# First Observations of Butterfly (*Pedaliodes*: Satyrinae: Nymphalidae) Visits to a Wild *Anthurium* (Araceae)

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## ABSTRACT

Aroids are visited by a diverse assortment of animals, including many arthropods and some birds. It is therefore surprising that reports of butterflies visiting aroids are limited to plants grown in Botanical Gardens or in cultivation. Thus, the role of butterflies in the biology of wild aroids remains unclear. Observations at *Anthurium bustamanteae* (Croat et al. 2020), a species recently discovered at 2700 m in upper montane cloud forests on the eastern slope of the Andes in northern Ecuador, advanced understanding of butterfly-aroid associations in several important respects. Over approximately five weeks, two species of *Pedaliodes* (Satyrinae, Nymphalidae) repeatedly visited both female-phase and male-phase inflorescences under a variety of weather conditions. The butterflies were observed to pick up pollen and feed at fluid secretions with their proboscises while they perched along male-phase spadices. One or both *Pedaliodes* species also formed apparent feeding queues of up to three individuals seeking to access a fluid-rich zone on the male-phase spadix. More direct interference competition over the surface of the spadix was expressed as aggressive dominance over butterflies by a wasp, which actively chased butterflies around the spadix. Evidence that *Pedaliodes* visit aroids even when they experience costs (weather, aggression, competition) and benefits (potentially nutritious aroid secretions) of exploiting aroids in the wild suggests a dependable ecological relationship. These data confirm an earlier report that butterflies are poised to provide pollination services to aroids, and that nymphalid butterflies in particular may have a special ecological relationship with Araceae, including *Anthurium*.

**KEY WORDS**

Ecuador, Montane, Cloud Forest, Mutualism, Pollination, Red Coloration, Spadix, Wasp

## INTRODUCTION

The pollination systems of Araceae remain poorly documented despite intensive studies into the family's biological systematics (Croat 1980; Chartier et al. 2013; Gibernau 2016). Inflorescence design in most aroids presents few physical barriers to the flower-bearing spadix, which typically emerges from the bract-like spathe over a protracted time period. Thus, it is not surprising that aroid visitors or pollinators include groups as different as arthropods (e.g. bees, beetles, and flies (Gibernau 2003, 2011, 2016; Prieto & Cascante-Marín 2017) and birds (e.g. hummingbirds, flowerpiercers, tanagers; Kraemer & Schmitt 1999; Bleiweiss et al. 2019). Butterflies combine attributes of these attendants, and therefore seem likely to visit aroid as well. However, associations between free-flying butterflies and aroids were completely unknown until recently, when several individuals of the common and widespread nymphalid, the Anna's 88 butterfly *Diaethria anna* (Guérin-Méneville), were observed feeding at inflorescence fluids of *Anthurium podophyllum* (Cham. & Schltdl.) cultivars in Costa Rica. During these visits the butterflies picked up pollen on their proboscises and abdomens and attended both female-phase as well as male-phase inflorescences (Hartley et al. 2017). With this one exception, however, all other documented association between butterflies and aroids are of a hodgepodge of captive species housed together in Botanical Gardens (e.g. Suvák 2015).

While studying *Anthurium bustamanteae* (Croat et al. 2020), a species recently discovered in upper montane cloud forests along the eastern slope of the Ecuadorian Andes, two nymphalid butterflies in the genus *Pedaliodes* were observed to repeatedly visit its inflorescences. Observations made intermittently over five weeks allowed us to characterize the association with respect to whether butterfly visits: 1) occurred under entirely natural (wild) conditions; 2) were of

**Figure 1.** Typical basking behaviors of *Pedaliodes asconia* (**A**) and *P. phaedra* (**B**) around Guango Lodge, revealing differences in dorsal wing surface coloration. Among possible traits of *Pedaliodes* that facilitate montane living are their thick hairy bodies, dark coloration, and sun basking. Both species folded their wings when visiting *A. bustamanteae* (see **Figure 2)**, which suggests they were not visiting the plant to thermoregulate. This difference reinforces the interpretation that butterflies were visiting the plants to feed.

sufficient frequency and duration to suggest a strong ecological relationship; 3) resulted in contact with plant sexual structures and exploitation of nutritive fluids; 4) could lead to mutualisms between butterflies and aroids. The resulting insights provide important steps towards understanding the role of butterflies in aroid biology and vice versa.

## MATERIALS AND METHODS

*Study Site and Anthurium Biology*.- Observations were made intermittently between February 26 and March 29, 2017 at 2700 m in upper montane cloud forests around Guango Lodge (0°22'46.56" S, 78°04'36.12" W), which is located approximately 4.8 km west of the larger town of Cuyuja, in Napo Province on the eastern slope of the Ecuadorian Andes. *Anthurium bustamanteae* is a member of section *Cardiolonchium* (Croat et al. 2020), and is characterized by its large and striking red spathe and spadix. Floral development followed the typical pattern for the genus, with dichogamous and protogynous sexual staging, resulting in asynchronous development of inflorescences within and among individual plants (Bleiweiss et al. 2019). Macrophotography suggested that floral sexual phases did not develop concurrently on the same spadix, and that male-phase flowers developed in time and space from the base to the tip of the spadix (see **Figure 1** in Bleiweiss et al. 2019). Thus, pollination of *A. bustamanteae* is likely to occur only by inter-spadix transfers.

As detailed elsewhere (Bleiweiss et al. 2019), inflorescences of *A. bustamanteae* produce fluids that appeared to be attractants for various arthropod (wasps, thrips) and bird (four species of hummingbird and one passerine, a flowerpiercer) visitors. The fluids on female-phase inflorescences appeared as distinct droplets over the entire spadix, each droplet being associated with a female-phase flower (stigmatic fluid). By contrast, fluid secretions by male-phase inflorescences are more copious, especially in a "transition zone" where new male-phase flowers are opening. Although the sugar or caloric content of any of these fluids was not analyzed, the behaviors of visitors suggest that these fluids have nutritive value (Bleiweiss et al. 2019; herein). Moreover, analysis of the fluid secretions of male-phase inflorescences for a related species also visited by birds, *A. sanguineum*, indicated appreciable glucose levels (up to 12%) in standing crops (Kraemer and Schmitt 1999). Thus, we consider inflorescence fluids secreted by either sexual phase of *A. bustamanteae* to be potentially nutritious for the butterflies, while refraining from any further characterizations (e.g. as "nectar").

*Visitors*.- Both butterfly species observed to visit *A. bustamanteae* were members of *Pedaliodes* (Satyrinae: Nymphalidae). These small to medium-sized butterflies are typical denizens of higher elevation habitats throughout the Andes, but are often very similar in appearance and challenging to identify (Pyrcz et al. 2016). Species-level identifications were made by comparing our photographs of wild butterflies both with individuals identified in on-line photographs taken at Guango Lodge, and with specimens housed in the collections of the Museum of Natural Sciences (MECN) in the National Biodiversity Institute (INABIO), Quito. The species with uniformly black upper wing surfaces was identified as *P. asconia* Thieme (**Figure 1A**), and the one with pairs of large white bands (forewings) or spots (hindwings) on upper wing surfaces was identified as *P. phaedra* Hewitson (**Figure 1B**).

Observations were made while conducting other studies, so our data probably underestimated the extent to which butterflies visit *A. bustamanteae*. However, overall patterns were consistent across the study period, suggesting that they portrayed the relationships accurately during this time. In addition, extended watches and digital photographs were used to document interesting behaviors. The latter were captured with a Canon f5.6 55–250mm zoom lens fitted to a Canon EOS Digital Rebel T5i camera set to ISO 400, AI Servo AF Mode, auto white balance, and sRGB color space. All photos were taken by Robert Bleiweiss.

**Table 1**. *Pedaliodes* visits to *Anthurium bustamanteae*, with accompanying physical, ecological, and behavioral data.

| Obs # | Species | Date[1] | Time[2] | Weather | Habitat[3] | Behavior[4] | Phase | Zone[5] | Visitors[6] |
|---|---|---|---|---|---|---|---|---|---|
| 1 | *P. asconia* | 02/26/17 | 11:55 | raining | riparian | visiting | female | tip | - |
| 2 | *P. asconia (2)*[7,8] | 03/01/17 | 10:07 | sunny | montane | feeding | male | transition | 2 spp. |
| 2 | *P. phaedra* | 03/01/17 | 10:07 | sunny | montane | feeding | male | transition | 2 spp. |
| 3 | *P. phaedra* (2) | 03/01/17 | 11:29 | sunny | montane | feeding | male | transition | 1 sp. |
| 4 | *P. asconia* | 03/01/17 | 11:59 | sunny | montane | feeding | male | transition | - |
| 5 | *P. asconia* | 03/02/17 | 10:01 | sunny | montane | feeding | male | transition | 2 spp. |
| 5 | *P. phaedra* | 03/02/17 | 10:01 | sunny | montane | feeding | male | transition | 2 spp. |
| 6 | *P. asconia* | 03/03/17 | 13:12 | overcast | montane | visiting | male | transition | - |
| 7 | *P. asconia* | 03/06/17 | 15:43 | overcast | montane | feeding | male | transition | - |
| 8 | *P. asconia* | 03/16/17 | 10:55 | sunny | montane | feeding x wasp | male | transition | - |
| 9 | *P. asconia(3)*[9] | 03/23/17 | 09:46 | sunny | montane | feeding x wasp | male | transition | 1 sp. |
| 10 | *P. asconia* | 03/27/17 | 12:07 | raining | montane | feeding | female | middle | - |
| 11 | *P. asconia* (2) | 03/29/17 | 13:11 | sunny | montane | feeding | male | transition | 2 spp. |
| 11 | *P. phaedra* | 03/29/17 | 13:11 | sunny | montane | feeding | male | transition | 2 spp. |

[1] Observations conducted on walks along trails, and during extended watches at individual plants.
[2] Twenty-four hour clock.
[3] Riparian habitat located along the río Papallacta. Both riparian and non-riparian forests share broken to closed canopy cover, but differ in other aspects of vegetation, such as abundance of *Alnus* at riparian sites.
[4] Feeding inferred from contact between proboscis and wet surface (usually on dry days without confounding effects of precipitation). "Visiting" indicates that butterfly was not feeding; "x" indicates inter-specific interaction with non-lepidopteran.
[5] "Transition zone" is the region of most copious fluid production.
[6] Simultaneous visits by individuals of one or both *Pedaliodes* species; "1 sp." = one species, "2 spp." = two species.
[7] Numbers in parentheses indicate multiple individuals of that *Pedaliodes* species visiting plant. Simultaneous records (time and date) and observation 3 are queues (of 2-3 individuals), with queue composition designated by observation number. All queues assembled on the spadix except for observation 3, when one individual waited on the spathe of the same inflorescence. See also data under "Multiple Visitors".
[8] **Figure 2A-C**. [9] **Figure 2D**.

**Table 2**. Butterfly visitors to aroids, as recorded from various sources.

| Aroid Species | Spathe Color[1] | Spadix Color | Butterfly Species | Family | Habitat | Reference |
|---|---|---|---|---|---|---|
| *Anthurium andreanum* | red | yellow | *Laparus doris* | Nymphalidae | Botanical Garden | Suvák 2015[3] |
| *Spathiphyllum sp.* | white | green | *Heliconius cydno* | Nymphalidae | Botanical Garden | Suvák 2015[3] |
| unknown *sp.* | N I[2] | N I | *Caligo telamonius* | Nymphalidae | Botanical Garden | Suvák 2015[3] |
| *Anthurium scherzeranum* | red | purple | *Morpho achilles* | Nymphalidae | Public Garden | Pacific Science Center[4] |
| *Spathiphyllum wallisii* | white | green | *Papilio rutulus* | Papilionidae | Botanical Garden | Pumpkin Beth[5] |
| *Spathiphyllum wallisii* | white | green | *Papilio thoas* | Papilionidae | Botanical Garden | Pumpkin Beth[5] |
| *Spathiphyllum wallisii* | white | green | *Papilio demoleu* | Papilionidae | Botanical Garden | Pumpkin Beth[5] |
| *Spathiphyllum wallisii* | white | green | *Cethosia cyane* | Nymphalidae | Botanical Garden | Pumpkin Beth[5] |
| *Anthurium* sp. | red | purple | *Anartia amathea* | Nymphalidae | unknown | R. Stickney37 (flikr)[6] |
| *Anthurium podophyllum* | green | purple | *Diaethria anna* | Nymphalidae | Cultivar, Mexico | Hartley et al 2017[7] |
| *Anthurium bustamanteae* | red | red | *Pedaliodes asconia* | Nymphalidae | Wild, Ecuador | this study[8] |
| *Anthurium bustamanteae* | red | red | *Pedaliodes phaedra* | Nymphalidae | Wild, Ecuador | this study[8] |

[1] Human-visible color names. [2] N I = no image available.
[3] The Victoria greenhouse of Botanical Garden of P. J. Sáfarik, University of Kosice.
[4] Pacific Science Center: https://www.pacificsciencecenter.org/life-sciences-blog/fresh-sheet-2018-04-07/
[5] RHS Hampton Court Palace Flower Show: https://www.pumpkinbeth.com/2017/07/tropical-butterflies-hampton-court-flower-show-2017/
[6] Https://hiveminer.com/Tags/anthurium%2Caroid/Recent
[7] Coatepec, Veracruz State, Mexico. [8] Guango Lodge, Napo Province, Ecuador.

## RESULTS

*Pedaliodes Visitation*.- Both *Pedaliodes* species were common in mature and regenerating forested habitats around Guango Lodge, which is located within the characteristic elevational and geographic range of the genus. *Anthurium bustamanteae* was one of the most common and conspicuous plants in these same habits. The *Pelaliodes* were observed at female-phase or male-phase spadices of the same or different *A. bustamanteae* plants fourteen separate times over approximately five weeks. Most visits were recorded along trails on forested slopes and during the morning hours of sunny days, but visits also occurred in riparian habitat and during inclement weather (**Table 1**). Overall, *P. asconia* outnumbered *P. phaedra* in both visits, and in numbers of individuals present on a spadix simultaneously. *Pedaliodes asconia* also was the only species observed to visit both male-phase (one or more individuals on 8 separate occasions) and female-phase (2 occasions) spadices (**Table 1**). These qualitative and quantitative patterns argue that the association between both *Pedaliodes* species and *A. bustamanteae* was a natural and regular occurrence around Guango Lodge.

Butterfly activities were examined more closely during extended watches at male-phase spadices that both *Pedaloides* species appeared to favor. On sunny days, it was easier to interpret the fluids (typically in the form of wetness or distinct droplets) observed on these spadices (**Figure 2A**) as plant secretions rather than as environmental condensations due to rain or mist. Typical of *A. bustamanteae* (Bleiweiss et al. 2019), more fluid appeared to be produced where fresh male-phase flowers were opening in the transition zone between open and unopened flowers (**Figure 2A**). At male-phase inflorescences, butterflies focused their visits on this zone of greatest fluid production (**Figure 2A**). The amount of fluid in this zone sometimes appeared to be depleted or evaporated (**Figure 2A**), though this could not be connected directly with butterfly visits.

On several days, up to three individuals of one or both *Pedaliodes* species occurred together on the same male-phase inflorescence (**Figure 2A**). The butterflies would appear to form "feeding queues" for access to the fluid-rich transition zone. The butterflies in these queues did not appear to be aggressive towards each other, consistent with their interactions in general. The competitive or co-operative nature of these queues could not be assessed. Invariably, however, one individual in any queue fed at the transition zone while the other waited below it, either on the spadix or more rarely, on the spathe (**Table 1, Figure 2A**).

Close inspection of these feeding queues revealed that the *Pedaliodes* were contacting the wet surfaces of the male-phase spadices with the tips of their extended proboscises. The tips of the proboscises were either bare and touching the fluid-producing zone (**Figure 2B**), or coated with pollen (**Figure**

**2C**). As male-phase flower development proceeds over time and space in the direction of the spadix tip (see **Figure 1** in Bleiweiss et al. 2019), the transition zone where the butterflies fed presumably presented the freshest flowers and the most viable pollen. Female-phase plants exuded stigmatic fluid over the length of the spadix, and no spatial visitation patterns were observed there (though the sample size was small; **Table 1**). Pollen transfer between sexual phases was not detected.

*Other Interactions*.-. We could not determine if the butterflies used the aroid as a mating station (cf. Hartley et al. 2017). Simultaneous visits by both *P. asconia* and *P. phaedra* were presumably due to other (feeding) considerations. On two separate occasions at the same inflorescence (**Table 1**), *P. asconia* visits overlapped with those of an unidentified wasp (family Vespidae, subfamily Polistinae). On both occasions, the wasp showed marked aggression towards the butterfly, chasing and physically pushing it around the circumference of the spadix, with the butterfly retreating as the wasp advanced (**Figure 2D**). These chases usually occurred just above the fluid-rich transition zone; the wasp appeared to defend, and the butterflies appeared to want, access to the zone's fluid. The tenacity and location of both participants suggested their strong affinities for *A. bustamanteae* as a resource, with possible territoriality expressed by the wasp. Butterflies were not observed to either overlap temporally or interact physically with hummingbirds or flowerpiercers at or around inflorescences of *A. bustamanteae* or elsewhere, though such behaviors remain possible.

*Comparative Data*.- Various butterfly species are known to visit an equally diverse taxonomic, morphologic, and ecologic array of tropical aroids maintained in Botanical Gardens or in cultivation (**Table 2**), suggesting a general potential of these insects to interact with aroids. Interestingly, most captive (mainly) and free-flying (exclusively) butterfly genera known to visit aroids are members of the diverse and widespread family Nymphalidae (**Table 2**). Although the pattern could arise from a bias in captive collections, the same bias in free-flying situations suggests a possible special taxonomic association.

## DISCUSSION

Our study makes important steps towards understanding *Anthurium*-butterfly interactions and possible mutualisms. We provide only the second report of free-flying butterflies visiting aroids, and the first evidence that butterflies visit aroids in natural settings, not just in Botanical Gardens or in cultivation. The distinction in settings is important because natural ones provide butterflies with more appropriate choices of which plants to visit. Moreover, plant secretions may accumulate in cultivated individuals due to ideal growing conditions and absence of competitors (Hartley et al. 2017), which could create artificial resource bonanzas for butterflies. Our evidence demonstrates that butterflies are dependable aroid visitors in the wild,

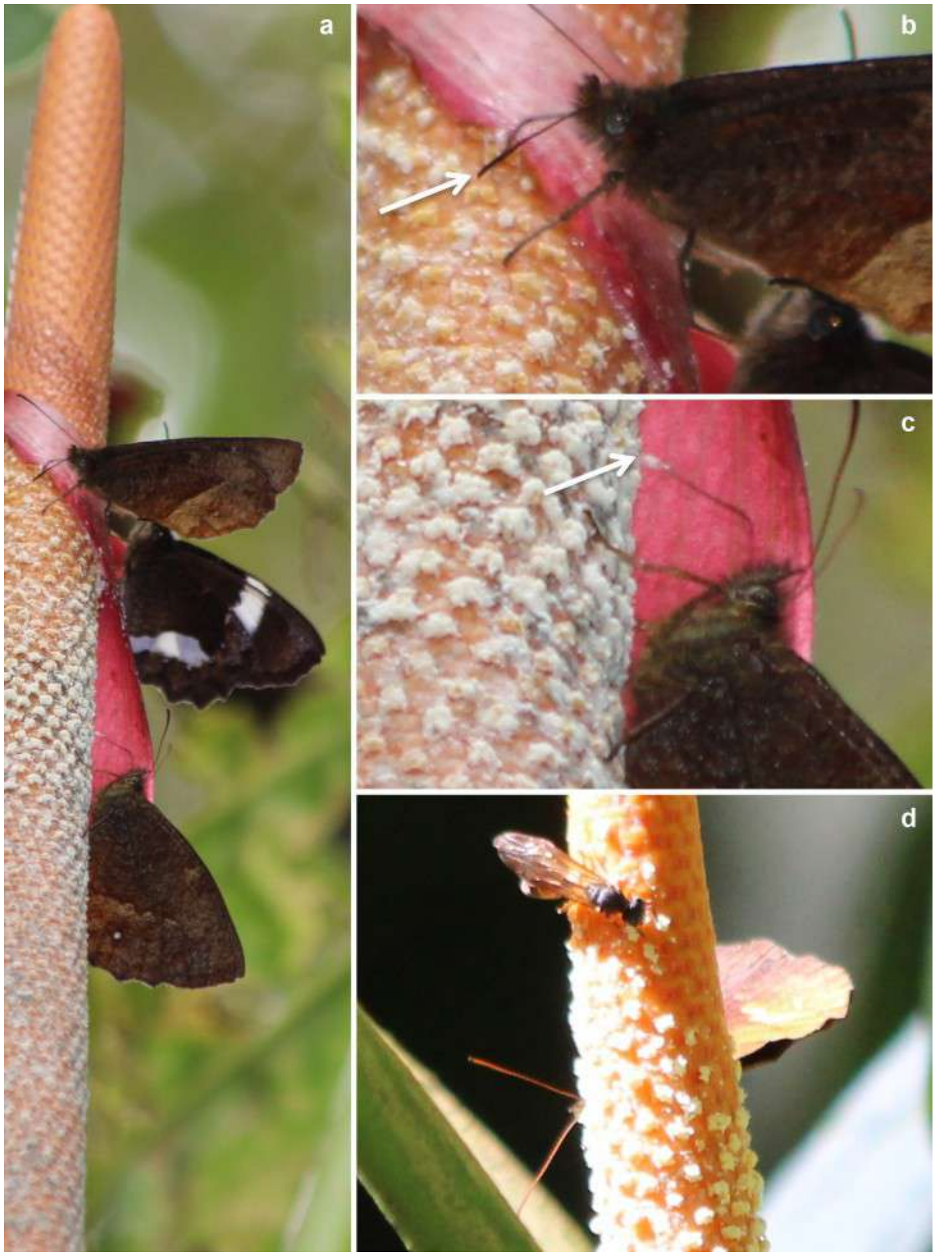


**Figure 2.** Butterfly foraging behaviors **on** *A. bustamanteae*, including a hetero-specific feeding queue of *Pedaliodes* (**A-C**), and a *Pedaliodes* being chased by a wasp (**D**). Pink plant tissues are part of the spathe, which has been pierced by the growing spadix. White dots along the surface of the spadix are pollen-producing male-phase flowers, which develop over time and space from the base towards the tip of the spadix (see **Figure 1** in Bleiweiss et al. 2019). Due to the sunny conditions, wetness of the spadix surface is likely to be a secretion by the plant. Note identifying marks for each *Pedaliodes* species in the feeding queue (**A**), including the absence (*P. asconia*) or presence (*P. phaedra*) of white coloration on the wing surface (less visible on the under-wing; compare to **Figure 1)**. Close-up of the feeding queue (**A**), revealed that the top and bottom butterflies (both *P. asconia*) were touching fluid secretions (**B**, arrow) or pollen (**C**, arrow) respectively, with their proboscises. The chase (**D**) of *P. asconia* by the wasp was proceeding around the circumference of the spadix when that image was captured.

even when they experience the interplay between costs (weather, aggression, competition) and benefits (potentially nutritious aroid secretions) typical of natural ecological conditions and interactions. Moreover, the potential for this relationship to be mutualistic is highlighted by observations that free-flying butterflies pick up pollen while feeding on nutritive fluids secreted by male-phase flowers, and also visit female-phase inflorescences. The one report of nocturnal moths (fruit-piercing Erebidae) visiting aroids in the wild found no evidence for actual or potential pollination services (Hartley et al. 2017). It remains for future studies, however, to gather evidence for actual pollination by lepidopterans that are active mainly during the day or at night (cf. Hartley et al. 2017, herein).

Behavioral interactions among visitors give some idea of possible pollination dynamics mediated through butterflies. Aggression by wasps resulted in butterflies being chased over the spadix surface rather than away from the plant, apparently extending the time the butterflies spent trying to feed there. Similarly, the formation of feeding queues among the *Pedaliodes* (one or both species) appeared to delay the departure of queued-up butterflies. Both of these more "laid-back" behaviors by butterflies suggest that these insects have less potential as outcrossers than do certain more mobile birds that also visit *A. bustamanteae* (Bleiweiss et al. 2019). Butterfly assiduity at male-phase inflorescences may therefore help explain why fewer of them were observed at female-phase inflorescences (**Table 1**). The aggressive, and possibly territorial wasp appeared to express even more sedentary dynamics. On the other hand, both butterflies (herein) and wasps (see **Figure 1A** in Bleiweiss et al. 2019) also visit female-phase inflorescences of *A. bustamanteae*. Moreover, extended time on the male-phase spadix may provide more opportunities for butterflies and wasps to pick up pollen, which could be advantageous for plant reproductive success if fertilization is limited by male function. Thus, the ways in which these various interactions balance out for the plant's overall reproductive success remain to be determined. However, these considerations highlight that potential contributions to pollination by the various participants in this mixed-visitor system may be highly idiosyncratic.

The mixed suite of vertebrate and invertebrate visitors to *A. bustamanteae* is intriguing given the frequent presumption that birds are more dependable flower visitors than arthropods under the wet and cool conditions that prevail in the high mountains (Cruden 1972; Stiles 1978). These physical factors could even reinforce behaviors that potentially make *Pedaliodes* less reliable pollinators than other aroid visitors (see above). However, many high-elevation butterflies have adaptations to montane living that enhance their ability to overcome thermal constraints (MacLean et al. 2016; **Figure 1)**, as is suggested for *Pedaliodes* by their ability to visit *A. bustamanteae* even during inclement weather

(**Table 1**). This more subtle interplay of factors that determine pollinator reliability may also apply to the sensory basis of food finding. Thus, although red is considered an attractant for birds, several arthropod visitors to *A. bustamanteae* (Bleiweiss et al. 2019, herein) belong to groups that can see these (long) wavelengths, including butterflies (Bleiweiss 2001; Frentiu & Briscoe 2008), thrips, and wasps (Blumenthal et al. 2005; Yaku et al. 2007). Thus red, along with many other colors **(Table 2)** may attract butterflies to aroids. The existence of any floral volatiles emitted by *Anthurium* also could attract butterflies (Hartley et al. 2017).

No butterflies or other arthropods were recorded at *A. sanguineum*, the other well-studied aroid in section *Cardiolonchium* that shares with *A. bustamanteae* many traits related to bird visitation (Kraemer and Schmitt 1999). This is a bit curious because butterflies are easier to detect than other arthropods, and the male-phase flowers of *A. sanguineum* secrete copious amounts of sugared fluids (nectar) that should make this species at least as attractive as *A. bustamanteae* to butterflies. Deterrence by weather or competitors also seem unlikely to explain the different visitors at the two sites given that *Pedaliodes* visited inflorescences under many weather and competitive conditions (see *Other Interactions*) around Guango Lodge. Another possibility is that *A. sanguineum* was flowering during a season or at elevations (2300 m; Kraemer and Schmitt 1999) unfavorable to butterflies that visit aroids (e.g. *Pedaliodes*; Pyrcz 2008, Pyrcz and Garlacz 2012). Regardless of the causes, butterfly visitation to only some available aroids is consistent with observations of *Diaethria anna*, which visited only one among several aroid species cultivated together in Costa Rica (Hartley et al. 2017). Much more study is therefore needed to determine why some aroids but not others might be attractive to butterflies.

In-depth, quantitative studies on possible pollination by the various visitors to *A. bustamanteae* and its relatives will be needed to understand the ecological implications of the various patterns described herein. More broadly, future studies should also follow up on observations that both free-flying butterfly taxa (*Diaethria*, and *Pedaliodes*) known to visit aroids belong to the diverse Nymphalidae, a tendency also consistent with associations documented in captivity (**Table 2**). Nymphalids in general, and even *Diaethria* and *Pedaliodes* alone, occur over most of the latitudinal and elevational range of the genus *Anthurium* (Vargas et al. 2004). Thus, there is a high potential for nymphalids to visit aroids. The interactions of these groups therefore deserve special attention.

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