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MYSTERY HERBIVORE OF CHARISMATIC EPIPHYTE DISCOVERED ON ANDROS

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ABSTRACT. While conducting a population ecological study of a distinctive epiphytic bromeliad, we witnessed a substantial amount of folivory in some populations on Andros, Bahamas. Finding two caterpillars on damaged plants, we reared a species of moth previously recorded only from Cuba. We report here on the damage to *Catopsis berteroniana* plants by larvae of *Dahana cubana*, and conclude from our data that both plant size and location (site) influence the amount of damage that plants experienced.

Additional Key Words: Bahamas, bromeliad, caterpillar, *Catopsis*, *Dahana*, folivory

The largest island of the Bahamas archipelago, Andros also has the greatest cover of pine forest of any of the islands. Lying east of the Florida peninsula, the Bahamas archipelago shares some climatic and geological characteristics with southern Florida. Though quite similar to rockland habitats in southern Florida, the pineyards and coppices of the Bahamas have many different species of plants and insects. An epiphyte considered rare in south Florida, *Catopsis berteroniana* (Schult.f.) Mez, Tillandsioideae: Bromeliaceae, occurs also on Andros, where it is locally abundant.

There are 15 native Bromeliaceae in the Bahamas (Correll & Correll 1982), including two *Catopsis* species (*C. berteroniana* and *C. floribunda*); in south Florida, *Catopsis berteroniana* is one of three in the genus, where *C. floribunda* and *C. nutans* also occur, in tropical hammocks and swamps. All three *Catopsis* species are rare in Florida (Wunderlin & Hansen 2011) and listed as state-endangered (Wunderlin et al. 2018). The white powder on the upper leaf surfaces has led some to call *C. berteroniana* partially carnivorous (Ward & Fish 1979), as the powder may lead to insects slipping on the surface into the leaf bases; it was shown to trap 12 times as many insects as similarly sized bromeliads (Frank & O'Meara 1984), and its leaf bases also serve as phytotelmata for mosquito larvae (ibid.). The waxy coating of its leaves may facilitate the trapping of insects (Gaume et al. 2004), but this epicuticular wax is also associated with greater sun exposure (Palaci et al. 2004). Though the plants occur in humid forests, the microhabitats on tree branches can be quite dry, and epiphytic bromeliads have photosynthetic pathways similar to desert plants. *Tillandsia* spp. use Crassulean-Acid Metabolism photosynthesis, allowing their stomata to be closed during the sunny daytime when they might lose too much water to the atmosphere, storing CO2 at night for sugar production the next day. All *Catopsis* spp. so far examined use C3 photosynthesis (Crayn et al. 2004; Matiz et al. 2013), but *C. berteroniana* leaves are succulent, and may be quite appealing to herbivores as a result (Palaci et al. 2004).

There are not many reports of herbivory on bromeliads in natural habitats. A study in a Mexican cloud forest found much lower rates of herbivory on epiphytic bromeliads and orchids than on ferns (Winkler et al. 2005). We were therefore surprised to find some individuals of *Catopsis berteroniana* on Andros, Bahamas, having lost large amounts of their leaf area to a chewing herbivore (Fig. 1). As part of a larger, longer-lasting demographic study (Gonsiska 2005), individual plants were marked and followed over a year, at four distinct sites on Andros Island. During the initial marking of individuals in spring 2004, and subsequent census in November of that year, we discovered substantial damage to the leaves of some individuals. As the plants vary not only in size, but in position in the habitat and resulting amount of sun exposure, we wondered if either of these factors influenced whether or not individual plants were subject to herbivory. We report here on the results of our systematic observations.

Materials and Methods

Study Sites. We chose coppice sites on the island of Andros, the largest of the 35 inhabited islands in the Bahamas archipelago (Smith & Vankat 1992), where *Catopsis berteroniana* populations were found. Andros is 45 km wide and 165 km long, and divided by shallow channels into three main sections; our work was conducted on North Andros, with all of our sites north of Andros Town. Similar to rocklands of southern Florida (Snyder et al. 1990), Andros has poorly developed soil, with a substrate of oolitic limestone (Sealey 1985). Weathering in rocklands karst produces pitted or honeycombed rock surfaces, as well as solution holes or sinkholes that may extend down to the

freshwater lens below (Smith & Vankat 1992). Andros is 210 km east southeast of Miami, and its annual rainfall (1300 mm) is similar to, though slightly less than, that of Miami (1340 mm). The coppices (dry evergreen forest communities) on Andros are more similar to hardwood hammocks of south Florida (sharing one-third of their species), and to the northern and central islands of the Bahamas, than to the drier, southern islands. Andros has the greatest expanse of pine forests in the Bahamas, and though these forests were all logged in the middle of the twentieth century, the land on which they grow has been left mostly intact, in contrast to the pine rocklands of southern Florida which are now greatly reduced in size due to development (Koptur 2006).

In March of 2004, we selected four sites on Andros Island based on the presence of *C. berteroniana*. These sites (with their numbers, and acronyms) are listed and described below.

Site 1: ATT (Atala Coppice) – The forest here is similar to hardwood hammocks in southern Florida, where various hardwood species grow on a limestone substrate that is slightly raised above the level of the surrounding pine rockland. This coppice has a sunken area in the middle that may be filled with water for part of the year. The canopy consists of pond apple (**Annona glabra**), poisonwood (*Metopium toxiferum*), signature plant (*Clusia rosea*), members of the Myrtaceae, and other tropical hardwoods. The coppice is surrounded by pine forest (*Pinus elliottii*). At this site, *C. berteroniana* co-occurs with epiphytic species that include several *Epidendrum* spp., *Prosthechea cochleata*, *Tillandsia fasciculata, T. utriculata,* and *C. floribunda*. We marked 26 individuals in this site.

Site 2: DBR (Don's Body Shop Road) - This site, near the town of Fresh Creek, is dominated by pond apple (*Annona glabra*) and cocoplum (*Chrysobalanus icaco*) and is located near a pine forest and a large tidal inlet. We marked 72 individuals in this site.

Site 3: QRN (Queen's Road North) and Site 4: QRS (Queen's Road South)- QRN is on the windward side of the mouth of Stafford Creek and has a short-statured canopy and windswept appearance, as compared with the site on the south (leeward) side of the creek's mouth (QRS). Vegetation at both QRS and QRN consists of wild dilly (*Manilkara bahamensis*), poisonwood (*Metopium toxiferum*), *Acacia choriophylla*, *Erythroxylon* sp., and other broadleaved trees. We marked 89 individuals at the QRN site, and 57 individuals at the QRS site.

At censuses in March and November, the amount of each individual *C. berteroniana* plant that had been consumed was estimated on a five-point scale, as follows: 0 = 0% herbivory; 1 = 1–24% herbivory; 2 = 25–49% herbivory; 3 = 50–74% herbivory; 4 = 75–100% herbivory. For data analysis, we used the mean value of each category as an estimate of the actual amount of damage, to create a numeric variable.

We assigned the exposure category for each individual in March, as a visual categorization of the canopy openness above each plant: none = closed canopy, fully shaded; half = partially open; and full = fully open canopy. As this is the dry season of the year, these assessments estimate the extreme exposures the individual plants would receive, when some drought-deciduous trees have lost their leaves. Only 20 of the marked individuals were in full sun; 92 in half-sun, and 131 were fully shaded.

Catopsis berteroniana individuals spend the first part of their development in an "atmospheric" form, with only their epidermis to absorb water. They transition to "tank" form after a year or more, when the leaf bases act as tanks to collect moisture as well. Individual plant sizes ranged from 0.5 to 42 cm in diameter. For our analysis, we placed the plants into size categories, putting those with diameters of less than 2.1 cm into category 1 (n = 87); those with diameters from 2.2–10 cm in category 2 (n = 92); those with diameters from 10.1–20 cm in category 3 (n = 30); and the largest ones, with diameters greater than 21 cm in category 4 (n = 35).

As both sunlight exposure and herbivory level were categorical variables, we used the nonparametric independent samples Kruskal-Wallis test as an alternative to ANOVA (SPSS v. 20). If significant differences were found, post-hoc comparisons between pairs were made using a 2-sided test of asymptotic differences.

RESULTS

The herbivore. While assessing damage to leaves we encountered fuzzy beige caterpillars (Fig. 2), whose hairs bore a dusting of the waxy bloom (Fig. 3) found on the leaves of *Catopsis berteroniana*, which aided their diurnal crypsis at the base of the leaves. We collected the larvae and reared them on a diet of the same leaves in containers. After one week, the larger of the two larvae had pupated and several weeks later, the adult eclosed (Fig. 4).

Although cryptically colored, these caterpillars were similar to wooly bears, and surmised to be larvae of moths of the family Arctiidae (Conner 2009). Similar to other ctenuchid moths, but unlike any we had previously seen, the single pinned specimen was photographed and shared with moth expert Charles Covell. Covell sent it to the expert in this group of moths, Rebecca Simmons, and she determined it to be

Figs. 1–4. **1.** Herbivory on *Catopsis berteroniana*. **2.** Caterpillar of moth hiding in base of leaves. **3.** Appearance of caterpillar on leaf surface, thumb for scale. **4.** Adult specimen of *Dahana cubana* (broken wings—pinning accident).

Dahana cubana Schaus (Ctenuchinae: Arctiidae; or Arctiinae, Erebidae).

Influence of site. Herbivory differed among the sites, with ATT having the greatest amount (average 12% over all plants), DBR and QRS similar amounts (2%), and close to nothing in QRN (< 1%). The Kruskal Wallis test was significant (test stat = 50.045, df = 3, n = 244; p. < 0.0001), and post-hoc tests showed that ATT differed substantially from all the other sites, and all the others were statistically equivalent to one another. Of the 26 plants followed at ATT, 10 experienced herbivore damage (38% of individuals); only 1 of 72 at DBR (1% of individuals), 1 of 89 at QRN (1%), and 6 of 57 at QRS (11%).

Influence of plant size. Size of the *Catopsis* individuals was associated with herbivory (Kruskal-Wallis test stat = 39.448, df = 3, n = 244, p < 0.0001), with the largest size category (plants larger than 21 cm in diameter) experiencing the greatest damage, significantly more than all the smaller size categories. None of the 87 plants in the smallest size category were damaged by herbivores, 3 individuals of 92 (3%) in the second size category, 3 of 30 (10%) in the third category, and 11 of 35 (31%) in the largest size category. Plants in all the smaller size categories experienced equivalent damage, as shown by post-hoc tests.

Influence of sun exposure. *Catopsis* individuals growing in full sunlight, across all sites and age classes, did not experience herbivory. Plants growing in half-sun and no-sun exhibited similar damage in both situations. None of these differences were shown to be significant with the Kruskal-Wallis test (test stat = 1.975, df = 3, n = 244; p = 0.578).

Discussion

An extensive review of animals associated with bromeliads cites some Lepidoptera known to eat leaves of various genera (Frank & Lounibos 2010). Riodinid caterpillars eat leaves of *Werauhia*, *Aechmea*, and *Tillandsia* species; Nymphalidae eat some South

American bromeliads; and a Lycaenid caterpillar has also been found eating leaves of *Tillandsia* (all sources cited in the review).

The damage we observed on *Catopsis berteroniana* on Andros appeared to be exclusively from the larvae of the Cuban *Dahana*, *Dahana cubana* Schaus (determined by Charles Covell and Rebecca Simmons from an adult reared from the larvae). Some adult tiger moths (Arctiidae) are brightly colored, and have evolved aposematic mimicry rings; the adult of *Dahana cubana* may give the illusion of a wasp-waist as do some *Syntomeida* species (Simmons 2009). The only prior records of the occurrence of this species, to our knowledge, are in Cuba (Schaus 1904).

The only congeneric moth species, the black-winged *Dahana* (*Dahana atripennis*), has larvae that feed on Spanish moss, *Tillandsia usneoides* (Garth 1964); they were found eating the young shoots in only a few of the many locations observed in an extensive survey (ibid.). Adults of *D. atripennis* have been observed every month of the year in Florida (Slotten 2003).

Dahana cubana caterpillars were observed eating plants in three of our four Andros sites. At Site 1, ATT many large plants had lost a substantial amount of foliage to *D. cubana* feeding, suggesting a possible larval outbreak. However, further studies are required to determine seasonal phenology of *D. cubana* across Andros, as well as corresponding levels of herbivory.

Although they lose leaf area to caterpillars, bromeliads may benefit from carnivorous ant species nesting beneath them provided they bring nitrogen-rich prey into their nests (Goncalves et al. 2016). The frass of leaf-feeding lepidopteran larvae may also provide nutrients, but perhaps not enough to offset the loss of 50% or more of the plant's foliage. In Mexican cloud forests, higher levels of herbivory were recorded on bromeliads that had fallen from trees without support than those with (Winkler et al. 2005). For *C. berteroniana* populations on Andros, levels of herbivory and the survival of individual plants may be influenced by more than only exposure to sunlight. Plants growing in areas where *D. cubana* have established may experience higher herbivory. However, during our demographic study only a single marked individual was observed to have been completely defoliated by larvae.

The Bahamas were logged in the early-mid twentieth century (Henry 1974; Allan 1986), as is evident from the relatively slim trunks in the present-day forests. Most of the fire in the pineyards is anthropogenic and set at often frequent intervals (O'Brien et al. 2006). As plants resprout after fires, recently burned areas are desirable for grazing and foraging by wildlife, which may be hunted for food. The impact of these rockland fires on epiphytic bromeliads and woodland insects is not well known, save for a study of ants that visit nectaries (Koptur et al. 2010). Hurricanes also take their toll on epiphytes in south Florida habitats (Oberbauer et al. 1994) and very likely do the same on Andros. They may also facilitate insect dispersal among islands that are normally too far apart for most insects under their own power (Morrison & Spiller 2008).

Having discovered the caterpillars of *Dahana cubana* on *Catopsis berteroniana* only in the Bahamas, additional surveys will focus on locating occurrences in southern Florida. As the native bromeliads in Florida have suffered greatly from an invasive herbivore/predator, the 'evil weevil' (*Metamasius callizona*), a beetle whose larvae eat the core of a plant and cause its mortality (Frank & Thomas 1994), minor leaf damage from a *D. cubana* larvae is not likely to be as noticeable or as devastating. Nonetheless it will be interesting to see if, and how much, this type of herbivore damage affects subsequent growth and reproduction of *C. berteroniana*.

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LITERATURE CITED

ALLAN, T. G. 1986. Management plan for the pine forests of the Bahamas. UTF/BHA/003/BHA Consultancy Report No. 2. Food and Agriculture Organization of the United Nations.

WUNDERLIN, R. P., B. F. HANSEN, A. R. FRANCK, AND F. B. ESSIG. 2018. Atlas of Florida Plants (http://florida.plantatlas.usf.edu/). [S. M. Landry and K. N. Campbell (application development), USF Water Institute.] Institute for Systematic Botany, University of South Florida, Tampa.

CONNER, W. E. (ed.) 2009. Tiger moths and woolly bears. Behavior, ecology, and evolution of the Arctiidae. Oxford University Press. 234 pp.

CORRELL, D. S. & CORRELL, H. B. 1982. Flora of the Bahama archipelago: including the Turks and Caicos Islands. Vaduz: J. Cramer. 1692 pp.

CRAYN, D.M., K. WINTER, & J. A. C. SMITH. 2004. Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. Proc. Nat. Acad. Sci. 101: 3703–3708; https://doi.org/10.1073/pnas.0400366101

Frank, J.H. & L.P. Lounibos. 2009. Insects and allies associated with bromeliads: a review. Terrestrial Arthropod Reviews 1(2): 125–153. doi:10.1163/187498308X414742

Frank, J. H. & G. F. O'Meara. 1984. The bromeliad *Catopsis berteroniana* traps terrestrial arthropods but harbors *Wyeomyia* larvae (Diptera: Culicidae). Florida Entomol. 67: 418–424.

Frank, J. H. & M. C. Thomas. 1994. *Metamasius callizona* (Chevrolat) (Coleoptera: Curculionidae), an immigrant pest, destroys bromeliads in Florida. Can. Entomol. 126: 673–682.

Garth, R. E. 1964. The Ecology of Spanish Moss (*Tillandsia usneoides*): Its Growth and Distribution. Ecology 45: 470–481.

Gaume, L., P. Perret, E. Gorb, S. Gorb, J. J. Labat, & N. Rowe. 2004. How do plant waxes cause flies to slide? Experimental tests of wax-based trapping mechanisms in three pitfall carnivorous plants. Arthrop. Struct. Develop. 33: 103–11.

Gonçalves, A. Z., R. S. Oliveira, P.S. Oliveira, & G.Q. Romero. 2016. Species-Specific Effects of Ant Inhabitants on Bromeliad Nutrition. PLoS ONE 11: e0152113. doi:10.1371/journal.pone.0152113

Gonsiska, P. A. 2005. Ecology of the endangered Florida bromeliad *Catopsis berteroniana* (Schult.f.) Mez (Bromeliaceae). MS thesis, Florida International University. 50 pp.

Henry, P. W. T. 1974. The pine forests of the Bahamas. British Foreign and Commonwealth Office Land Resource Study. No. 16.

Koptur, S. 2006. The conservation of specialized and generalized pollination systems in subtropical ecosystems: a case study. Ch. 15, pp. 341–361. *In* N. Waser & J. Ollerton (eds.) Plant–pollinator interactions: from specialization to generalization. University of Chicago Press.

Koptur, S., P. William, & Z. Olive. 2010. Ants and plants with extrafloral nectaries in fire successional habitats on Andros (Bahamas). Florida Entomol. 93: 89–99.

Matiz, A., P. T. Mioto, A. Y. Mayorga, L. Freschi & H. Mercier. 2013. Ch. 4 in Matiz et al. (eds.): CAM Photosynthesis in Bromeliads and Agaves: What Can We Learn from These Plants? http://dx.doi.org/10.5772/56219

Morrison, L. W. & D.A. Spiller. 2008. Patterns and processes in insular floras affected by hurricanes. J. Biogeogr. 35: 1701–1710.

O'Brien, J. J., C. Stahala, G. P. Mori, M. A. Callaham, Jr, & C. M. Bergh. 2006. Effects of prescribed fire on conditions inside a Cuban parrot (*Amazona leucocephala*) surrogate nesting cavity on great Abaco, Bahamas. Wilson J. Ornithol. 118: 508–512.

Oberbauer, S. F., K. Von Kleist III, K. R. T. Whelan, & S. Koptur. 1996. Effects of Hurricane Andrew on epiphyte communities within cypress domes of Everglades National Park. Ecology 77: 964–967.

Palací, C. A., G. K. Brown, & D. E. Tuthill. 2004. Vegetative Morphology and Leaf Anatomy of *Catopsis* (Tillandsioideae: Bromeliaceae). Selbyana 25: 138–50. http://www.jstor.org/stable/41760152.

Schaus, W. 1904. New species of American Heterocera. Syntomidae. Trans. Amer. Entomol. Soc. 30: 135–178. [*Dahana cubana* – p. 136]

Sealey, N.E. 1985. Bahamian landscapes, an introduction to the geography of the Bahamas. Collins Caribbean, London.

Simmons, R. B. 2009. Adaptive Coloration and Mimicry. Chapter 7: pp. 115–126. *In* W. E. Conner (ed.) Tiger Moths and Wooly Bears: Behavior, Ecology, and Natural History of the Arctiidae. Oxford University Press.

Slotten, J. R. 2003. The life history of *Dahana atripennis* (Grt.) (Lepidoptera: Arctiidae). South. Lepid. News. 25: 57 (Insert D).

Smith, I.K. & J.L. Vankat. 1992. Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. Bull. Torrey Bot Club 119: 181–191.

Snyder, J. R., A. Herndon, & W. B. Robertson. 1990. South Florida rockland, pp. 230–277. *In* Myers, R. L. & J.J. Ewel (eds.) Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.

Ward, D. B. & D. Fish. 1979. Powdery *Catopsis*. pp. 74–75. *In* Ward, D.B. (ed.) Rare and endangered biota of Florida. Volume 5, Plants. University Presses of Florida; Gainesville, Florida, U.S.A.

Winkler, M., K. Hülber, K. Mehltreter, J. García Franco, & P. Hietz. 2005. Herbivory in Epiphytic Bromeliads, Orchids and Ferns in a Mexican Montane Forest. J. Tropical Ecol. 21: 147–154.

Wunderlin, R. P. & B. F. Hansen. 2011. Guide to the Vascular Plants of Florida. 3rd edition. University Press of Florida; Gainesville, Florida, U.S.A. 783 pp.

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