0.078 mm, SD = 0.0044 mm, n = 9). Head black, bearing a pair of very short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body with a pattern of light brown, reddish and white longitudinal stripes; caudal filaments very short. Legs and prolegs light brown. Setae light brown, all dorsal and subdorsal setae clubbed at tip. Maximum length 7 mm. Duration 8-12 days (mean = 9.3 days, SD = 1.58 days, n = 9).

Second instar (Figs. 2E, F). Head capsule width 1.10-1.22 mm (mean = 1.160 mm, SD = 0.0432 mm, n = 10); head scoli 0.20-0.26 mm (mean = 0.218 mm, SD = 0.0199 mm, n = 10). Head dark brown with chestnut brown areas, with two short scoli on vertex. Body brown, with reddish brown and white longitudinal stripes; caudal filaments short. Legs and prolegs light brown. Maximum length 10 mm. Duration 7-10 days (mean = 8.4 days, SD = 1.13 days, n = 9).

Third instar (Figs. 2G, H). Head capsule width 1.50-1.76 mm (mean = 1.605 mm, SD = 0.0826 mm, n = 8); head scoli 0.30-0.36 mm (mean = 0.320 mm, SD = 0.0185 mm, n = 8). Similar to second instar in color and general shape; head light brown with a dark brown dorsal area extending to the posterior region of head scoli, head scoli short; body with longitudinal zigzag patterns. Maximum length 14 mm. Duration 7-10 days (mean = 8.8 days, SD = 0.88 days, n = 9).

Fourth instar (Figs. 2I, J). Head capsule width 2.20-2.50 mm (mean = 2.329 mm, SD = 0.0980 mm, n = 9); head scoli 0.40-0.50 mm (mean = 0.456 mm, SD = 0.0345 mm, n = 9). Similar to third instar but larger and with whitish subdorsal areas in the abdominal segments. Maximum length 22 mm. Duration 9-15 days (mean = 11.4 days, SD = 2.61 days, n = 9).

Fifth (last) instar (Figs. 2K, L). Head capsule width 3.08-3.64 mm (mean = 3.345 mm, SD = 0.1713 mm, n = 8); head scoli 0.62-0.68 mm (mean = 0.636 mm, SD = 0.0229 mm, n = 8). Head similar to previous instars, light brown with a dark brown dorsal area extending to the posterior region of head scoli, with two stubby scoli on vertex. Body light brown with several zigzag longitudinal stripes of different shades of brown and whitish subdorsal areas in the abdominal segments; legs and prolegs light brown; caudal filaments short.

Maximum length 30 mm. Duration 9-22 days (mean = 18.3 days, SD = 6.42 days, n = 7).

Pupa (Figs. 2M, N, O). Short and smooth; mostly dark rusty brown with white areas on wing caps appearing after two days and with short squared ocular caps; cremaster broad, dark in ventral portion; dorsal abdomen with a paired series of short subdorsal white protuberances. Total length 12-13 mm. Duration 14-15 days (mean = 14.2 days, SD = 0.55 days, n = 6).

Behavior and natural history: Oviposition behavior was not observed in the field, and the natural host plant is unknown. In the laboratory, larvae easily accepted cultivated broadleaf carpetgrass Axonopus compressus (Sw.) P. Beauv. ("grama missioneira") (Poaceae), a grass species native to Brazil, and also accepted by other Euptychiina larvae in the laboratory (Freitas, 2003; Freitas et al., 2012; Kaminski & Freitas, 2008; pers. obs.). Larvae are isolated and moved slowly. Adults (Figs. 1C-D, 2P) are present in montane semi-deciduous forests from 700 to 1100 m. In Serra do Japi, adults were only recorded in bait traps (mostly in the canopy, see below), and behaviors such as territorialism and courtship were never directly observed. Two seasonal forms are known: the wet season form is slightly darker with larger and more numerous and conspicuous ocelli on the ventral hindwing (Fig. 1C), while the dry season form is paler with reduced ocelli (Fig. 1D, 2P); intermediates were observed in transitions between seasons (Fig. 1E).

Adult population biology: In total, 137 individuals were captured over nine years sampling in Serra do Japi, 130 in the forest canopy (52 males, 71 females and seven with sex not recorded) and only seven in the understory (three males and four females), indicating a clear preference for the upper stratum ($X^2 = 110.431$, P < 0.0001, DF = 1). A single recapture was recorded in 2015, when a male was recaptured in the following day at the same canopy trap. Adults showed low abundance over the sampling period, being more abundant in 2014 and 2015 (Fig. 3). The sex could be attributed to 130 of the captured individuals, totaling 55 males and 75 females, a sex ratio not significantly different from 1:1 (0.73:1, $X^2 = 3.077$, P = 0.0956, DF = 1). The forewing length of females varied from 2.4 to 3.0 cm (mean = 2.59 cm, SD = 0.106, n = 67) and of males from 2.2 to 2.9 cm (mean = 2.40 cm, SD = 0.113, n = 52), with females being significantly bigger than males (t = 9.687, P < 0.0001, DF = 117).

DISCUSSION

The immature stages of *Y. borasta* follow the most common pattern reported for Euptychiina: eggs are laid singly and larvae are isolated, larvae are slow-moving, with a pair of short head horns on the vertex, a pair of caudal filaments and no body scoli, and the pupae are stubby and smooth, with short ocular caps. In particular, larvae and pupae are very similar to those reported for other species of *Yphthimoides* and related species belonging to the "*Megisto* clade" of Peña *et al.* (2010), such as *Moneuptychia* Forster, 1964, *Pharneuptychia* Forster, 1964, *Carminda* Ebert & Dias, 1998, and *Cissia* Doubleday, 1848 (Barbosa *et al.*, 2018, 2020; Singer *et al.*, 1983 and references therein, AVLF unpublished data). Among the shared characteristics, the brown last instar patterned with longitudinal zigzag stripes, the general profile of the head capsule, the shape of head horns and the

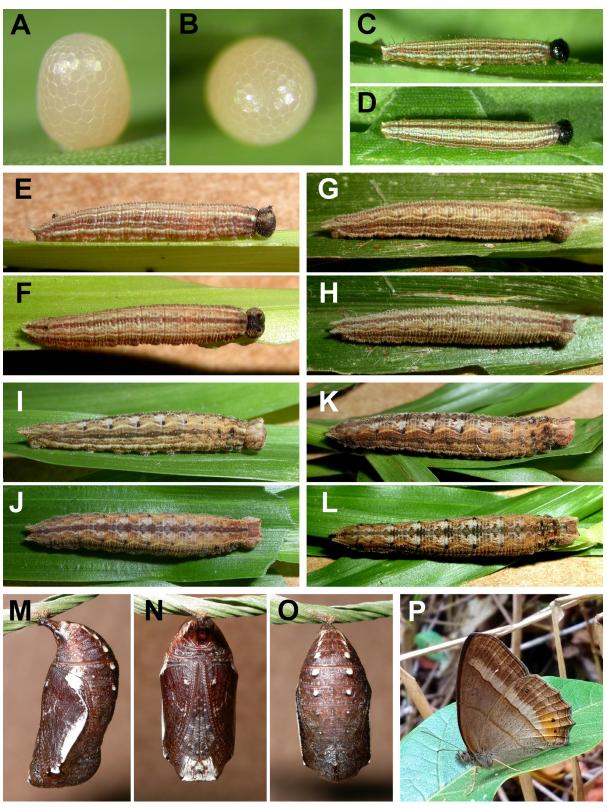


Figure 2. Life stages of *Yphthimoides borasta*. A, B. egg, lateral and dorsal. C, D. first instar, lateral and dorsal. E, F. second instar, lateral and dorsal. G, H. third instar, lateral and dorsal. I, J. fourth instar, lateral and dorsal. K, L. fifth (last) instar, lateral and dorsal. M, N, O. pupa, lateral, ventral and dorsal. P. adult male from Minas Gerais (photo courtesy of Laura Braga).

general pupal shape and profile are notable. Even though the immature stages resemble those of other known *Yphthimoides* (see Freitas, 2004; Freitas *et al.*, 2012; Barbosa *et al.*, 2018), curiously the larvae are not remarkably similar to those of *Y*.

cipoensis, a closely related species according to Barbosa *et al.* (in prep.); larvae of *Y. cipoensis* passed through only four instars and last instar are more slender, grayish, with a well-marked dorsal dark brown stripe (Freitas, 2004), while larvae

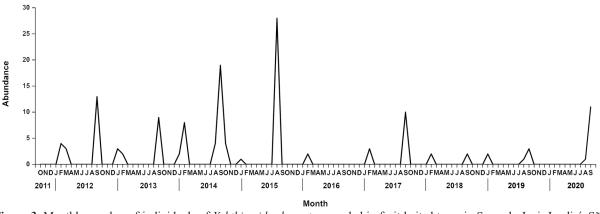


Figure 3. Monthly number of individuals of *Yphthimoides borasta* recorded in fruit-baited traps in Serra do Japi, Jundiaí, São Paulo State, Brazil, from October 2011 to September 2020.

of *Y. borasta* have five instars, are more stubby, brownish and show no conspicuous dorsal stripe (present study).

All reared adults displayed a wing pattern with six larger ocelli on the ventral hindwing, quite distinct from most field-collected specimens, which usually showed only four small black ocelli (Figs. 1 C-E and Fig. 2P). Seasonal forms are known in several other species of Satyrini (including *Yphthimoides*), with the summer forms presenting larger and more numerous ocelli than the winter forms (e.g. Brakefield & Larsen, 1984; Brakefield & Reitsma, 1991; Freitas *et al.*, 2010; Barbosa *et al.*, 2018). In addition, larvae reared in laboratory conditions usually give rise to summer form adults, possibly as a consequence of controlled temperature and high humidity inside the containers (AVLF unpublished). In this sense, the phenotype obtained here could represent an extreme summer form, usually rare in the mostly cold montane habitats where *Y. borasta* occurs.

Most species of Yphthimoides are locally common and easily observed on open areas and forest edges, usually flying near the ground (Brown, 1992; Freitas, 2004; Freitas et al., 2012; Barbosa et al., 2015, 2016, 2018). However, Y. borasta diverges from these patterns, being rarely recorded during field work and with usually very few specimens observed on a single day (AVLF pers. obs.), making it relatively scarce in collections and inventories (see data in Santos et al., 2018 and Shirai et al., 2019). A second characteristic is even more remarkable: at least at Serra do Japi, 95% of all individuals were captured in canopy traps, suggesting that this is a canopy-dwelling species, a pattern distinct from all other Yphthimoides species and for most Euptychiina (DeVries, 1987; Brown, 1992 and unpublished results from the authors). This could explain why Y. borasta remained undetected for three decades of inventories in Serra do Japi, until its first capture on February 8, 2012 in a canopy trap. Although most known Euptychiina fly low to the ground, as additional ecological studies have become available, several canopy-dwelling species have been revealed, such as Megeuptychia antonoe (Cramer, 1775) (DeVries & Walla, 2001; Ribeiro & Freitas, 2012), Atlanteuptychia ernestina (Weymer, 1911) (Freitas et al., 2013) and Caeruleuptychia ca. cyanites (Lourenço et al., 2019). In fact, as suggested by Singer et al. (1983), several species of Euptychiina that are rare and scarce in collections could be in fact canopy-dwelling species that are seldom observed in the understory.

In summary, a better knowledge of other aspects than just adult morphology and molecular data is crucial to advance understanding of the evolution of Euptychiina butterflies. These include knowledge of the immature stages and host plants, natural enemies, population ecology and general behavior (of both adults and immatures), all aspects that have been neglected for many species-rich groups of Neotropical butterflies.

ACKNOWLEDGMENTS

Thanks to André Tacioli and all members of the LABBOR for helping in the field work in Serra do Japi. Jessie Santos and Leila Shirai helped with some information on adults of Y. borasta. Laura Braga and Wolfgang Walz kindly sent us pictures of adults photographed in the field. Thamara Zacca and an anonymous referee revised the submitted version. EPB and JYOC thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for their graduate fellowships (CAPES Finance Code 001). EPB thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for post-doc fellowships (2016/15873-8, 2018/21432-0). JYOC also thanks the Brazilian Research Council - CNPq for graduate and technical fellowships (141443/2018-9, 381029/2019-0, respectively). AVLF acknowledges support from FAPESP (Biota-Fapesp - grants 2011/50225-3, 2013/50297-0), from the Brazilian Research Council - CNPq (fellowship 302585/2011-7, 421248/2017-3) and from the National Science Foundation (DEB-1256742). This publication is part of the RedeLep 'Rede Nacional de Pesquisa e Conservação de Lepidópteros' SISBIOTA-Brasil/CNPg (563332/2010-7). The butterfly species is registered in the SISGEN (AB6BCEF).

LITERATURE CITED

- Barbosa, E. P., Silva, A. K., Paluch, M., Azeredo-Espin, A. M. L., Freitas, A. V. L. 2015. Uncovering the hidden diversity of the Neotropical butterfly genus *Yphthimoides* Forster (Nymphalidae: Satyrinae): description of three new species based on morphological and molecular data. *Organisms, Diversity & Evolution* 15: 577-589.
- Barbosa, E. P., Marín, M. A., Giraldo, C. E., Uribe, S., Freitas, A. V. L. 2016. Description of two new species of the Neotropical genus *Yphthimoides* Forster, 1964 (Lepidoptera: Nymphalidae: Satyrinae) from the 'renata clade'. *Neotropical Biodiversity* 2(1): 87-98.

- Barbosa, E. P., Siewert, R. R., Mielke, O. H. H., Lamas, G., Willmott, K. R., Freitas, A. V. L. 2018. Redescription of *Yphthimoides patricia* (Hayward, 1957), with taxonomic notes on the names *Euptychia saltuensis* Hayward, 1962 and *Yphthimoides manasses* (C. Felder & R. Felder, 1867) (Nymphalidae: Satyrinae). *Zootaxa* 4422: 537-557.
- Barbosa, E. P., Aguiar, T. M. C., Rosa, A. H. B., Zacca T., Freitas, A. V. L. 2020. A new species of butterfly (Lepidoptera: Nymphalidae) from the highlands of southeastern Brazil. *Zootaxa* 4819: 128-142.
- Brakefield, P. M., Larsen, T. B. 1984. The evolutionary significance of dry and wet season forms in some tropical butterflies. *Biological Journal of the Linnean Sociey* 22: 1-12.
- Brakefield, P. M., Reitsma, N. 1991. Phenotypic plasticity, seasonal climate and the population biology of *Bicyclus* butterflies (Satyridae) in Malawi. *Ecological Entomology* 16: 291-303.
- Brown, K. S. Jr. 1992. Borboletas da Serra do Japi: Diversidade, hábitats, recursos alimentares e variação temporal, pp. 142-187. In: Morellato, L. P. C. (Ed.), História natural da Serra do Japi. Ecologia e preservação de uma área florestal no Sudeste do Brasil. Campinas, Editora da Unicamp/Fapesp.
- Cosmo, L. G., Barbosa, E. P., Freitas, A. V. L. 2014. Biology and morphology of the immature stages of *Hermeuptychia atalanta* (Lepidoptera: Nymphalidae: Satyrinae). *Annales de la Société entomologique de France* (N.S.) 50: 82-88.
- **DeVries, P. J.** 1987. *The Butterflies of Costa Rica and their Natural History. Papilionidae, Pieridae, Nymphalidae*. Princeton, Princeton University Press. 327 pp.
- DeVries P. J., Walla, T. R. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society* 74: 1-15.
- Espeland, M., Breinholt, J., Barbosa, E. P., Casagrande, M. M., Huertas, B., Lamas, G., Marín, M. A., Mielke, O. H. H., Miller, J. Y., Nakahara, S., Tan, D., Warren, A. D., Zacca, T., Kawahara, A., Freitas, A. V. L., Willmott, K. R. 2019. Four hundred shades of brown: Higher level phylogeny of the problematic Euptychiina (Lepidoptera, Nymphalidae, Satyrinae) based on hybrid enrichment data. *Molecular Phylogenetics and Evolution* 131: 116-124.
- Forster, W. 1964. Beiträge zur Kenntnis der Insekten fauna Boliviens XIX Lepidoptera III. Satyridae. Veröffentlichungen der Staatssammlung München 8: 51-188.
- Freitas, A. V. L. 2003. Description of a new genus for "Euptychia" peculiaris (Nymphalidae: Satyrinae): Immature stages and systematic position. Journal of the Lepidopterists' Society 57: 100-106.
- Freitas, A. V. L. 2004. A new species of *Yphthimoides* (Nymphalidae, Satyrinae) from southeastern Brazil. *Journal of the Lepidopterists' Society* 58: 7-12.
- Freitas, A. V. L. 2007. A new species of *Moneuptychia* Forster (Lepidoptera: Satyrinae, Euptychiina) from the highlands of southeastern Brazil. *Neotropical Entomology* 36: 919-925.
- Freitas, A. V. L. 2017. Immature stages of the Neotropical satyrine butterfly *Taygetis acuta* (Nymphalidae: Euptychiina). *Tropical Lepidoptera Research* 27: 1-5.
- Freitas, A. V. L., Peña, C. 2006. Description of genus *Guaianaza* for "*Euptychia*" pronophila (Lepidoptera: Nymphalidae: Satyrinae) with a description of the immature stages. *Zootaxa* 1163: 49-59.
- Freitas, A. V. L., Emery, E. O., Mielke, O. H. H. 2010. A new species of Moneuptychia Forster (Lepidoptera: Satyrinae: Euptychiina) from Central Brazil. Neotropical Entomology 39: 83-90.
- Freitas, A. V. L., Kaminski, L. A., Mielke, O. H. H., Barbosa, E. P., Silva-Brandão, K. L. 2012. A new species of *Yphthimoides* (Lepidoptera: Nymphalidae: Satyrinae) from the southern Atlantic forest region. *Zootaxa* 3526: 31-44.
- Freitas, A. V. L., Barbosa, E. P., Santos, J. P., Mielke, O. H. H. 2013. A new genus, Atlanteuptychia gen. nov., for Euptychia ernestina (Lepidoptera: Nymphalidae: Satyrinae). Zoologia 30: 661-668.
- Freitas, A. V. L., Iserhard, C. A., Santos, J. P., Carreira, J. Y. O., Ribeiro, D. B., Melo, D. H. A., Rosa, A. H. B., Marini-Filho, O. J., Accacio, G. M., Uehara-Prado, M. 2014. Studies with butterfly bait traps: an overview. *Revista Colombiana de Entomologia* 40: 209-218.
- Freitas, A. V. L., Barbosa, E. P., Siewert, R. R., Mielke, O. H. H., Zacca, T., Azeredo-Espin, A. M. L. 2015. Four new species of *Moneuptychia* (Lepidoptera: Satyrinae: Euptychiina) from Brazil. *Zootaxa* 3981: 521-541.

- Freitas, A. V. L., Barbosa, E. P., Marín, M. A. 2016a. Immature stages and natural history of the Neotropical satyrine *Pareuptychia ocirrhoe interjecta* (Nymphalidae: Euptychiina). *Journal of the Lepidopterists' Society* 70: 271-276.
- Freitas, A. V. L., Carreira, J. Y. O., Santos, J. P., Barbosa, E. P. 2016b. Immature stages and natural history of two species of *Forsterinaria* from southeastern Brazil (Lepidoptera: Nymphalidae). *Tropical Lepidoptera Research* 26: 13-18276.
- Freitas, A. V. L., Mota, L. L., Barbosa, E. P., Carreira, J. Y. O. 2019. Immature stages of the *Selaginella*-feeding *Euptychia mollina* (Nymphalidae: Satyrinae) from the Brazilian Amazon. *Zoologia* 36: e32053.
- García-Barros, E., Martín, J. 1995. The eggs of European satyrine butterflies (Nymphalidae): external morphology and its use in systematics. *Zoological Journal of the Linnean Society* 115: 73-115.
- Kaminski, L. A., Freitas, A. V. L. 2008. Immature stages of the butterfly Magneuptychia libye (L.) (Lepidoptera: Nymphalidae, Satyrinae). Neotropical Entomology 37: 169-172.
- Lamas, G. 2004. Nymphalidae. Satyrinae. Euptychiina, pp. 217-223. In: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea Papilionoidea. In: Heppner, J. B. (Ed.), Atlas of Neotropical Lepidoptera. Volume 5A. Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- Lourenço, G. M., Luna, P., Guevara, R., Dáttilo, W., Freitas, A. V. L., Ribeiro, S. P. 2019. Temporal shifts in butterfly diversity: responses to natural and anthropic forest transitions. *Journal of Insect Conservation* 24: 353-363.
- Marín, M. A., Peña, C., Freitas, A. V. L., Wahlberg, N., Uribe, S. I. 2011. From the phylogeny of the Satyrinae butterflies to the systematics of Euptychiina (Lepidoptera: Nymphalidae): History, progress and prospects. *Neotropical Entomology* 40: 1-13.
- Marín, M. A., Peña, C., Uribe, S. I., Freitas, A. V. L. 2017. Morphology agrees with molecular data: phylogenetic affinities of Euptychiina butterflies (Nymphalidae: Satyrinae). *Systematic Entomology* 42: 768-785.
- Morellato, L. P. C. 1992. História Natural da Serra do Japi: ecologia e preservação de uma área no sudeste do Brasil. Campinas, Editora da UNICAMP/FAPESP.
- Murray, D. L. 2001. Immature stages and biology of *Taygetis* Hübner (Lepidoptera: Nymphalidae). *Proceedings of the Entomological Society of Washington* 103: 932-945.
- Peña, C., Nylin, S., Freitas, A. V. L., Wahlberg, N. 2010. Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera, Nymphalidae, Satyrinae). *Zoologica Scripta* 39: 243-258.
- Ribeiro, D. B., Freitas, A. V. L. 2012. The effect of reduced impact logging on fruitfeeding butterflies in Central Amazon, Brazil. *Journal of Insect Conservation* 16: 733-744.
- Santos, J. P., Freitas, A. V. L., Brown, K. S., Carreira, J. Y. O., Gueratto, P. E., Rosa, A. H. B., Lourenço, G. M., Accacio, G. M., Uchara-Prado, M., Iserhard, C. A., Richter, A., Gawlinski, K., Romanowski, H. P., Mega, N., Oliveira, M. T., Oliveira, A. M., Ribeiro, D. B., Araujo, P. F., Filgueiras, B., Cordeiro, K., Melo, D. H. A., Leal, I. R., Beirão, M. V., Ribeiro, S. P., Cambuí, E. C. B., Vasconcelos, R. N., Cardoso, M. Z., Paluch, M., Greve, R. R., Voltolini, J. C., Galetti, M., Regolin, A. L., Sobral-Souza, T., Ribeiro, M. C. 2018. Atlantic butterflies: a data set of fruit-feeding butterfly communities from the Atlantic forests. *Ecology* 99: 2875-2875.
- Seraphim, N., Marín, M. A., Freitas, A. V. L., Silva-Brandão, K. L. 2014. Morphological and molecular marker contributions to disentangling the cryptic *Hermeuptychia hermes* species complex (Nymphalidae: Satyrinae: Euptychiina). *Molecular Ecology Resources* 14: 39-49.
- Shirai, L. T., Machado, P. A., Mota, L. L., Rosa, A. H. B., Freitas, A. V. L. 2019. DnB, the Database of nymphalids in Brazil, with a checklist for standardized species lists. *Journal of the Lepidopterists' Society* 73: 93-108.
- Singer, M. C., DeVries, P. J., Ehrlich, P. R. 1983. The Cissia confusa speciesgroup in Costa Rica and Trinidad (Lepidoptera: Satyrinae). Zoological Journal of the Linnean Society 79: 101-119.
- Stehr, F. W. 1987. Order Lepidoptera, pp. 288-305. In: Stehr F. W. (Ed), Immature Insects. Volume 1. Dubuque, Kendall-Hunt Publishing Company.
- Triplehorn, C. A., Johnson, N. F. 2005. *Borror and Delong's Introduction to the Study of the Insects*. Belmont, Thomson Brooks/Cole. 864 pp.
- Zacca T., Barbosa, E. P., Freitas, A. V. L. 2018. *Euptychiina Species Checklist*. https://www2.ib.unicamp.br/labor/site/?page_id=1020.