

Chemical defense and aposematism: the case of *Utetheisa galapagensis*

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Summary. The moth *Utetheisa galapagensis* (Lepidoptera, Arctiidae) is an endemic of the Galápagos Islands. Unlike other species of *Utetheisa*, which are gaudily aposematic, it is uniformly grayish in appearance. Our initial presumption that *U. galapagensis* lacks the plant-derived systemic pyrrolizidine alkaloids that account for the aposematism of its congeners was erroneous. *U. galapagensis* feeds on species of *Tournefortia* (Boraginaceae), one of which, *T. rufo-sericeae*, was found to contain pyrrolizidine alkaloids (5% of dry weight). *U. galapagensis* of both sexes contain these compounds. The drabness of *U. galapagensis* may be attributable to the fact that the moth is nocturnal, unlike its aposematic congeners. Two additional species of *Utetheisa* from the Galápagos (*U. devriesi*, and *U. perryi*) are also non-aposomatic. Whether the three Galápagos *Utetheisa* are primitively drab, or whether their cryptic condition is secondarily derived from an aposematic ancestry, remains unsettled.

Key words. Chemical defense – Arctiidae – pyrrolizidine alkaloids – Boraginaceae – *Tournefortia*

The genus *Utetheisa* (Lepidoptera: Arctiidae), of primarily Old World affinity, is cosmopolitan in distribution and includes nearly 40 species and subspecies (Strand 1919; Hayes 1975; Holloway 1988), almost all gaudily colored as adults. The coloration, which manifests itself as a sprinkling of yellow, white, and black markings, against a varying background of pink and white, is generally considered to be aposematic. Indeed, *Utetheisa* that have been studied in some detail, such as the New World *Utetheisa ornatix*, although crepuscular in its mating habits, is as likely to be seen on the wing in the daytime as at night (Hayes 1975; Conner *et al.* 1980). Aposematism in *Utetheisa* is thought to be linked to adult distastefulness, which in turn appears to be a consequence of the larval feeding habits. *Utetheisa* larvae, as far as is known, feed on plants containing pyrrolizidine alkaloids, bitter toxins that they sequester and retain through metamorphosis into the adult stage. In

U. ornatix, the larval foodplants are legumes of the genus *Crotalaria* (Fabaceae) (Grossbeck 1911; Pease 1968; Tietze 1972; Newman and Walker 1977). Other species of the genus feed on *Crotalaria* as well, or on species of *Messerschmidia*, *Heliotropium*, *Myosotis*, *Bothriospermum*, *Echium*, and *Trichodesma* (Boraginaceae) (Robinson 1975; Holloway 1988).

It has been known for some time that there exist four species of *Utetheisa* on the Galápagos Islands, of which one is the widely distributed, aposematic *U. ornatix* (Fig. 1B, C). The other three species – *U. galapagensis*, *U. devriesi*, and *U. perryi* – are endemic to the islands (Hayes 1975), and non-aposomatic. They are evenly grayish in appearance and entirely lacking in colored markings. We were interested in securing these drab species for chemical study to check whether they too acquired systemic alkaloid. There were four possibilities. They could be alkaloid-free and diurnal, and therefore cryptic because they could not “afford” to be aposematic, or they could be alkaloid-laden and nocturnal, and hence in no “need” to be warningly colored. Alternatively, they could be alkaloid-free and nocturnal and for both reasons non-aposomatic, or alkaloid-laden and diurnal, and non-aposomatic possibly because of cryptic behavioral habits. We have now had the opportunity to look into these possibilities with one species, *U. galapagensis*, and were able to show that the second alternative held true. We found both the moth and one of its food plants to be alkaloid-laden, and the moth to be inactive during the day. We here present the data.

Material and methods

The moth

The *U. galapagensis* adult (Fig. 1A) is cryptic in appearance. The forewings are darker than the hindwings, and both wings bear black markings, particularly along the margins. *Utetheisa* typically have a wingspread of about 4 cm; *U. galapagensis*, with a wingspread of about 3 cm, is conspicuously smaller.

The *U. galapagensis* larvae are black and white, unlike the more colorful black-yellow-and-red larvae of other species of the genus (e.g. *U. ornatix*) (Eisner & Meinwald 1995). *U. galapagensis* differs further from such species as *U. ornatix* in that it lays its eggs singly rather than in clusters.

The food plants of *U. galapagensis* are three congeneric species of the family Boraginaceae: *Tournefortia rufo-sericeae*, *T. psilostachya*, and *T. pubescens*.

U. galapagensis occurs from sea level to the Pampa zone, on the following Galápagos Islands: Baltra, Fernandina, Floreana, Genovesa, Isabela, Marchena, Pinta, Santiago, San Cristóbal, Santa Cruz, and Santa Fe.

Moths were sent in dried condition from their collecting site (Volcano Darwin, Isabela Island) to our Cornell laboratories for analysis.

The plant

Cuttings of *T. rufo-sericeae* (from Santa Cruz Island) were sent in air-dried condition to our Cornell laboratories for analysis.

Chemical analysis (plant)

Powdered leaves and stems (50 g) were extracted with methanol for 24 h. After filtration, the solvent was removed *in vacuo*, and the residue was partitioned between dichloromethane and 0.2 N aqueous HCl. The aqueous phase was separated, basified by the addition of concentrated aqueous NH₃, and extracted with dichloromethane. After evaporation and filtration, the extract was analyzed by electrospray mass spectrometry (MS), using a Micromass Quattro I mass spectrometer, operated in positive-ion electrospray mode. For analyses of the plant's N-oxide content the aqueous phase was acidified with 1 N HCl and treated with Zn dust for 24 h at 25°C. After filtration and adjusting to pH 9 by addition of concentrated aqueous NH₃, the solution was saturated with sodium chloride and then extracted repeatedly with a mixture of dichloromethane and methanol (9/1, v/v). Evaporation yielded 1.5 g of a slightly yellowish oil, which was analyzed by ¹H NMR spectroscopy, indicating the presence of large amounts of pyrrolizidine alkaloids. Part of this material (0.4 g) was then chromatographed over a short silica column (length 5 cm) using a mixture of methanol and dichloromethane (1/6, v/v) containing 2% aqueous NH₃ as a solvent. The fractions thus obtained were analyzed by ¹H- and ¹³C-NMR spectroscopy using CDCl₃ and acetone-d₆ as solvents, which indicated the presence of four alkaloids, the tetrahydropyrrolizines **1** and **2** and the hexahydropyrrolizines **3** and **4**. NMR spectra were recorded at 298 K using a Varian UNITY+ (500 MHz proton, 126 MHz carbon) spectrometer.

Spectroscopic data of **3** and **4**

(1*R*,7*R*,8*R*)-1-({2*R*,3*S*}-2,3-Dihydroxy-2-[1-methylethyl]-propylcarbonyloxymethyl)-7-hydroxyhexahydropyrrolizine (tournefortine A, **3**). ¹H NMR (500 MHz, acetone-d₆): 2.72 (J_{1,2a} = 8.1 Hz, J_{1,2b} = 7.6 Hz, 1H, 1-H), 1.76 (J_{2a,2b} = 12.0 Hz, J_{2a,3a} = 9.3 Hz, J_{2a,3b} = 7.0 Hz, 1H, 2-Ha), 2.14 (J_{2b,3a} = 7.0 Hz, J_{2b,3b} = 3.3 Hz, 1H, 2-Hb), 2.56 (J_{3a,3b} = 8.9 Hz, 1H, 3-H_a), 3.11 (1H, 3-H_b), 2.67 (J_{5a,5b} = 9.3 Hz, J_{5a,6a} = J_{5a,6b} = 8 Hz, 1H, 5-H_a), 2.95 (J_{5b,6a} = J_{5b,6b} = 4.5 Hz, 1H, 5-H_b), 1.91-1.95 (2H, 6-H_a and 6-H_b), 4.19 (J_{7,8} = 4.5 Hz, J_{7,6a} = J_{7,6b} = 2.8 Hz, 1H, 7-H), 3.13 (J_{8,1} = 5.5 Hz, 1H, 8-H), 3.94 (J_{9a,9b} = 10.6 Hz, J_{9a,1} = 6.0 Hz, 1H, 9-H_a), 4.54 (J_{9b,1} = 4.6 Hz, 1H, 9-H_b), 3.95 (J_{12,13} = 6.5 Hz, 1H, 12-H), 1.11 (3H, 13-H), 2.08 (J_{14,15} = J_{14,16} = 6.9 Hz, 14-H), 0.89 (3H, 15-H), 0.90 (3H, 16-H). ¹³C NMR (126 MHz, acetone-d₆): 37.0 (C-1), 31.8 (C-2), 55.85 (C-3), 52.6 (C-5), 37.4 (C-6), 70.8 (C-7), 74.0 (C-8), 67.6 (C-9), 175.7 (C-10), 83.5 (C-11), 69.6 (C-12), 17.6 (C-12), 33.05 (C-13), 17.0 (C-15), 17.5 (C-16). Electrospray MS: 302.2 {M+H}⁺.

(1*R*,7*R*,8*R*)-1-({2*R*,3*R*}-2,3-Dihydroxy-2-[1-methylethyl]-propylcarbonyloxymethyl)-7-hydroxyhexahydropyrrolizine (tournefortine B, **4**). ¹H NMR (500 MHz, acetone-d₆) [ppm]: 2.76 (J_{1,2a} = 9.3 Hz, J_{1,2b} = 6.0 Hz, 1H, 1-H), 1.75 (J_{2a,2b} = 12.0 Hz, J_{2a,3a} = 10.1 Hz, J_{2a,3b} = 6.7 Hz, 1H, 2-H_a), 2.11 (J_{2b,3a} = 5.8 Hz, J_{2b,3b} = 3.3 Hz, 1H, 2-H_b), 2.54 (J_{3a,3b} = 8.6 Hz, 1H, 3-H_a), 3.04 (1H, 3-H_b), 2.65 (J_{5a,5b} = 9.3 Hz, J_{5a,6a} = J_{5a,6b} = 8 Hz, 1H, 5-H_a), 2.96 (J_{5b,6a} = J_{5b,6b} = 4.5 Hz, 1H, 5-H_b), 1.92-1.96 (2H, 6-H_a and 6-H_b), 4.18 (J_{7,8} = 4.3 Hz, J_{7,6a} = J_{7,6b} = 2.8 Hz, 1H, 7-H), 3.19 (J_{8,1} = 6.8 Hz, 1H, 8-H), 4.11 (J_{9a,9b} = 10.7 Hz, J_{9a,1} = 6.9 Hz, 1H, 9-H_a), 4.20 (J_{9b,1} = 6.6 Hz,

1H, 9-H_b), 3.89 (J_{12,13} = 6.5 Hz, 1H, 12-H), 1.20 (3H, 13-H), 2.15 (J_{14,15} = J_{14,16} = 6.9 Hz, 14-H), 0.85 (3H, 15-H), 0.87 (3H, 16-H). ¹³C NMR (126 MHz, acetone-d₆) [ppm]: 36.6 (C-1), 32.0 (C-2), 55.75 (C-3), 52.4 (C-5), 37.5 (C-6), 70.45 (C-7), 73.3 (C-8), 67.05 (C-9), 174.8 (C-10), 84.1 (C-11), 71.6 (C-12), 17.8 (C-12), 32.85 (C-13), 16.2 (C-15), 18.15 (C-16). Electrospray MS: 302.2 {M+H}⁺.

Hydrogenation of **1** and **2**

For comparison purposes, a solution of 50 mg of a 5:2 mixture of compounds **1** and **2** in methanol (2 ml) was hydrogenated at 10 bar for 8 h using palladium on charcoal (10% Pd) as catalyst. Subsequently, the mixture was filtered and evaporated, and the residue analyzed by ¹H NMR spectroscopy.

Alkaline Hydrolysis of **1** and **2**

A solution of 30 mg of a 5:2 mixture of alkaloids **1** and **2** and 100 mg of potassium carbonate in 20 ml of a 2:1 mixture of methanol and water was stirred for 16 h at 55 °C. After evaporation of the solvent *in vacuo* the semi-solid residue was extracted with dichloromethane. The combined extracts were filtered and evaporated, yielding 1 mg of yellow crystals, which was compared to (+)-retronecine obtained in a similar fashion from (-)-monocrotaline.

Quantification

In order to determine the ratio of these alkaloids on the original extract, a small sample of the mixture of alkaloids obtained after N-oxide reduction was analyzed by ¹H-NMR spectroscopy. Using acetone-d₆ as the solvent, the signals corresponding to the methyl group adjacent to the secondary hydroxyl group in **1-4** are sufficiently separated in order to determine the relative abundance of these compounds via integration.

Chemical analysis (moth)

Air-dried bodies of two female and two male *U. galapagensis* adults were extracted each with 1 ml of a 1:1 (v/v) mixture of dichloromethane and methanol for 12 h at 25 °C. After filtration, the extracts were concentrated and directly submitted to analysis via ¹H NMR spectroscopy using acetone-d₆ as the solvent.

For HPLC analysis, air dried bodies of two female and two male *U. galapagensis* were extracted for 24 h with 500 ml of buffer solution (2.7 g monopotassium phosphate/2 mL of triethylamine/0.4 mL of trifluoroacetic acid in 4 L of water: pH adjusted to 3.0 with phosphoric acid). The samples then were centrifuged for 15 min and the extracts analyzed by HPLC with a Hewlett-Packard 1090 Series II instrument with a diode array detector (column: C-18 BDS Hypersil; 250 4.6 mm: 5-μl particle size). The column was eluted (1 mL/min) with a mixture of buffer solution and acetonitrile (94:6 v/v). The pyrrolizidine alkaloid ridelline served as internal standard.

Results

Plant and moth chemistry

The analyses of *T. rufo-sericeae* plant material revealed the presence of four alkaloids, which were separated by silica gel chromatography into two fractions, containing two tetrahydropyrrolizines (**1**, **2**) and two hexahydropyrrolizines (**3**, **4**), respectively (Fig. 2). The known retronecine derivative indicine (**1**) along with smaller amounts of its epimer morifoline (**2**) were identified through comparison of their proton and carbon NMR spectra with published data (Nishimura *et al.* 1987, Wiedenfeld & Cetto 1998) and

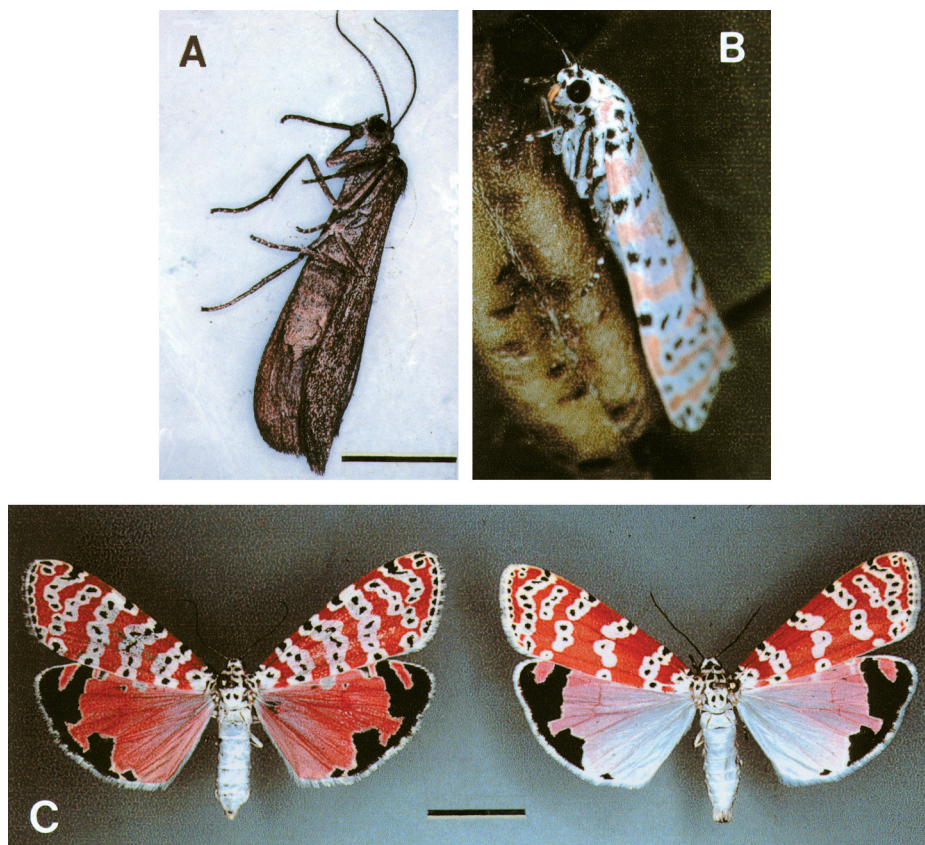


Fig. 1 (A) *Utetheisa galapagensis*. (B) *Utetheisa ornatrix*, on pod of *Crotalaria mucronata*, its foodplant (Florida specimen). (C) *Utetheisa ornatrix*, female and male (right) (Florida specimens). Bars (A) 5 mm; (C) 10 mm

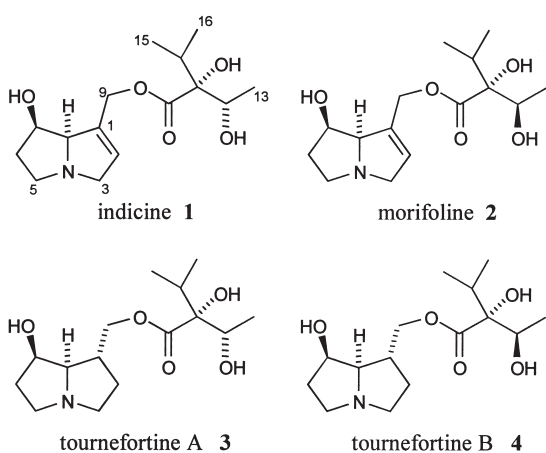


Fig. 2 Pyrrolizidine alkaloids identified from *T. rufosericeae*

comparison by NMR spectroscopy and HPLC to authentic samples of intermedine and lycopsamine obtained from *Eupatorium* roots (Conner *et al.* 2000). The diastereomers **1** and **2** occurred in a ratio of about 5:2, respectively, as determined by ^1H NMR spectroscopy. Their absolute configuration was established through alkaline hydrolysis, which yielded (+)-(7*R*,8*R*)-retronecine.

The unsaturated alkaloids **1** and **2** were accompanied by about equal amounts of their saturated derivatives, **3** and **4**, which were identified through a standard set of two-dimensional NMR experiments, including double-quantum filtered COSY, NOESY, gHSQC, and gHMBC as two diastereomers of 1-(2,3-dihydroxy-2-[1-methylethyl]propylcarbonyloxymethyl)-7-hydroxyhexahydropyrrolizine (Fig. 2). The ratio of the relative abundances of **3** and **4** closely resembled that of their unsaturated analogs, **1** and **2**. We anticipated the relative configuration of **3** and **4** at carbons C-7, C-8, C-11, and C-12 to parallel the configuration of the corresponding carbons in **1** and **2**, which was corroborated *via* analysis of NOESY spectra in combination with a hydrogenation experiment. Strong NOE correlation signals observed for the pair of protons (7-H, 8-H) established *cis* orientation for these two protons, whereas NOE signals observed for the pairs of protons (8-H, 9-H_a), (8, 9-H_b), (2-H_a, 9-H_a), (2-H_a, 9-H_b), and (1-H, 2-H_b), indicated *trans* orientation for protons H-8 and H-1 as well as *cis* orientation for H-1 and H-2_b. These assignments were corroborated further by NOE correlation signals observed for the pairs (H-1, 3-H_a) and (H-3_a, H-5_a), which indicates *cis* orientation of H-1, H-3_a, and H-5_a. Therefore, the configuration of the hexahydropyrrolizine unit in **3** and **4** was established as (1*R*,7*R*,8*R*). Hydrogenation of the two tetrahydropyrrolizine derivatives **1** and **2** yielded a mixture of diastereomers of the corresponding hexahydropyrrolizines, among them as two of

the major products **3** and **4**, indicating that the naturally more abundant hexahydropyrrolizine **3** is derived from (2*R*,3*S*)-trachelanthic acid, while the less abundant isomer **4** is derived from (2*R*,3*R*)-viridifloric acid. Compounds **3** and **4** represent two hitherto unknown diastereomers of 1-(2,3-dihydroxy-2-[1-methylethyl]propylcarbonyloxymethyl)-7-hydroxy-hexahydropyrrolizine for which we propose the names tournefortine A and tournefortine B, respectively.

The isolation of these pyrrolizidine alkaloids from *T. rufo-sericeae* came as no surprise, given that structurally closely related alkaloids have been identified from other species of the genus (Ogihara *et al.* 1997). However, the sheer amount of alkaloid present in the leaves of *T. rufo-sericeae* is fascinating, considering that the pyrrolizidine alkaloids **1-4** - mostly in the form of their respective N-oxides - make up about 5% of the dry weight of the analyzed plant material (leaves and stems). The four compounds **1-4** occur in a ratio of 5:2:5:2, respectively, as determined via integration of the ¹H-NMR signal of the protons in position 13.

Analyses of extracts obtained from *U. galapagensis* of both sexes using NMR spectroscopy, HPLC, and electrospray MS revealed the presence of the four alkaloids **1-4** as well as of the corresponding N-oxides. The relative abundances of these compounds varied significantly among the four individuals analyzed. HPLC analysis indicated that the moths contained between 50 and 300 µg of these alkaloids per individual.

Moth habits

Unlike *U. ornatrix*, with which we have field experience, both in Florida and in the Galápagos, and which we know to be active at dusk and during the day, *U. galapagensis* seems to be exclusively nocturnal. One rarely sees *U. galapagensis* on the wing during the day, and the moth flies regularly to lights, which occurs less frequently with *U. ornatrix*. A further characteristic of *U. galapagensis* is that it does not readily take to flight when disturbed in the daytime, with the result that it is not usually flushed from its perches. *U. ornatrix*, in contrast, is readily flushed in the daytime. We assume that aposematic *Utetheisa* other than *U. ornatrix*, are similarly active in the daytime, and that the two cryptic endemic congeners of *U. galapagensis* - *U. devriesi* and *U. perryi* - are also nocturnal.

Discussion

U. galapagensis evidently is unexceptional in that it sequesters pyrrolizidine alkaloids from its larval food plant and stores the compounds systemically. While we did not obtain direct evidence of such sequestration, the presence of the alkaloids in both the moth and one of its *Tournefortia* food plants, leaves little doubt that the moth derives its alkaloid from the larval diet. Since presence of pyrrolizidine alkaloids appears to be a common feature of *Tournefortia* (Ogihara *et al.* 1997), we assume the other two food plants of *U. galapagensis* - *T. psilostachya* and *T. pubescens* - to

be alkaloid laden as well, and to be used by the moth with equal effectiveness for alkaloid uptake.

We assume that *U. galapagensis* benefits from the possession of its acquired alkaloid, just as *U. ornatrix* does (Dussourd *et al.* 1988, Eisner & Eisner 1991, Hare & Eisner 1993, González *et al.* 1999, Eisner *et al.* 2000), and assume further that by being nocturnal the moth avoids diurnal, visually-oriented predators such as birds and reptiles, providing an explanation, possibly, for why the moth is not aposematic.

One wonders whether there are special advantages for a moth in the Galápagos to being strictly nocturnal. Is bat predation less of an issue in the Galápagos? Whatever the answer, we discovered that *U. galapagensis* has ears (tympanal organs) typical of those of arctiids (Fullard & Barclay 1980), indicating that it might have the capacity to hear the echolocating calls of approaching bats and take evasive action. Moreover we found also that, like other *Utetheisa*, *U. galapagensis* lacks sound producing organs by which to warn pursuing bats of its distastefulness. Aside from the issue of bat predation, could it be that the daytime hours on the Galápagos are fraught with unusual dangers? The possibility certainly cannot be dismissed that some diurnal, visually-oriented predators on the Galápagos are unaffected by *Utetheisa*'s chemical defenses. On the other hand, it should be noted that one species of *Utetheisa*, *U. ornatrix*, does survive in the Galápagos as an aposematic diurnal species.

By the same token one wonders whether drabness in the Galápagos *Utetheisa* is a primitive condition retained unchanged from ancestral times, from before the acquisition of aposematic traits by the *Utetheisa* lineage, or whether it is a secondary condition evolved by divergence from an aposematic ancestry. The former alternative would imply that the Galápagos provided refuge from the selective pressure that forced the evolution of aposematism elsewhere, while the latter alternative would indicate that special adaptive conditions on the islands made retention of aposematism maladaptive. Either way, it is clear that drabness in *U. galapagensis*, as very probably also in *U. devriesi* and *U. perryi*, should the latter two also sequester pyrrolizidine alkaloids, is a correlate of nocturnal habits, not absence of defense.

We are at a loss in explaining why *U. galapagensis* lays its eggs singly, rather than in clusters. In *U. ornatrix*, which does lay clusters, the eggs are protected by parental endowment with pyrrolizidine alkaloid. Being clustered, when thus endowed, provides better protection against some egg predators (chrysopid larvae) than being laid singly (Eisner *et al.* 2000), but this is not to say that the singly laid eggs of *U. galapagensis* are alkaloid free. All in all, there is much that could be learned by further study of *U. galapagensis*. Its courtship alone is deserving of investigation, if for no other reason than to determine whether it is similar, and subject to the same sexual selective strategy on the part of the female, as it is in *U. ornatrix*. In the latter species the female receives pyrrolizidine alkaloid from the male by seminal infusion, a gift that she bestows, together with alkaloid of her own, upon the eggs (Eisner & Meinwald 1995). We had no *U. galapagensis* eggs available for analysis, to see if these too are alkaloid-endowed.

Acknowledgements

Study supported in part by grants AI02908 and GM 53830 from the National Institutes of Health. This is paper no. 184 in the series "Defense mechanisms of arthropods". Paper no. 183 is Smedley *et al.*: Proc Nat Acad Sci USA 99:6822–6827.

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Received 13 February 2002; accepted 8 March 2002.



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