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BUTTERFLY KLEPTOPARASITISM AND FIRST ACCOUNT OF IMMATURE STAGES, MYRMECOPHILY, AND BAMBOO HOST PLANT OF THE METALMARK *ADELOTYPA ANNULIFERA* (RIODINIDAE)

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ABSTRACT. This paper describes the life history, host plant use, and myrmecophily of the Neotropical riodinid butterfly *Adelotypa annulifera* (Godman, 1903) in Tambopata, Peru. Eggs of *A. annulifera* are laid at the tips of new growth bamboo culm sheaths bearing extrafloral nectary sites where adult butterflies and ants gather to feed. *Adelotypa annulifera* larval stages are actively tended by multiple species of ants and were observed feeding on the extrafloral nectaries of the bamboo. Pupation of *A. annulifera* occurs on the host plant near the base of the bamboo. We also document the potential kleptoparasitic behavior of adult butterflies on ant species that tend the caterpillars. To our knowledge, this is the first account describing the immature stages and life history of a species belonging to the genus *Adelotypa* and the first account of adult riodinid butterfly kleptoparasitism on ants.

Additional key words: bamboo, extrafloral nectaries, Nymphidiini, Peru, Tambopata

The metalmark butterflies of the family Riodinidae are diverse, small bodied, and primarily confined to the Neotropics, where approximately 1300 described species occur (Heppner 1991, Robbins 1993, Hall & Harvey 2002). Members of this family exhibit substantial phenotypic diversity, utilize a wide array of host plant families, and many immatures of these species engage in relationships with ants (myrmecophily) (DeVries 1997, Pierce et al. 2002, Kaminski et al. 2013). In these myrmecophilous relationships, caterpillars feed and communicate with ants in exchange for the ants' active protection from parasitoids and predators. Among the Lepidoptera, myrmecophily is unique to the family Riodinidae and their larger sister family Lycaenidae (Fiedler 1991, Pierce et al. 2002). Riodinidae are monophyletic, originated in the Neotropics, and are estimated to have split from Lycaenidae around 96 Mya in the mid-Cretaceous (Espeland et al. 2015).

Myrmecophily in riodinid larvae is associated with specialized organs that produce nutritional resources and semiochemicals as well as an organ to communicate acoustically with ants (Ross 1964, Fiedler et al. 1996, DeVries 1988). Myrmecophilous butterfly larvae secrete substances that attract and appease their attendant ants, including sugars and amino acids that the ants harvest from specialized exocrine glands (Pierce 1983). The majority of myrmecophilous larvae feed exclusively on plant tissue, but some feed on insect-derived food sources including ant eggs, larvae, pupae, and ant regurgitation (Cottrell 1984). Myrmecophilous butterflies, their attendant ants, host plants, and natural enemies have become a model for the study of insect-plant interactions, chemical communication, mutualism, biodiversity, conservation, and the evolution of complex life history traits (Pierce 1984). The family Riodinidae is interesting not only for its species diversity but also for its great morphological and ecological diversity. Butterflies in this family exhibit the greatest variation in wing shape, color and pattern relative to any other butterfly family and mimic species belonging to other lepidopteran families (DeVries 1997). Their biology is poorly known relative to other butterfly groups, yet the study of riodinids has the potential to provide insights into several aspects of evolutionary biology, including mimicry-driven phenotypic plasticity and myrmecophily (D'Abrera 1994, DeVries 1991).

The study organism *Adelotypa annulifera* (Godman, 1903) is a Neotropical riodinid butterfly currently placed in the tribe Nymphidiini that ranges from the Guyana Shield to Bolivia. Nymphidiini is the largest of the tribes in the Riodinidae (Hall 1999) with over 300, often rare, species and it is thought to be an entirely myrmecophilous tribe (Hall & Harvey 2002). The majority of riodinid species have unknown life histories (DeVries et al. 1992) and until now, there are no published accounts on the larval biology of members belonging to the genus *Adelotypa* (Penz & DeVries

2006). Here we provide the first detailed description of the biology and behavior of *A. annulifera* immatures and adults.

METHODS

Field observations were carried out in proximity of the Tambopata Research Center (TRC, 13°8'1.13" S, 69°36'46.11" W) in the Tambopata National Reserve of Southeastern Peru during May and August 2013, December 2014, January and May 2015. The Tambopata rainforest has five major forest types: terra firme (upland forest, mature floodplain forest), primary successional floodplain forest, swamp forest, and bamboo forest. Mean annual rainfall at TRC is approximately 3,150 mm and greater than 80% of the rainfall in this region occurs during the October–May wet season. The monthly temperature ranges between 21–27° C year-round, and there is a weak seasonal signal in temperature (Brightsmith 2004).

Initial observations of adult *A. annulifera* butterflies feeding on bamboo sap in association with ants were made in May 2013. Bamboo plants were visually scanned for the presence of eggs, larvae and tending ants. During daily inspections of plants containing larvae and ants we documented and photographed larval instars, the adult feeding behavior in association with ants, and the species of ants. Four pupae of unknown age were collected at a bamboo culm sheath in December 2014 and brought to the Tambopata Research Center to be reared. Measurements were taken with a ruler and general aspects of larval morphology observed using a stereomicroscope. Color patterns of *A. annulifera* immature stages and adults in vivo were recorded using a Canon 70D DSLR camera equipped with a 100mm macro lens. Terminology for early stage descriptions follows Downey and Allyn (1980) for eggs, Stehr (1987) for general morphology of larvae, Mosher (1916) for pupae, and DeVries (1988) for ant-organs.

RESULTS

Natural history of *Adelotypa annulifera*. This species occurs in primary rainforest at altitudes between about 400–700m. In this study, six male butterflies and five female butterflies were observed in the field feeding on the extrafloral nectaries at the tips of bamboo shoots, always in association with ants. Up to three *A. annulifera* butterflies were observed feeding at the same time at a nectary and while the males fed throughout the day and would return when disturbed, the females only fed for short periods of time (less than one hour) and did not return to the site when disturbed. The behavior typically started with the butterflies fluttering around various shoots and they were only observed landing and feeding in the presence of ants. Upon landing, the butterflies walked towards the location of the flowing sap while probing with their proboscis. Once the location of the sap flow was located, the butterflies spent up to several hours at the same location. One butterfly, identified by a missing part of its left hind wing, was seen at the same flow three days in a row. Though observations were not continuous throughout each day, the butterfly was seen at the same location as early as 0900 h and as late as 1730 h on the same day. If disturbed, the butterflies would fly away and often land on the underside of a nearby leaf. After several minutes to an hour the butterflies eventually returned to the plant, though not always to the same nectary location, as each bamboo often had multiple areas of ants feeding. Despite seeing males and females share nectaries for extensive periods of time, no mating attempts were observed.

A total of 13 eggs laid in clusters of four to five were observed on early growth bamboo near the culm sheath tips approximately 0.5–1.0 meter above ground. The larvae were solely observed feeding at bamboo extrafloral nectaries and remained present on the bamboo in association with ants throughout all instars. On 8 December 2014, two final instar larvae and two pupae of unknown age were found at the base of a bamboo culm sheath. On 10 December 2014 the two larvae pupated at the same location and the four pupae total were collected and brought to the Tambopata Research Center to be reared. Only one of the pupae eclosed to an adult four days after collection, which was identified as a female *A. annulifera*.

Description of immature stages. Egg: Dorso-ventrally flattened, grayish color, general spherical shape, convex, exochorion with hexagonal cells in lateral view, slightly depressed micropylar area centered on the top surface (Fig. 1A). Oviposition occurs at the tips of new growth bamboo culm leaves.

First instar: Head capsule light brown, body dorso-ventrally compressed, body reddish with four longitudinal light bands, total length 2.1 mm (n=2) (Fig. 1B). Prothoracic and anal plate same color as body. Body with short setae in lateral areas and in prothoracic and anal shields. The larvae remain in physical contact with an individual bamboo host plant and feed on the liquid extrafloral nectar produced at the tips of new growth shoots.

Mid instars: Head capsule light brown, body reddish to light brown with four longitudinal light bands, total length ranges from 5.6–6.4 mm (n=3) (Fig. 1C–D, Fig. 2). Prothoracic and anal shields light brown. Ant-organs present, including tentacle nectary organs (TNOs) on

FIG. 1. Immature stages of *Adelotypa annulifera* on bamboo and their association with ants. (**A**) Eggs with *Megalomyrmex balzani.* (**B**) First instar larva with *Ectatomma tuberculatum*. (**C**) Mid-instar larva with *Pheidole* sp. (**D**) Mid-instar larvae with *Paraponera clavata*. (**E**) Final instar larvae with *E. tuberculatum*. (**F**) Pupae.

FIG. 2. Dorsal (left) and lateral (right) views of early instar *Adelotypa annulifera*.

FIG. 3. Final instar larva (left) dorsal, lateral, and ventral view. Presence of tentacle nectary organ (TNO) on abdominal segment 8. Pupa (right) dorsal, lateral, and ventral view.

the eighth abdominal segment which appear similar to those described in *Lemonias caliginea* (in Ross, 1964, as *Anatole rossi*) and *Thisbe irenea* (DeVries 1988) and one pair of vibratory papillae (VPs) located on anterior border of the prothoracic shield, anteriorly directed, similar in overall appearance to those described by Ross (1964, 1966) and DeVries (1988). Later instar body becomes greenish in color (Fig. 2), head capsule lighter yellow color, general aspects of morphology similar to preceding instars'.

Final instar: Head brown, body turns to a light brown and beige color, total length 12.5 mm (n=2) (Fig. 1E, Fig. 3). Prior to pupation, final instars found at base of bamboo host plant under tan colored culm leaf. Prominent tentacle nectary organs on abdominal segment 8.

Pupa: Body variegated coloring with light brown, beige, and dark spots, abdominal segments mobile, total length 12.1 mm (n=2) (Fig. 1F, Fig. 3) Tegument is entirely sculptured with irregular striations and lacking prominent tubercles. Silk girdle crossing the A1 segment near one pair of dark spiracles. Pupation occurs on the same host plant near the base of the bamboo under the culm leaf.

DISCUSSION

Interactions of immature stages with ants on bamboo. All life stages of *A. annulifera* were observed in association with ants on young bamboo shoots. At least four different species of ants were observed in association with *A. annulifera* immatures: *Ectatomma tuberculatum* (Fig. 1B, 1E), *Pheidole* sp. (Fig. 1C), *Megalomyrmex balzani* (Fig. 1A), and *Paraponera clavata* (Fig. 1D). In each case, only one species of ant was present on each bamboo plant. It is possible that the ants claim and defend their bamboo from other ant species for access to the extrafloral nectaries and caterpillar secretions.

Ectatomma tuberculatum (Formicidae) was one of the most prevalent ant species at the study site. The genus *Ectatomma* is unusual in that all species spend large fractions of their life harvesting secretions from extrafloral nectaries (EFNs), sap-feeding hemipterans, and myrmecophilous butterfly larvae (DeVries 1991, Bentley 1977, Wheeler 1986). At one site, *E. tuberculatum* ants were observed feeding at the same extrafloral nectary as both larval and adult *A. annulifera*. This relationship contrasts with the observations by Ross (1964 and 1966) in which the myrmecophilous riodinid larvae of *Lemonias caliginea* (in Ross, 1964, as *Anatole rossi*) are preyed upon by *E. tuberculatum* workers in Mexico. However, DeVries (1988) observed the riodinid larvae of *Thisbe irineae* associating primarily with *E. ruidum* as well as *E. tuberculatum* workers in Panama and devised an experiment to explain this difference in *Ectatomma* behavior. *Thisbe irineae* larvae were exposed to a species of *Azteca* ant and were then offered to *E. ruidum* workers where they were subsequently attacked and killed, presumably because the riodinid larvae had acquired an *Azteca* ant chemical odor (DeVries 1988). Future experiments on *A. annulifera* could be performed to determine if larvae are attacked by workers of one ant species after exposure to another ant species.

At another site, high numbers of *Pheidole* ant workers (n=6-33) were observed surrounding early instar *A. annulifera* larvae (Fig. 1C). When the caterpillars were physically disturbed, *Pheidole* soldiers and more workers were recruited to defend the caterpillar. *Megalomyrmex balzani* were seen at two different bamboo shoots (May and August 2013) and were only observed in association with adults and eggs. Interestingly, *Paraponera clavata* were observed tending numerous *A. annulifera* larvae in May 2015 and would aggressively fend off invading insects, as well as one of the researchers, on the bamboo stalk (Fig. 1D).

Based on our observations, *A. annulifera* appears to be an ant generalist and future work will help to reveal further details of the butterfly-ant relationships. A satisfying evolutionary explanation is unknown as to why some myrmecophilous riodinids and lycaenids are allied with only a single species of ant whereas others are generalists (Pierce 1984, Pierce et al. 2002).

Bamboo as a host plant. Two common species, *Guadua sarcoparpa* Londono and Peterson and *Guadua weberbaueri* Pilger (Poaceae: Bambuseae) dominate the bamboo forests in southwestern Amazonia (Griscom & Ashton 2006). Bamboo forests cover approximately 180,000 km^2 in southwestern Amazonia, representing the largest bamboo-dominated forest in the Neotropics. These plants are biologically interesting because they primarily occur as mono-dominant forests with a patchy distribution throughout terra firma and floodplain forests (Nelson 1994, Griscom & Ashton 2003). Bamboo forests have been assumed to be a species-poor, weedy habitat, but researchers are discovering that bamboo forests are an important component of the regional ecosystem in southwestern Amazonia (Emmons & Feer 1990, Kratter 1997).

It is common for many species of ants, wasps, beetles, flies, bees, hemipterans, and other insects to forage on the extrafloral nectaries of the bamboo (personal observation). Using their mandibles, ants appear to manipulate the tips of the shoots to improve the flow of nectar and will guard bamboo stalks against other insects. Young bamboo grows rapidly and, considering nectaries were the only observed food source for the *A. annulifera* larvae, the fluids secreted from the nectaries likely contain sugars and amino acids. Future research should investigate the contents of this bamboo extrafloral nectar and potential nutritional benefits for Neotropical arthropod fauna, including the immature stages of *A. annulifera*.

The family Riodinidae contains immature stages with diverse diets, which include live and dead leaves, flower buds, fungi, extrafloral nectar, and cases of entomophagy (DeVries et al. 1997; DeVries & Penz 2000). Bamboo is a relatively unusual host plant choice for Lepidoptera immatures and this appears to be the first record as a host plant for a species belonging to Riodinidae. For Riodinidae, it has been proposed that obligate symbiotic relationships with ants are associated with an expansion in the number of host plants (polyphagy) (DeVries et al. 1992, DeVries 1997, Hall & Harvey 2001). The tendency of female butterflies to oviposit in the presence of ants could lead to 'mistakes' in plant selection and as a result, polyphagy could evolve more easily in myrmecophilous butterflies than in non-myrmecophilous ones (Pierce 1984; Pierce & Elgar 1985). Perhaps the utilization of bamboo as a host plant by *A. annulifera* was initiated by the butterflies ovipositing near bamboo nectary sources in the presence of ants.

As the bamboo grows and develops, portions of the shoots and leaves change color. Interestingly, *A. annulifera* instar coloration changes as well and seems to match the appearance of the host plant. For instance, early instar caterpillars appear to be reddish in color, as are the young bamboo tips they feed under. Later instars become more greenish in color, like the green bamboo they are exposed on, and final instars and pupae become beige colored which coincides with the color of the dead culm leaves.

Adult butterfly-ant interactions: a case of kleptoparasitism. There are few reports of ants interacting with the adult butterflies of myrmecophilous riodinids or lycaenids, or if they do, ants treat the butterflies much as they would any insect prey. To investigate the specificity of the butterfly-ant relationship, one of the authors presented the *M. balzani* ants with three live unidentified species of moth, similar in size to *A. annulifera* adults, which the ants immediately proceeded to attack. While adult *A. annulifera* were feeding, ants would investigate various parts of the butterflies with their antennae and at times crawl over their head, legs, and open wings (Fig. 4A-D). Taken together, these observations support the idea that *A. annulifera* has co-evolved in the presence of ants and the adult butterflies are somehow able to reduce their aggressive behavior.

These ants not only tolerate the presence of the butterflies, but the butterflies appear to display a kleptoparasitic behavior by taking a nectar resource from the ants. Butterflies were seen feeding exclusively from bamboo nectary flows, a resource which the ants were protecting, feeding upon, and maintaining (Fig. 4D–F). The ants attempted to remove the butterflies' proboscises to gain better access to the fluid, but would eventually settle with little to no access and wait. In addition, butterflies were twice observed drinking bamboo fluid directly out of an ant's mandibles, essentially stealing a resource with no consequence (Fig. 4F). Ants were seen antennating the terminal portion of the butterfly's abdomen for extensive periods

FIG. 4. Adult *Adelotypa annulifera* interactions with ants on bamboo. (**A**) Antennation of adult butterfly wings. (**B**) Ant crawling on butterfly wing. (C) Antennation of butterfly abdomen. (**D-E**) Butterflies and ants utilizing extrafloral nectary source on bamboo. (**F**) Butterfly drinking bamboo fluid directly from *Ectatomma* ant mandibles.

FIG. 5. Adult *Adelotypa annulifera* putative wing pattern mimicry. (**A**) Male (left) and female (right) butterflies perched on bamboo shoot in presence of *Megalomyrmex balzani* ants. View of *A. annulifera* wing pattern: (**B**) Ventral (**C**) Dorsal (**D**) Lateral.

of time, not unlike when the ants antennate the caterpillars in return for a nectar reward (Fig. 4C), however, extensive observations revealed that the butterflies did not provide any apparent resource for the ants. Thievery of a food source (kelptoparasitism) occurs in many arthropod groups (Eisner et al. 1991; Sivinsky et al. 1999) and in this case, *A. annulifera* adult butterflies appear to display a kelptoparasitic behavior towards attendant ants by taking a nutritive resource, in this case bamboo sap secretions (Fig. 4D–F).

Several observations in the Lycaenidae suggest that chemical interactions between adult butterflies and ants may be more complex than currently appreciated and some adults may appease ants that would otherwise attack them. In *Curetis regula*, butterfly adults feed on leaf tissue damaged by their larvae alongside the larvae's attendant ants (DeVries 1984). The butterflies could emit a chemical signal which appeases the ants or mimics cuticular hydrocarbons to reduce aggressive behavior. Future studies should investigate the chemical profiles emitted from *A. annulifera* larvae and adults. Overall, this potentially kleptoparasitic interaction between *A. annulifera* and ants is, to our knowledge, the first documented case of this behavior in the family Riodinidae.

Finally, the red markings on the *A. annulifera* butterfly wings, at least to a human observer, are strikingly ant-like in appearance (Fig. 5A–D). For example, the size and color of the wing spots are similar to the body segment size and color of the *Megalomyrmex* and *Ectatomma* ants that *A. annulifera* adults were observed associating with (Fig. 4, Fig. 5), suggestive of mimicry. Cases of myrmecomorphy (arthropods that mimic ants morphologically and/or behaviorally) have been described in over 2000 arthropods and include groups such as spiders, beetles, and hemipterans (McIver 1993). Some salticid spiders mimic ants to avoid being preyed upon by them and other ant-mimics likely gain protection from all predators that tend to avoid ants (Cushing 2012). In a striking case of a lepidopteran mimicking a predator, the metalmark moth *Brenthia hexaselena* has evolved to mimic jumping spiders with wing markings, wing positioning, posture, and movement (Rota and Wagner 2006). Members of Riodinidae exhibit a wide array of wing shapes and patterns (DeVries et al. 1992; Robbins & Busby 2015) and it is possible that selective pressures by predation have resulted in butterfly wing-patterns resembling noxious ants. While this observation requires more scrutiny, the red wing markings on *A. annulifera* adults could serve as visual mimicry of the ants that the butterflies associate with and could function to ward off would-be visual predators.

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LITERATURE CITED

BENTLEY, B. L. 1977. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). J. Ecology 65:27–38.

BRIGHTSMITH, D. J. 2004. Effects of weather on avian geophagy in Tambopata, Peru. Wilson Bulletin 116:134–145.

COTTRELL, C. B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. Zool. J. Linn. Soc. 79:1–57.

CUSHING, P. E. 2012. Spider-ant associations: an updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders. Psyche. vol. 2012, Article ID 151989, 23 pages, 2012. doi:10.1155/2012/151989.

D'ABRERA, B. 1994. Butterflies of the Neotropical Region, pp. 880–1096. Part VI: Riodinidae. Hill House, Victoria, Australia.

DEVRIES, P. J. 1984. Of crazy-ants and Curetinae: are *Curetis* butterflies tended by ants? Zool. J. Linn. Soc. 79:59–66.

DEVRIES, P. J. 1988. The larval ant-organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. Zool. J. Linn, Soc. 94:379–393.

DEVRIES, P. J. 1991. Mutualism between *Thisbe irenia* butterflies and ants, and the role of ant ecology in the evolution of larval-ant associations. Biol. J. Linn. Soc. 43:179–195.

DEVRIES, P. J. 1997. The butterflies of Costa Rica and their natural history. Vol II. Riodinidae. Princeton University Press. xxv + 288 pp.

DEVRIES, P. J. 2000. Entomophagy, behavior, and elongated thoracic legs in the myrmecophilous Neotropical butterfly *Alesa amesis* (Riodinidae). Biotropica 32:712–721.

DEVRIES,, P. J., I. A. CHACON, & D. MURRAY. 1992. Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera). J. of Res. Lep. 31:103–126.

DOWNEY, J. C., & A. C. ALLYN. 1980. Egg of Riodinidae. J. Lep. Soc. 34:133–145.

EISNER, T., M. EISNER, & M. DEYRUP. 1991. Chemical attraction of kleptoparasitic flies to heteropteran insects caught by orb-weaving spiders. Proc. Natl. Acad. Sci. USA. 88:8194–8197.

EMMONS, L. H., & F. FEER. 1990. Neotropical rainforest mammals: a field guide. University of Chicago Press, Chicago, IL.

ESPELAND, M., J. P. W. HALL, P. J. DEVRIES, D. C. LEES, M. CORNWALL, Y. HSU, L. WU, D. L. CAMPBELL, D. TALAVERA, R. VILA, S. SALZMAN, S. RUEHR, D. J. LOHMAN, & N. E. PIERCE. 2015. Ancient Neotropical origin and recent recolonization: Phylogeny, biogeography and diversification of the Riodinidae (Lepidoptera: Papilionoidea). Mol. Phyl. Evo. 93: 296–306.

FIEDLER, K. 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). Bonner Zool. Monogr. 31:1–210.

FIEDLER, K., B. HOLLDOBLER, & P. SEUFERT. 1996. Butterflies and ants: the communicative domain. Experentia 52:14–24.

GRISCOM, B. W., & P. M. S. ASHTON. 2003. Bamboo control of forest succession: Guadua sarcocarpa in Southeastern Peru. Forest Ecol. Man. 175:445–454.

GRISCOM, B. W., & P. M. S. ASHTON. 2006. A self-perpetuating bamboo disturbance cycle in a Neotropical forest. J. Trop. Ecol. 22:587–597.

HALL, J. P. W. 1999. The genus *Theope* and relatives: their systematics and biology (Lepidoptera: Riodinidae: Nymphidiini). Ph.D. Dissertation, University of Florida, Gainesville.

HALL, J. P. W., & D. J. HARVEY. 2001. A phylogenetic analysis of the Neotropical riodinid butterfly genera *Juditha, Lemonias, Thisbe* and *Uraneis*, with a revision of *Juditha* (Lepidoptera: Riodinidae: Nymphidiini). Syst. Entom. 26:453–490.

HALL, J. P. W., & D. J. HARVEY. 2002. Basal subtribes of the Nymphidiini (Lepidoptera: Riodinidae): phylogeny and myrmecophily. Cladistics 18:539–569.

HEPPNER, J. B. 1991. Faunal regions and the diversity of Lepidoptera. Trop. Lep. 2:1–85.

KAMINSKI, L. A., L. M. MOTA, A. V. L. FREITAS, & G. R. P. MOREIRA. 2013. Two ways to be a myrmecophilous butterfly: natural history and comparative immature-stage morphology of two species of *Theope* (Lepidoptera: Riodinidae). Biol. J. Linn. Soc. 108:844–870.

KRATTER, A. W. 1997. Bamboo specialization by Amazonian birds. Biotropica 29: 100–110.

MCIVER, J. D., & G. STONEDAHL. 1993. Myrmecomorphy: morphological and behavioral mimicry of ants. Ann. Rev. Entom. 38:351–379.

MOSHER, E. 1916. A classification of the Lepidoptera based on characters of the pupa. Bulletin of the Illinois State Laboratory of Natural History, vol. 12, pp. 17–159.

NELSON, B. W. 1994. Natural forest disturbance and change in the Brazilian Amazon. Remote Sensing Rev. 10:105–125.

PENZ, C. M., & P. J. DEVRIES. 2006. Systematic position of *Apodemia paucipuncta* (Riodinidae), and a critical evaluation of the nymphidiine transtilla. Zootaxa 1190:1–50.

PIERCE, N. E. 1983. The ecology and evolution of symbiosis between lycaenid butterflies and ants. Ph.D. dissertation, Harvard University.

PIERCE, N. E. 1984. Amplified species diversity: A case study of an Australian lycaenid butterfly and its attendant ants, pp. 197–200. *In* R. I. Vane-Wright, and P. R. Ackery (Eds.). The biology of butterflies, Symposium of the Royal Entomological Society of London Number 11, Academic Press, London, UK.

PIERCE, N. E., & M. A. ELGAR. 1985. The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. Behav. Ecol. Sociobiol. 16:209–222.

PIERCE, N. E., M. F. BRABY, A. HEATH, D. J. LOHMAN, J. MATHEW, D. B. RAND, & M. A. TRAVASSOS. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Ann. Rev. Entom. 47:733–771.

ROBBINS, R. K. 1982. How many butterfly species? News Lepid. Soc. 1982: 40–41.

ROBBINS, R. K. 1993. Comparison of butterfly diversity in the Neotropical and Oriental regions. J. Lepid. Soc. 46:298–300.

ROBBINS, R. K., & R. C. BUSBY. 2015. Evolutionary gain of male secondary sexual structures in the widespread Neotropical montane genus *Lathecla* (Lepidoptera, Lycaenidae, Eumaeini). Ins. Syst. Evol. 46:47–78.

ROSS, G. N. 1964. II. Early stages of *Anatole rossi*, a new myrmecophilous metalmark. J. Res. Lep. 3:81–94.

ROSS, G.N. 1966. Life-history studies on Mexican butterflies. IV. The ecology and ethology of *Anatole rossi*, a myrmecophilous metalmark (Lepidoptera: Riodinidae). Ann. Entomo. Soc. Am. 59:985–1004.

ROTA J., & D. L. WAGNER. 2006. Predator mimicry: metalmark moths mimic their jumping spider predators. PLoS One 1:e45 doi:10.1371/journal.pone.0000045.

SIVINSKI J., S. MARSHALL, & E. PETERSSON. 1999. Kleptoparasitism and phoresy in the Diptera. Flor. Entomo. 82:179–197.

STEHR, F. W. 1987. Order Lepidoptera. *In* Immature Insects, pp. 293–294. Vol. I, F. W. Stehr, Ed, Kendall/Hunt Publishing, Dubuque, Iowa.

WHEELER, D. E. 1986. *Ectatomma tuberculatum* foraging biology and association with *Crematogaster* (Hymenoptera Formicidae). Ann. Entom. Soc. Amer. 79:300–303.

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