

OVOPOSITION BEHAVIOR, HOST PLANT USE, AND DIET
BREADTH OF *ANTHANASSA* BUTTERFLIES (LEPIDOPTERA:
NYMPHALIDAE) USING PLANTS IN THE ACANTHACEAE IN A
COSTA RICAN COMMUNITY

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ABSTRACT

Oviposition behavior and use of host plants by populations of *Anthanassa ardys* and *A. tulcis* (Nymphalidae: Melitaeinae) were investigated in two different habitats near Monteverde, Costa Rica. We observed oviposition behavior and collected egg clusters for experimental rearings. To explore their diet breadth, both species were reared on nine locally growing plant species in the Acanthaceae, including *Hypoestes phyllostachya*, a naturalized exotic from Africa. *A. ardys* oviposited in nature on four acanth species (*Dicliptera unguiculata*, *Hypoestes phyllostachya*, *Justicia valerii*, and *Pseuderanthemum cuspidatum*) and was reared with varied success on eight species. *A. tulcis* oviposited on two acanth species (*Dicliptera unguiculata* and *Hypoestes phyllostachya*), and was reared successfully on seven. Though both species laid eggs on *Hypoestes* (5 of 14 egg clusters found), neither species successfully completed development on this plant. This oviposition "mistake" might be explained by the fact that *Anthanassa* butterflies have only recently been exposed to this plant.

Two other butterfly species, *Anartia fatima* and *Siproeta epaphus*, known to use Acanthaceae as host plants, were also unsuccessful in completing development on *Hypoestes*. Neither species was observed to oviposit on *Hypoestes* in nature.

Key Words: Acanthaceae, *Anthanassa*, exotic, *Hypoestes*, Lepidoptera, Melitaeinae, Nymphalidae, oviposition mistake

RESUMEN

Fué investigada la conducta de oviposición y el uso de plantas huésped por las poblaciones de *Anthanassa ardys* y *A. tulcis* (Nymphalidae: Melitaeinae) en dos ambientes diferentes cercanos a Monteverde, Costa Rica. Se colectaron grupos de huevos para su crianza. Con el objetivo de investigar la variedad de dietas de estas mariposas, ambas especies se criaron en nueve especies de plantas de la familia Acanthaceae, incluyendo *Hypoestes phyllostachya*, que es una planta exótica, introducida de Africa.

Las observaciones mostraron que en el campo *A. ardys* ovipositó en cuatro especies de acantáceas (*Dicliptera unguiculata*, *Hypoestes phyllostachya*, con éxito en ocho especies. *A. tulcis* ovipositó en dos especies de acantáceas en el campo (*Dicliptera unguiculata* y *Hypoestes phyllostachya*), y fué criada con éxito en siete especies en el laboratorio. A pesar de que las dos especies de mariposas ovipositaron en *Hypoestes* sp. (cinco de catorce grupos encontrados), ninguna de ellas completó su crecimiento con éxito en esta planta. Esto posiblemente se deba a que *Anthanassa* spp. ovipositaron por equivocación en esta especie porque estas mariposas habían sido expuestas a esta planta recientemente.

Se conoce que otras dos especies de mariposa, *Anartia fatima* y *Siproeta epaphus*, utilizan las plantas de la familia Acanthaceae como plantas pero éstas tampoco completaron su crecimiento con éxito en el género *Hypoestes phyllostachya*. En el campo, no se observó ninguna especie que ovipositará en el género *Hypoestes*.

Anthanassa (Nymphalidae: Melitaeinae) is a genus of butterflies common in forest clearings, pastures, and disturbed open areas in tropical America. Five species of *Anthanassa* occur in Monteverde, Costa Rica: *A. ardys* (Hewitson 1864), *A. atronia* (Bates 1866), *A. crithona* (Salvin 1871), *A. otares sopolis* (Godman & Salvin 1878) and *A. tulcis* (Bates 1864). The host plants and early stages of these butterflies are poorly known in Costa Rica and indeed in the whole neotropics (De Vries 1987). Haber observed oviposition in the field and reared *A. ardys* on *Pseuderanthemum cuspidatum* (Acanthaceae), in Monteverde (this study). Scott (1986), listing *A. tulcis* as *Phyciodes frisia* ssp. *tulcis*, cites hosts in both the Acanthaceae (*Beloperone guttata*, *Dicliptera*, *Ruellia*) and the Euphorbiaceae (*Drypetes lateriflora*). In 1997, Feldman observed *Anthanassa drusilla lelex* (Bates, 1864) ovipositing on *Justicia comata* (Acanthaceae) at La Selva Research station in Heredia, Costa Rica. We focused on the diet breadth of *A. ardys* and *A. tulcis* in Monteverde from January to March 1996 when both species were abundant.

The study site was located between 1300 and 1520 meters elevation on the Pacific slope in evergreen montane forest (Premontane Wet Forest life zone) and in areas transitional to cloud forest (Lower Montane Wet Forest life zone) (Bolaños & Watson 1993). The habitat consisted of a mosaic of primary and secondary forest patches and pasture lands. At this site the dry season begins in November, with mean monthly rainfall between 30 and 80 mm. Mean annual precipitation is 2429 mm and mean annual temperature is 19°C (Stiles & Skutch 1989).

We observed host use by *Anthanassa ardys* and *A. tulcis* at five locations spanning four km at Monteverde and determined the diet breadth for these two species by test rearings on nine species of Acanthaceae that commonly grew in the area where *Anthanassa* were active. We also wanted to determine if the exotic *Hypoestes phyllostachya* ("Polka-dot plant") served as a suitable host for any of the butterflies that use acanths at Monteverde. *Hypoestes phyllostachya* was introduced to Monteverde as an ornamental plant originating in Africa by Richard Hartmann between 1958 and 1966 (Rockwell pers. comm. 1996). In addition, we observed differences in oviposition behavior between *Anthanassa* butterflies and two other nymphalid butterflies with acanth hosts: *Anartia fatima* (Godart 1820) and *Siproeta epaphus* (Latreille 1811).

METHODS

We conducted a brief survey of the acanths commonly occurring below the Monteverde Cloud Forest Preserve, and found ten species: *Blechum pyramidatum* (Lam.) Urb., *Buceragenia glandulosa* Leonard, *Dicliptera unguiculata* (Nees), *Habracanthus blepharorhachis* (Lindau) Gomez-Laur., *Hypoestes phyllostachya* Baker, *Justicia costaricana* Leonard, *Justicia oerstedii* Leonard, *Justicia valerii* Leonard, *Pseuderanthemum cuspidatum* (Nees) Radlk., and *Razisea spicata* Oerst. *Buceragenia* is now considered to be a cleistogamous form of *P. cuspidatum* (M. Grayum, pers. comm.). In our study area, *Buceragenia* grew as small, frequently grazed or chopped plants in pastures, while *Pseuderanthemum* reached heights of 20 to 50 cm in shady forest edges. All ten acanths occurred in close proximity to areas where adult *Anthanassa* were abundant and active.

Anthanassa:

We observed *Anthanassa ardys* and *A. tulcis* at five locations in the Monteverde vicinity between the hours of 0900 and 1400 hr. We observed no oviposition behavior for the three other species of *Anthanassa* that occur in Monteverde: *A. atronia*, *A. cri-*

thona, and *A. otaes*. We followed females that appeared to be searching for host plants, and collected ovipositing females (whenever possible) after they stopped laying. We also noted oviposition behaviors.

From 20 January to 1 February, 1996, we collected all egg clusters found (either by observation of ovipositions or by haphazardly overturning leaves of potential acanth hosts). We witnessed seven oviposition events by *Anthanassa ardys* and two by *A. tulcis*, and collected fourteen egg clusters. Once the eggs had hatched, we transferred larvae to fresh plants and reared them in clear plastic bags in the lab, replacing fresh plant leaves every 2 or 3 days.

A. ardys

On 31 January 1996, we transferred 10 larvae from either clutches 1, 2, or 3 to each of the acanths except *Blechum*. On 3 February, we augmented these with five to ten larvae from egg cluster 6. Eleven larvae were transferred to *Blechum*. The intent was to even out the numbers of larvae on each plant as of 3 February. Total numbers of larvae placed on each plant are listed in Table 1 under "Number of Larvae." Clutches 4 and 5 died before hatching. We kept egg clusters 8, 9, and 12 on *Hypoestes*, exposing larvae to both young and mature leaves. We reared clutches 10 and 14 on *Dicliptera*, and brood 11 on *Justicia valerii*.

A. tulcis

On 4 February, we transferred four to eight larvae from brood 7 onto each of ten acanth species. We transferred 20 larvae from egg cluster 13 to *Hypoestes* including plants of varying ages, and 41 larvae from clutch 13 to *Dicliptera*.

Anartia fatima and *Siproeta epaphus*:

We observed oviposition behaviors of *A. fatima* and *S. epaphus* in the same five locations and collected eggs (laid singly) from the hostplants. On 3 February 1996, we transferred one *A. fatima* larva to *Hypoestes*, and on 9 February, we transferred one to *Dicliptera*. On 3 February, we exposed three *S. epaphus* larvae to each of these two potential hosts.

RESULTS

Oviposition Behavior

A. ardys and *A. tulcis* displayed similar oviposition behaviors. Females basked or took nectar, until around 1130 (C.S.T.), when they started flying low over clearings, roadsides, and forest edges, frequently alighting on low-growing grasses and herbaceous dicots. After landing, females appeared to test the leaves by curling their abdomens and touching them to the upper leaf surfaces. This post-landing behavior has previously been documented in other butterflies (Chew & Robbins 1984). Females did this once or twice before rejecting even a non-acanth.

Upon reaching an acceptable acanth, females alighted and rotated their bodies (either direction) in a circle on the upper surface of the leaf, touching their abdomens down many times, and beating their wings slowly and rhythmically (1-2 times per second). They performed this "dance" on the leaf surfaces for up to a minute on any one

TABLE 1. *ANTHANASSA* OVIPOSITION TIMES.

Butterfly Species Brood	Start time ² (hrs)	Total time (min)	# of eggs	Date	Plant Species
<i>Anthanassa ardys</i> 1	1241	15	48	20/1/96	<i>Buceragenia glandulosa</i> ¹
<i>Anthanassa ardys</i> 6	1319	14	55	24/1/96	<i>Buceragenia glandulosa</i>
<i>Anthanassa ardys</i> 8	1220	11	67	26/1/96	<i>Hypoestes phyllostachya</i>
<i>Anthanassa ardys</i> 9	1236	6	38	26/1/96	<i>Hypoestes phyllostachya</i>
<i>Anthanassa ardys</i> 11	1202	7	55	30/1/96	<i>Justicia valerii</i>
<i>Anthanassa ardys</i> 14	1230	7	28	1/2/96	<i>Dicliptera unguiculata</i>
	Means:	10	48		
<i>Anthanassa tulcis</i> 7	1149	20	73	26/1/96	<i>Hypoestes phyllostachya</i>
<i>Anthanassa tulcis</i> 13	1153	19	96	1/2/96	<i>Dicliptera unguiculata</i>
	Means:	19.5	85		

Number of eggs laid by *Anthanassa ardys* was not significantly correlated with the Total time ($R = 0.467$, $P = 0.35$).

¹*B. glandulosa* is considered to be a cleistogamous form of *P. cuspidatum*.

²Earliest time at which oviposition was observed.

leaf, or for several minutes of rotating on several adjacent leaves. While based only on qualitative observation, this behavior seemed to be related to the available leaf surface area on the potential hosts: if the leaf surface area was relatively large (e.g., *Pseuderanthemum*: 4-8 sq cm), the female remained on one leaf surface, but if the plant leaves were small (e.g., *Justicia valerii*: 1-3 sq cm), she moved between a few adjacent leaves and danced on them for several minutes before selecting or rejecting the plant as an oviposition site. Quantitative data is needed to test this hypothesis.

Once a leaf was selected, the female gradually stopped beating her wings while curling her abdomen onto the lower surface of the leaf, and began to oviposit. In all nine observed cases, the head and the front walking legs remained over the dorsal leaf surface. Except for the abdominal movements necessary for oviposition, the *Anthanassa* remained still, unless disturbed—in which case, rhythmic and then more rapid wing beats followed (based upon one instance where I inadvertently disturbed an ovipositing female). The earliest observed ovipositions started at 1220 hr (*A. ardys*) and 1149 hr (*A. tulcis*), and the latest began at 1319 hr (*A. ardys*) and 1153 hr (*A. tulcis*) (Table 1). Oviposition lasted 6-15 minutes in *A. ardys*, and 19-20 minutes in *A. tulcis* (Table 1). Clusters of 28-67 (*A. ardys*) and 73-96 (*A. tulcis*) eggs were laid; on one occasion two large clusters and one singly laid egg (*A. ardys*) were found on one leaf. It is not known if the clusters were from the same or different females. Eggs of *A. adys* were greenish white and bullet-shaped, with muted surface sculpturing. Eggs were

0.55mm in diameter and 0.6-0.7mm in height. Eggs of *A. tulcis* were yellow-green, spherical to bullet-shaped, and smooth with barely visible scaling on the surface. The eggs were 0.5mm in diameter and 0.4-0.5mm in height. There was no significant correlation between the duration of oviposition and the number of eggs deposited ($R = 0.467$, $P = 0.35$, Table 1—this regression was performed for *A. ardys* only). When finished ovipositing, females returned to the upper surface of the leaf and beat their wings slowly, basking for up to five minutes before flying away.

S. epaphus:

Females exhibited searching behavior similar to that of *Anthanassa*. When a female alighted on an acceptable oviposition site, she lowered her abdomen to the leaf surfaces a few times, and then extended her abdomen to lay a single egg over the course of 10-20 seconds. Females stopped beating their wings for only a few seconds while ovipositing. On the only observed host, *Blechnum pyramidatum*, eggs were placed in curled leaves, the junctions of leaves and stems, or between flower bracts. Sometimes, a female returned to the same plant to deposit another egg. The eggs are spherical, 2 mm in diameter, and green with strong, vertical ribbing.

Anartia fatima:

The behavior of this butterfly was similar to that of *S. epaphus*. Single eggs (blue-green, spherical, approximately 1 mm in diameter) were laid on leaf surfaces or between flower bracts on *Blechnum*, as observed at one lower-elevation site. Females also oviposited on leaf surfaces of low-growing *Hydrocotyle* sp. (Apiaceae) and *Spermacoce assurgens* (Rubiaceae), growing near small patches of *Blechnum*. The five ovipositions observed lasted from 5-10 seconds each. On 22 and 24 March 1997, Feldman observed ovipositing females of *Anartia fatima* at La Selva Research Station in Heredia, Costa Rica, and found that females would land on the host (*Blechnum browneii*) and take off again, subsequently ovipositing on the first plant she encountered (based on five observations of one female, one observation of another). Oviposition sites included *Blechnum browneii*, *Hydrocotyle mexicana* (Apiaceae), a fern, and a dead leaf—grasses were not used as oviposition sites by these individuals.

REARING RESULTS

A total of 14 egg clusters were collected from 20 January to 1 February (Table 2). Six of these came from observed ovipositions of *A. ardys*, two were from observed ovipositions of *A. tulcis*, and four were found by searching acanth leaves (Table 2). All of the individuals in egg clusters 4, 5 and 12 (found by searching leaves) died before or soon after hatching, so the *Anthanassa* species were unknown for these clusters. Clusters 4 and 12 were found on *Hypoestes*, and cluster 5 was found on *J. valerii*. These data were not included in Table 2.

At least one *A. ardys* survived on each of the acanth species used in this study, except for *Hypoestes* (Table 2). Although we found two egg clusters on *Hypoestes* (the two "unknown" egg masses were found on *Hypoestes*), no larvae survived past the first instar on this plant. The larvae did not appear to feed on *Hypoestes*. Although they were provided with both young and mature leaves, all larvae on *Hypoestes* died within 4-7 days. Survival rates varied among different acanth species: larvae seemed to be most successful on *Blechnum*, *Dicliptera*, *Justicia* spp., and *Pseuderanthemum* (Table 2).

TABLE 2. RESULTS FROM REARING *ANTHANASSA ARDYS* AND *A. TULCIS* ON VARIOUS ACANTH SPECIES.

Butterfly Species	Cluster #	Oviposition Site Plant	Reared on	Number of Eggs ¹	Number of Larvae	Number of Adults
<i>A. ardys</i> ²	1,2,3,6	<i>B. glandulosa</i> ⁴	<i>B. pyramidatum</i>	146 total	10	7
" "	" " " "	" "	<i>B. glandulosa</i>	(48, 42, 1, 55)	13	6
" "	" " " "	" "	<i>D. unguiculata</i>		19	6
" "	" " " "	" "	<i>H. blepharorhachis</i>		10	3
" "	" " " "	" "	<i>H. phyllostachya</i>		20	0
" "	" " " "	" "	<i>J. costaricana</i>		14	6
" "	" " " "	" "	<i>J. oerstedii</i>		20	4
" "	" " " "	" "	<i>J. valerii</i>		16	3
" "	" " " "	" "	<i>P. cuspidatum</i>		15	7
" "	" " " "	" "	<i>R. spicata</i>		10	1
<i>A. ardys</i>	8,9	<i>H. phyllostachya</i>	<i>H. phyllostachya</i>	67, 35	no data ⁵	0
<i>A. ardys</i>	10	<i>D. unguiculata</i>	<i>D. unguiculata</i>	42	no data	22
<i>A. ardys</i>	11	<i>J. valerii</i>	<i>J. valerii</i>	55	no data	18
<i>A. ardys</i>	14	<i>D. unguiculata</i>	<i>D. unguiculata</i>	28	defunct ³	
<i>A. tulcis</i>	7	<i>H. phyllostachya</i>	<i>B. pyramidatum</i>	73 total	7	1
" "	" "	" "	<i>B. glandulosa</i>		7	2
" "	" "	" "	<i>D. unguiculata</i>		7	2
" "	" "	" "	<i>H. blepharorhachis</i>		4	1

¹The "number of eggs" refers to the original number of eggs in the egg mass laid on the "Oviposition Site Plant" (host) listed on the same line in the second column. The larvae hatching out of these egg masses (the "Number of Larvae") were partitioned amongst the plants listed in the righthand column.

²Larvae from broods 1, 2, 3, and 6 were combined. The number of adults resulting from rearings on each host are also listed.

³Egg masses from which no larvae hatched are listed as "defunct."

⁴*B. glandulosa* is considered to be a cleistogamous form of *P. cuspidatum*.

⁵In these cases, larvae were not counted after the eggs hatched.

TABLE 2. (CONTINUED) RESULTS FROM REARING *ANTHANASSA ARDYS* AND *A. TULCIS* ON VARIOUS ACANTH SPECIES.

Butterfly Species	Cluster #	Oviposition Site Plant	Reared on	Number of Eggs ¹	Number of Larvae	Number of Adults
<i>A. tulcis</i>	"	<i>H. phyllostachya</i>	<i>H. phyllostachya</i>		7	0
" "	"	" "	<i>J. costaricana</i>		7	1
" "	"	" "	<i>J. oerstedii</i>		8	8
" "	"	" "	<i>J. valerii</i>		7	2
" "	"	" "	<i>P. cuspidatum</i>		5	2
" "	"	" "	<i>R. spicata</i>		5	0
<i>A. tulcis</i>	13	<i>D. unguiculata</i>	<i>D. unguiculata</i>	96 total	41	18
	"	" "	<i>H. phyllostachya</i>		20	0

¹The "number of eggs" refers to the original number of eggs in the egg mass laid on the "Oviposition Site Plant" (host) listed on the same line in the second column. The larvae hatching out of these egg masses (the "Number of Larvae") were partitioned amongst the plants listed in the righthand column.

²Larvae from broods 1, 2, 3, and 6 were combined. The number of adults resulting from rearings on each host are also listed.

³Egg masses from which no larvae hatched are listed as "defunct."

⁴*B. glandulosa* is considered to be a cleistogamous form of *P. cuspidatum*.

⁵In these cases, larvae were not counted after the eggs hatched.

At least one *A. tulcis* survived on eight of the ten acanths used. No larvae survived past the first instar on *Razisea spicata* or *Hypoestes*, even though we observed oviposition and collected one *A. tulcis* egg cluster on *Hypoestes*. All larvae on these plants died within four days, not developing beyond the first or second instar. Again, survival rates varied among the larvae on different plants.

The one larva of *Anartia fatima* we attempted to rear on *Hypoestes* did not survive, but the one fed *Dicliptera* reached adulthood. We found no *A. fatima* eggs or larvae on *Dicliptera*. However, it is listed as a host by DeVries (1987).

When larvae of *Siproeta epaphus* were given a choice between *Hypoestes*, *Dicliptera* and *Blechum*, they fed only on *Blechum*.

DISCUSSION

Oviposition Behaviors

Orientation toward and selection of potential oviposition sites by lepidopteran females is mediated by a combination of chemical and visual stimuli (Chew & Robbins 1984, Papaj 1986, Renwick & Chew 1994). Visual stimuli include leaf shape and color. Searching *Anthanassa* females landed on both acanths and non-acanths. Most often, the plants on which they landed were similar to the acanths in leaf shape (ovate), hinting that prior to landing on plants, these butterflies used visual cues to search for hosts.

The representatives of three genera of butterflies observed (*Anthanassa*, *Siproeta epaphus*, and *Anartia fatima*) all exhibited different oviposition behaviors. *Anthanassa* spp. invested more time for each oviposition event. Eggs were laid in clusters, which may serve as protection from predators or parasites (Haber 1978, Schmidt & Smith 1985), perhaps by reducing the surface area exposed to ovipositing parasitoids. Some lepidopteran larvae that feed in groups also have been shown to stimulate each other to feed (Chew & Robbins 1984). Females remained still during egg deposition, so unless females are tracked to the oviposition site, both laying females and egg clusters could be difficult for visually-oriented predators to find.

Siproeta laid eggs singly, relatively rapidly, and "on the move." In some instances, the host plants appeared to be too small or structurally weak to support the weight of the butterfly for more than a second or two. Eggs were laid where they were difficult to see in curled leaves, at leaf nodes, and between flower bracts. This may help hide them from visual predators. Also, many *Blechum* plants were only 5-10 cm tall, and therefore possibly too small to support more than one or two larvae.

Anartia fatima exhibited two different behaviors—one very similar to that of *Siproeta*. In two locations in Monteverde, females laid eggs near, but not on their host plants. Eggs were instead laid on small Apiaceae or Rubiaceae growing in close proximity to *Blechum*. This type of oviposition behavior was documented in *Anartia* (Silberglied 1983 and included references), in Ithomiinae (Haber 1978, this study), in satyrid butterflies (Singer 1984) and in Papilionidae (Young 1979). Young (1979) and Singer (1984) speculate that this strategy protects eggs from predators or parasites that search for eggs using visual or phytochemical cues of the host plants. There is evidence that some parasitoids may use phytochemicals to locate their hosts (Hendry et al. 1976).

Interspecific constraints to larval host selection in *Anthanassa* spp.

Our observations indicated no apparent partitioning of resources or microhabitats (shade or sun) between the *Anthanassa ardys* and *A. tulcis*. Both species oviposited on

Hypoestes plants in fairly close proximity and under apparently similar levels of light. Also, both species oviposited on *Dicliptera* on the same hectare of land. This could either mean that there are some unobserved differences in the microhabitats used by *A. ardys* and *A. tulcis*, or that the abundance of host plants was not limiting enough to lead to partitioning of resources.

Neither species was observed to oviposit on *Blechum* growing in the same habitat. *S. epaphus* and *A. fatima* laid eggs only on (or near) this species: they were not observed to oviposit on *Dicliptera*, *Hypoestes*, *Justicia valerii*, or *Pseuderanthemum* growing nearby. Resource partitioning between related species using different larval hosts has been documented for papilionids by Emmel & Emmel (1969) and Shapiro and Carde (1970). However, our data are insufficient to suggest competition or resource partitioning between *Anthanassa* and these other two species. Data on host use by *Anthanassa* species in other habitats and in other parts of their range are needed before reaching further conclusions.

Physiological and environmental constraints to oviposition site selection

Both *Anthanassa* species oviposited on plants along forest edges and in clearings (many acanth species grew in partial shade). Also, *Anthanassa ardys* and *A. tulcis* basked for 2-3 hours before beginning host plant searches. The shaded forest may be too cold for them. The possibility of thermoregulatory constraints to butterfly-host-plant use is discussed in Courtney (1982) and Renwick & Chew (1994). Since *Anthanassa* rarely ventured into the cooler forest, they would be less likely to encounter the shade-adapted species e.g., *Razisea spicata*, *Habracanthus blephororhachis*, *Justicia costaricana*, and *J. oerstedii*. This may explain why no oviposition was observed on these shade tolerant species. *Blechum* was most often observed growing in small patches or patches of very small plants in pastures or banana groves. It is possible that these plants were not sufficiently abundant or that resource partitioning (mentioned above) may be occurring.

Williams et al. (1996) found that females of *Phyciodes tharos* (Nymphalidae) oviposited on a range of possible hosts, while *Chlosyne harrisii* females oviposited on one host only, even though their larvae fed successfully on a range of hosts in the lab. Phytochemical as well as environmental (e.g. temperature) cues may be involved in the restricted oviposition range of *Chlosyne harrisii*. Phytochemistry plays a role in determining intraspecific differences in host plant ranges for some pierids (Huang and Renwick 1993).

Why did *A. ardys* and *A. tulcis* oviposit on *Hypoestes phyllostachya*?

Oviposition "mistakes" are documented in many lepidopteran species, such as *Anartia* and various ithomiids (Haber 1978 and pers. obs.). These "mistakes" sometimes involve females ovipositing on unrelated plants growing in close proximity to established hosts (as with *Anartia fatima*, discussed above). This has been documented by Courtney (1982), Neck (1973), and Singer (1984). Other "mistakes" involve females ovipositing on related plants that do not support larval development. These plants are often introduced species (Bowden 1971, Chew 1977 and 1981, Sevastopulo 1964, Straatman 1962).

Hypoestes phyllostachya was introduced into the Monteverde area as an ornamental plant between 1958 and 1966. The time during which *Anthanassa* spp. have been exposed to this plant species in Monteverde (a maximum of 40 years) may have been too short to allow *Anthanassa* larvae to adapt to *Hypoestes* either by rejecting this

plant as an oviposition site or by using it as a viable host. Though the visual and/or phytochemical cues are present to stimulate oviposition by *Anthanassa ardys* and *A. tulcis*, phytochemicals that stimulate feeding behavior in larvae may be absent, or phytochemicals that are present in *Hypoestes* but are absent in the native acanthus may be toxic to the larvae. It appeared that the *Anthanassa* larvae did not feed on either young or mature leaves of the *Hypoestes* plants to which they were exposed. In addition, early instar larvae of *Anthanassa* spp. appear to be rather sessile, so it seems unlikely that larvae might crawl from *Hypoestes* to a normal host. Thus, it seems unlikely that this behavior in *Anthanassa* is similar to the non-host ovipositions of *Anartia fatima*.

Survival rates of *Anthanassa* spp. on various Acanthaceae

Survival rates of *Anthanassa* varied among the acanth species studied, but due to the small number of larvae reared on each plant, these findings do little more than suggest possible trends for further study. The larvae reared were most successful on *Blechnum*, *Dicliptera*, *Justicia* spp., and *Pseuderanthemum* (Table 2).

CONCLUSIONS

Various factors may influence the oviposition site choices of *Anthanassa* butterflies. *Anthanassa* spp. may overlook (or simply not encounter) some potential host plant species on which they can survive (e.g., in the forest, shade or low temperatures may inhibit oviposition behavior). Alternatively, they oviposit on at least one species of Acanthaceae that is unsuitable for larval development (e.g., *Hypoestes*). However, more study is needed to determine whether acanth host plant resources are partitioned by the butterflies at Monteverde. It would also be useful to determine exactly what visual and/or phytochemical cues stimulate *Anthanassa* spp. to select oviposition sites and initiate oviposition, what chemical differences exist between *Hypoestes* and the other acanthus at Monteverde, and what effects this plant might have (if any) on populations of *Anthanassa* at this site.

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