

HOST PLANT TOXICITY AND MIGRATION
IN THE DAYFLYING MOTH *URANIA*

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“October 15th, 1936. Referring to that point about high death rate in captive broods, it is of interest to note that when this took place there was an almost equal death rate in wild larvae left on trees—death not due to parasitism.”

“I believe that this is one method of natural control by means of a change in the chemical composition of the foliage—retarding larval growth and even causing death.”

Quoted from letter to Sir Edward Poulton from V.G.L. van Someren in Nairobi. (van Someren, 1937). His insight has been overlooked.

The diurnal members of the moth family Uraniidae are familiar insects because most “coffee table” books on the Lepidoptera figure the spectacular *Chrysidia madagascariensis*, the uraniid of that island, and almost all depict one of the forms of *Urania* described in this paper (Fig. 1). These handsome black and green *Papilio*-like moths sometimes have spectacular annual flights throughout the Neotropics (Williams, 1958; Skutch, 1970; Smith, 1972 and 1982). The numbers involved varied greatly from year to year (Fig. 2 and Smith, 1982). *Urania* are not always nomadic, and populations with all life stages may be found in aseasonal wet forest during every month of the year. They burst out of such areas, usually in July or August in Central America and northern South America (Fig. 3). “Return” flights that can be detected by casual observation are not annual nor widespread. Thus the obvious conclusion—*not* all moths participate in the annual “emigration” flight.¹ Why do some, often many, emigrate each year? Why do some not emigrate? I think I have discovered part of the answer.

The sole larval food plants of *Urania* moths (including the *Chrysidia* of Madagascar, Catala, 1940) are species of *Omphalea* (Euphorbiaceae) which are mainly big, woody lianas, though some are trees. The distribution of the Uraniidae coincides exactly with that of *Omphalea* spp., and is peculiar: the lowland Neotropics including Cuba and Jamaica, extreme eastern Tanzania, Madagascar, Papua, and the southern Philippines. No other insect to my knowledge regularly eats the leaves of *Omphalea*, which are apparently full of defensive compounds, although some beetle nips holes in the youngest leaves.² In the wild adult *Urania* apparently feed only on nectar of certain species with fluffy-white mimosoid-like flowers like *Inga* or *Eupatorium* spp. (Smith, 1982). If they do not feed as adults they do not breed and they die.³

Female *Urania* lay eggs on the undersides of the leaves usually in

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Fig. 1. The Central American form, *U. fulgens*, of the day-flying moth *Urania*.

clutches of about 80 but single eggs and small clutches are also found. There are usually five instars; the early ones graze the surface of the leaves while the later ones are capable of eating an entire leaf. The typical generation time from egg to adult is about 46 days (Smith, 1982). Up to seven generations a year may be produced in a big flight year, with three

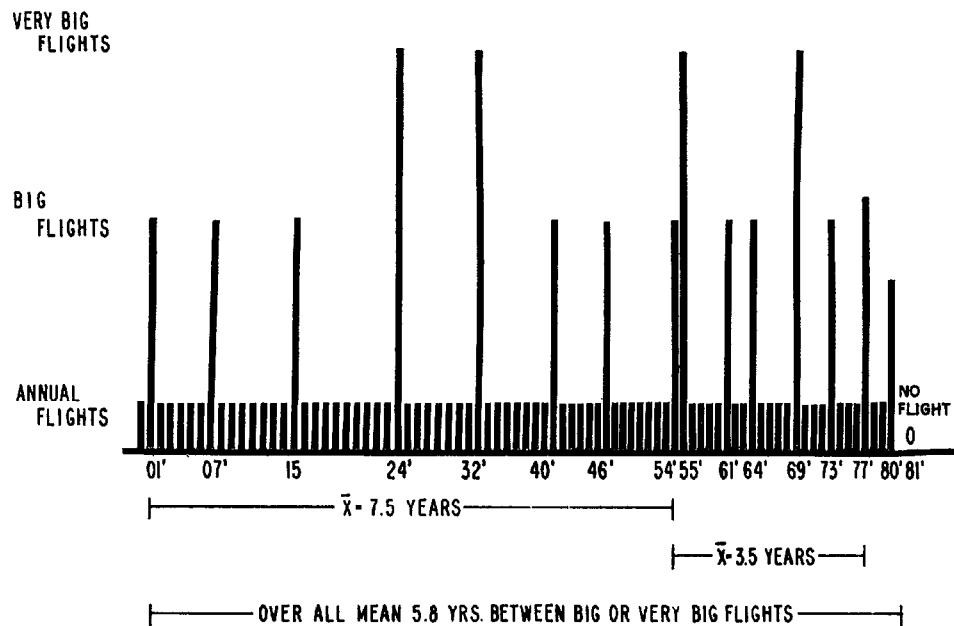


Fig. 2. Summary of population fluctuations and emigratory flights of *Urania* moths in Central America and northern South America.

or four of these coming out during the nomadic period. Adults have lived up to 66 days in the lab and I would not be surprised if they lived at least as long as this in the wild.

O. diandra is the only species of *Omphalea* in lower Central America and South America. This often huge woody liana sends its tendrilled branches above the supporting canopy in swamp forests behind mangroves, in forests at the edge of sandy beaches, and in deep monsoon-type forests far removed from the ocean. I suspect that it occurs in patches separated from other such pockets by many kilometers. The ranges of *Urania* and *Omphalea* do not coincide at all times. In the dry season *Urania* (as adults or larvae) are found only in those *Omphalea* "patches" located in wet relatively aseasonal areas (eg. certain areas on the Atlantic side of Central America). And then not all "patches" in those areas will contain *Urania*. It is only during the nomadic phase that *Urania* are capable of nearly filling up the entire range of *Omphalea*. There are "patches" of low-lying *Omphalea* on both sides of Panama that I have repeatedly censused for *Urania* and found none for 3-6 years. But, in all such areas, *Urania* eventually moved in, sometimes persisting for several years and in others disappearing within months. There is yet no clear picture of how *Omphalea* is distributed.

The results of *Urania* rearing experiments from 1973 suggested that some aspect of the *Urania* caterpillars' consumption of *Omphalea* leaves determined whether they would emerge as emigratory or sedentary adults.⁴ A rearing experiment in which Jeff Waage and I put field-collected larvae and adults on clones of *Omphalea* was responsible for focusing attention on a key to the solution. The adults laid eggs and these hatching larvae and ones from the wild were placed on potted clones of *Omphalea* "A" (collected in 1970). They did well (too well in fact, for we feared that



Fig. 3. Distribution of *Urania* moths and their general flight directions when in nomadic phase. The former population in Jamaica is now apparently extinct. The Cuban form differs only slightly in appearance from the others. It is said to also undergo population fluctuations and north-south flights.

they would consume all potted clones!). In the field *Omphalea* "A" had been heavily hit by the 1973 flight but looked in good shape in 1974.⁵ We brought back leaves from it to feed the larvae in the lab. There were no larvae on it.⁶ Some lab larvae refused to eat it, others ate it but grew slowly, and others died. Assuming that the plant had been sprayed with insecticide we put the remaining larvae back on the potted clones where they did well. We noted that when larvae were moved from one *Omphalea* to another (for more convenient observation) they often left the plant and wondered why it was adaptive for larvae to "imprint" on the plant on which they were hatched.

At this point by chance I had a conversation with a plant pathologist to whom I described my *Urania-Omphalea* dilemma. "Sounds like a phytoalexin response (Cruickshank, 1963) or probably more like that wound response' that Green and Ryan (1972) have described." I had expected that plants would respond in evolutionary time to pest pressure and evolve chemical defenses and other mechanisms. But the thought that a plant could respond to grazing by the induced production of "anti-herbivore compounds" in a matter of days or even hours was completely new and gave me an entirely different view of the *Omphalea* problem. My records showed that the larvae of 1974 were either on vines that had escaped attack (reason?) for the previous three years, or were vines that I had missed in my censuses.

The obvious experiment was to treat genetically identical clones to different grazing regimes and to bioassay their acceptability on *Urania* larvae. No matter where the eggs were laid, *Urania* larvae always climb up to the most actively growing part of the vine and begin surface grazing the youngest leaves. I grazed with a razor the leaves of 3 meter long clones. At about day 10 larvae usually moult to 3rd instar and begin to disperse. At this stage they can bite through a mature leaf. I mimicked this with a paper punch (Fig. 4) and caused over the next 12-15 days as much damage as 80 larvae would do before they pupate. I then waited the appropriate time—a "*Urania* generation"—and repeated the process with some of the clones again, and finally some clones received three grazings.

The new leaves of each of the four groups were fed to sib larvae *after* the new leaves had appeared on the thrice grazed clones. Larvae grown on leaves from thrice grazed clones grew significantly slower and had much higher mortality rates than did larvae fed leaves from the other groups (Smith, 1982, Fig. 5). Grazing could have resulted in an increase in toxic compounds or a decrease in the nutritive quality of the clone. Since the clones grew at about the same rate and there seemed to be no difference in the color or size of the new leaves, I favor the toxicity hypothesis. However this experiment did not adequately control for the "recovery" of the once or twice grazed plants since I tested the leaves *only after* the new leaves came out on the thrice-grazed plants. The other clones could have "recovered" during that time (about 220 days). My present doubts are further reinforced by reviewing the mixed results that came from the 1973 experiments⁴ (Smith, 1982). Clearly leaf quality (grazing history) was one of the major uncontrolled factors. It is "biologically reasonable" that a plant ought to refrain from expending valuable energy on toxic compounds unless provoked by repeated attacks. In addition, it is usually the third generation after the last flight of the previous nomadic phase



Fig. 4. Experimental simulation of *Urania* grazing using a paper punch.

that becomes nomadic. If toxicity goes up slowly and comes down slowly, this would suggest that the cycles in *Urania* (Fig. 2) reflect the chemical cycles in *Omphalea* (Smith, 1982).⁷

It is interesting to note that the consequences of the grazing history of a plant seem not only to act as the *ultimate* factor for emigration but the apparent increase in level of toxic compounds may also be the *proximate* clue producing emigrating or non-emigrating individuals.⁴ Figure 6 suggests a model of *Urania* nomadic flights.

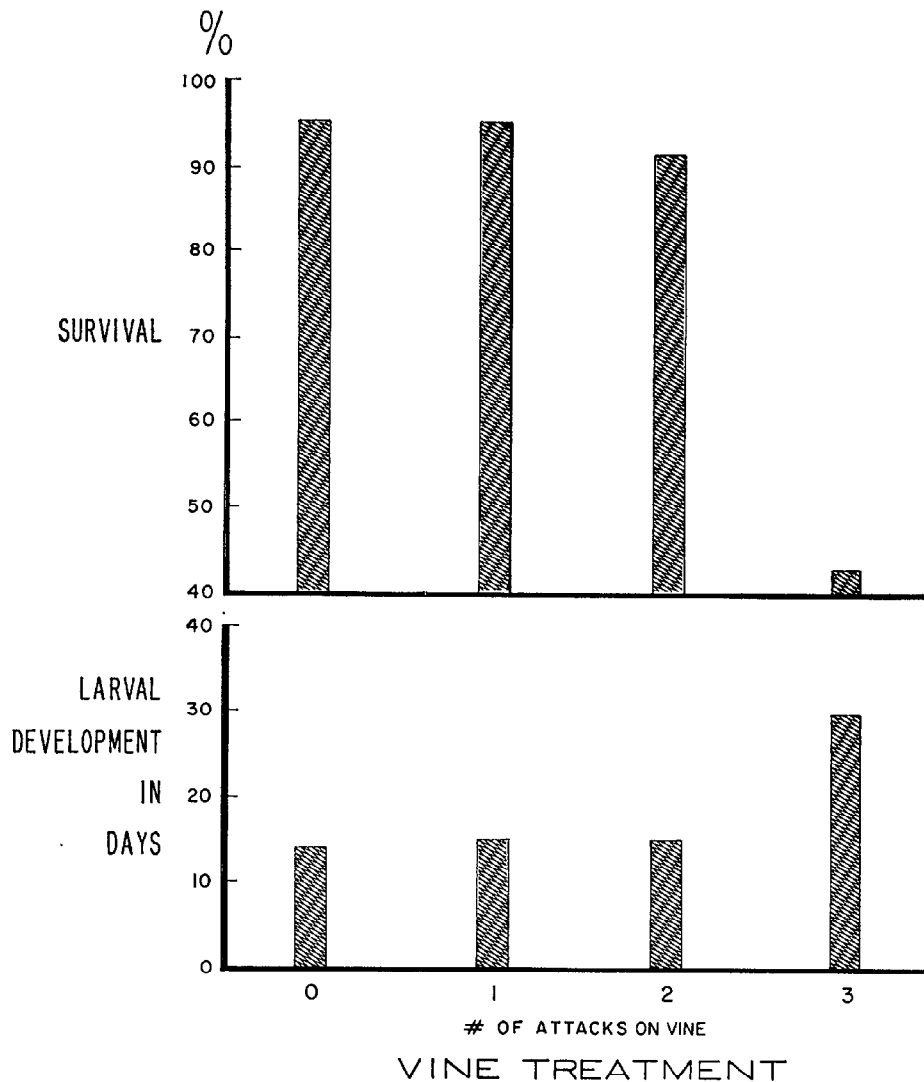


Fig. 5. The effects of the number of previous grazings of genetically identical clones of *Omphalea diandra* on the development and mortality of *Urania* larvae which were eating new leaves.

SUMMARY

Day-flying Neotropical *Urania* moths undergo cyclical population fluctuations and massive one-way flights. There may be "return" flight several months later, but these are scattered, not always annual, and composed of relatively few recently emerged individuals that are usually in reproductive diapause. Presumably not all moths emigrate in the southward flight. Why do some leave and others remain? The sole larval food plant are species of the woody, often huge lianas *Omphalea* spp (Euphorbiaceae). The distribution of *Omphalea* and *Urania* coincide exactly but not all patches of *Omphalea* are occupied by *Urania* at any given time. Few insects and no other Lepidopteran eat *Omphalea*. Imitating feeding of *Urania* larvae,

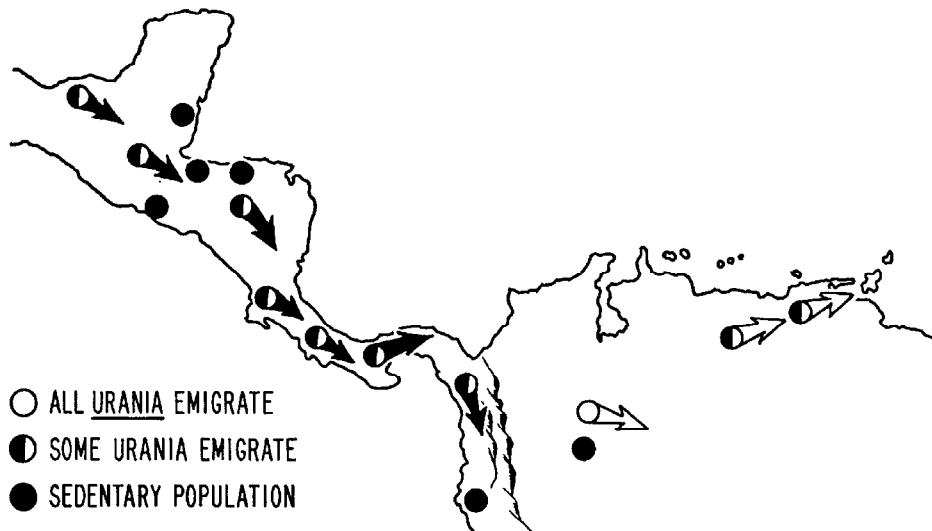


Fig. 6. A suggested model of *Urania nomadic* flights. Not all individuals in a population emigrate, and not all populations contribute to the emigration flight. Return flights may consist of few individuals and thus are difficult to detect. These individuals may also be many generations removed from the original immigrants.

I experimentally grazed with razor and later paper punched the leaves of genetically identical clones of *Omphalea*. Larvae grew normally on the controls, and on leaves from clones earlier "grazed" once or twice. But when presented with leaves from clones "grazed" the third time, they either refused to eat them, ate them and died, or grew slowly and had higher pupal mortality. A hypothesis is proposed that the chemical response of the plants also provides not only the ultimate cause but also that the level of toxicity provides the proximate clue as to whether the adults emigrate or not. They may be seeking vines which have received less grazing and or have escaped grazing entirely for several years and thus have lowered toxicity. I also suggest that it is the plant's response that determines the four or eight year cycle in *Urania*.

APPENDIX

¹A one way migration poses some problems most of which I feel are more apparent than real. If all the "migrating" genes moved out of an area, say Veracruz, Mexico, how then does this area continue to give rise to successive generations of migrants? One explanation is that one does not detect the few individuals that move back from other locales to the south. This need not occur very often, perhaps every few years, but the females are quite fecund and population build up could be very rapid. We simply do not know how far an individual migrates, nor do we have any idea of the genetics as they directly relate to the nomadic tendency.

²Leaf-cutting ants (*Atta* spp.) also occasionally attack. I have examined specimens of all the described species and all possess extra floral nectaries in one place or another on their leaves. In *O. diandra*, pugnacious ants (not *Atta* spp.) move up and down the liana seeking out secreting nectaries—yet another defensive line against herbivores.

³The absence of an adult food source in an area could certainly be a factor causing adults to leave. In 1978 I released several hundred recently emerged adults in an area with much *Omphalea* but apparently lacking flowers suitable to the adults. Approximately one half of the individuals were fed before release on sugar water, honey and desolved bullion. All of the adults disappeared within a few hours and were not seen again during the following week.

⁴In those experiments I assumed that there was a migratory type and non-migratory type, and that something during the larval period determined which emerged. Two sets of hypotheses were tested, first, abundant larval food would give rise to non-migratory adults; scarcity would produce migratory adults. Second, low larval density would produce non-migratory adults; high density would give rise to migratory adults. In both cases the experimental groups behaved one way or the other, but the results were neither consistent nor predictable.

⁵The flight of 1973 was a big one (Fig. 2). As noted by several authors (e.g., Smith, 1972) the year following big flights is often (note exception 1954-55, Fig. 2) a poor one for *Urania* emigration. The obvious explanation—that they ate all the *Omphalea*—I believe, is not, the correct one. Plants that had been badly chewed up by October 1973 were completely leafed out again by January 1974.

⁶*Urania* populations at nadir in both wild and lab. Gregarine parasites were thought to be implicated, but later were judged not to be a serious source of mortality. Larvae found to “imprint” on particular plants but significance of such behavior not understood.

⁷Experiments would have been repeated in 1981 except that there was no *Urania* flight in 1981, a unique occurrence with reliable data back to 1954, and anecdotal data back to 1900. The year 1981 was the wettest year in recorded meteorological history in Panama, but how this might have affected *Urania* is not known.

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