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Authors: Long, Isaac, and Sourakov, Andrei

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REMARKABLE LONGEVITY OF THE CHEMICALLY DEFENDED MOTH, *UTETHEISA ORNATRIX*
(LEPIDOPTERA: EREBIDAE) AND THE FACTORS THAT AFFECT IT

ISAAC LONG AND ANDREI SOURAKOV*

McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida, USA.

* Corresponding author: asourakov@flmnh.ufl.edu

ABSTRACT. Most butterflies and moths, with the exception of *Heliconius*, live only a week or two in their non-hibernating state. In the present study, we evaluated the longevity of the chemically defended Ornate Bella Moth, *Utetheisa ornatrix*, using a sample of 214 individuals from two broods. On a diet of 6% sugar water or Gatorade®, a quarter of the moths survived for one month or longer, with a maximum survival of 50 days. A glimpse into the genetic component offered by using two broods suggests that one can expect to find greater variability in longevity between different populations of this species. Males lived on average longer than females, and moths from heavier pupae lived longer than their smaller siblings. The nutrition of caterpillars, translated into pupal weight, appears to have a positive effect on the longevity of resultant adults. While it was not surprising to find that sugar played a positive role in the longevity and fecundity of adult moths, the fact that *Utetheisa ornatrix* can subsist solely on water for up to 36 days and that males tended to live longer than females, which is reverse of most species for which such data is available, were intriguing findings. The chemically defended nature of this species, its high fecundity (251±64 eggs in this study) paired with its habit of laying eggs in small batches, and its propensity to disperse as adults help explain why these moths evolved prolonged life spans.

Additional key words: community ecology, herbivores, trophic interactions, tiger moths

According to mark-recapture studies of temperate butterflies, most live only a week or two in a non-hibernating state, and males tend to live slightly shorter lives than females (e.g., Scott 1973). There are exceptions to the rule, however. In the tropics, *Heliconius* butterflies, which feed not only on nectar but also on pollen, can live as long as five months (Turner 1971, Ehrlich & Gilbert 1973, Boggs 1979). For moths, the longevity data is mostly derived from the laboratory cultures of several economically important species. For instance, females of the European Corn Borer Moth, *Ostrinia nubilalis* (Hübner, 1796) (Pyralidae), live around 13–14 days on 8% sucrose solution (Royer & McNeil 1993), females of the Cotton Bollworm Moth, *Helicoverpa armigera* (Hübner, [1809]) (Noctuidae), live 10–12 days on 10% honey solution (Hou & Sheng 1999), and both males and females of Dolichos Armyworm Moth, *Spodoptera dolichos* (Fabricius, 1794) (Noctuidae), live 12–13 day on a diet of 7% honey/sucrose solution (Montezano et al. 2015). Based on two species, Murphy et al. (2011) found that female limacodids (the group that does not feed as adults), live 8–9 days on average, but some female Saddleback Caterpillar Moths, *Acharya stimulea* (Clemens, 1860), lived as long as three weeks in the lab.

In the present study, we evaluated the longevity of the Bella Moth, *Utetheisa ornatrix bella* (Linnaeus, 1758) (Erebidae) in the lab. The moth has intriguing and intricate relationships with its hostplants in the genus *Crotalaria*, which determine its ecology (Conner 2008). As the primary focus of the second author's interest in *U. ornatrix* are these relationships, we explored here how caterpillar performance, interpreted as greater or

smaller pupal weight, may be influencing the longevity of adult moths. As *U. ornatrix* is a nectar-feeder for which the nectar and rain may be scarce in early spring or late fall/winter when this moth flies in north-central Florida (Sourakov 2015), we also investigated the roles that sugar and water play in determining longevity. There exists anecdotal evidence that butterflies live longer on Gatorade® (Daniels, pers. com.), and adult butterflies are routinely maintained in colonies on that diet (e.g., Trager 2009, Saarinen 2009). Because of this and considering the salt-seeking, puddling behavior of many Lepidoptera species in the tropics, we also tested if Gatorade® would have any benefits compared to sugar water of the same concentration. We evaluated longevity separately by sex, as the biological objectives, physiology, and pupal weights of males are all different from those of the females.

MATERIALS AND METHODS

A total of 214 pupae from two broods were obtained in the laboratory of the McGuire Center for Lepidoptera and Biodiversity, by rearing larvae from eggs, which were laid in late April 2016 by two *U. ornatrix* females netted on the University of Florida campus. These females, similar in color pattern and size, flew in close proximity to each other, were collected a few minutes apart, and represented a very isolated population located in the middle of urban development; hence we assume that they are genetically similar. The resultant larvae were fed on the foliage and seeds of *Crotalaria lanceolata* E. Mey. collected from the same location. As it has been demonstrated that adding green seeds of this host to the diet has a positive effect on pupal weight, which in turn

corresponds to wing size (Sourakov 2015, Long & Sourakov 2016), we varied the amount of seeds provided to larvae in later instars to achieve a greater variation in pupal weight.

As the larvae grew, they were divided into smaller and smaller groups feeding in 2 oz. clear plastic cups, until they pupated individually in these cups and were assigned voucher numbers. Pupae were weighed using a Mettler Toledo AL104 analytical balance. The mean (\pm SD) pupal weights of the two broods were more similar in females (154 ± 21 mg (N=40) vs. 155 ± 23 mg (N=62), $P=0.8$) than in males (179 ± 27 mg (N=38) vs. 166 ± 22 mg (N=74), $P=0.06$).

Upon emergence, moths were randomly placed in one of the three experimental groups which were provided with water, 6% sugar-water solution, or Gatorade® (fruit punch flavor), which, in addition to 6% sugar solution, contains sodium, potassium, food starch, phosphoric acid, flavors and preservatives. The liquids were delivered via soaked cotton tips (halved Johnson's baby-proof swabs were used as they retained moisture to a

much greater degree than the regular kind) inserted into the lid of the cup. The swabs were changed every two days to avoid molding and drying, during which time the mortality was assessed and the swabs were re-wetted with solution. A small control group of moths was kept in similar cups with holes but without any sustenance. Cups were kept at 23°C and organized in a checkerboard manner to reduce potential biases. Females of *U. ornatatrix* will lay eggs on the walls and lid of the cups even when they are not mated, and we randomly chose 5 females from each experimental group to compare fecundity. The data analysis (T-test and Ordinary Least Squares (OLS) regression analysis) was conducted using PAST statistical program (Hammer et al. 2001).

RESULTS

The results of correlating pupal weight and longevity are summarized in Table 1. Greater pupal weight appears to have had a positive influence on the longevity of *Utetheisa ornatatrix*, regardless of diet or sex, except for one group (females, brood 2, on Gatorade®). The

TABLE 1. Survival rates of *Utetheisa ornatatrix* adult moths in the lab in relation to sex and diet

Sex / Diet	Brood	Regression analysis (OLS)			50% surv.(days) \pm SE, variance & sample size
		Slope	P	r ²	
Males / Sugar Water	1	57.8	0.75	0.02	41.5 \pm 3.5 (var 99.1) (N=8)
	2	133.6	0.12	0.09	28 \pm 1.9 (var 101.2) (N=27)
Females / Sugar Water	1	117.6	0.12	0.20	25 \pm 1.5 (var 30.9) (N=13)
	2	29.1	0.71	0.005	22 \pm 1.6 (var 71.8) (N=29)
Males / Gatorade®	1	41.9	0.50	0.06	29 \pm 1.7 (var 29.8) (N=10)
	2	71.7	0.45	0.03	22 \pm 2.0 (var 84.4) (N=21)
Females / Gatorade®	1	91.7	0.37	0.05	24.5 \pm 2.1 (var 77) (N=18)
	2	-53.4	0.34	0.003	21 \pm 1.3 (var 52.9) (N=30)
Males / Water only	1	108.2	0.13	0.13	21 \pm 1.8 (var 58.4) (N=19)
	2	133	0.03	0.24	22.5 \pm 1.2 (var 30.1)(N=20)
Females / Water only	1	92.9	0.17	0.41	22 \pm 0.8 (var 4.3) (N=6)
	2	-167.2	0.74	0.15	15 \pm 3.5 (var 42.2) (N=3)
Control – no sustenance	1&2	9.1	0.36	0.11	6.5 \pm 0.3 (var 0.7) (N=10)
All males	1&2	104.6	0.007	0.06	23 \pm 0.9 (var 99.8) (N=112)
All females	1&2	49.0	0.18	0.02	22 \pm 0.8 (var 64.8) (N=102)

variance is great and hence, this correlation is weakly supported for each group separately. When all groups are combined and analyzed by sex (Table 1, bottom), the increase in sample size strengthens this conclusion. Increase in pupal weight appears to have stronger positive effect on the longevity of males than of females.

As illustrated by 50% survival data (Table 1) and the 25% survival graph (Fig. 1), males lived longer than females in all test groups, with the longest living male surviving 50 days, but with as many as a quarter living over a month on the sugar-containing diet. While males that were provided only water lived shorter lives on average, several also lived past the 30-day mark. Moths fed sugar-water and Gatorade® had similar fecundity (Mean \pm SD = 249 \pm 70 eggs and 253 \pm 63 eggs, respectively, $P=0.94$), and these two groups differed significantly ($P=0.02$; $P=0.03$) from the group maintained on water only, which laid average of 127 \pm 30 eggs.

DISCUSSION

Our results have demonstrated that *Utetheisa ornatrix* is an exceptionally long-lived moth, approaching *Heliconius* butterflies in longevity, but without the benefits of digesting nitrogen from the pollen—the way in which *Heliconius* are thought to achieve their remarkable longevity and in which they differ from other butterflies. While surviving up to the 20-day mark did not require that *U. ornatrix* adults feed on sugar, beyond approximately 25 days, the availability of sugar became essential for their survival. One can speculate that a freshly emerged *U. ornatrix* must be storing sufficient body-fat resources which it can convert into water, as, even when deprived of water, they lived for 8–9 days—almost as long as the limacodids in the study by Murphy et al. (2011). While limacodids, with their vestigial proboscises and thick bodies, evolved as non-feeders, *U. ornatrix* is a slim, seemingly delicate moth and an active nectar feeder with a well-developed proboscis.

Brood 1 and Brood 2 show slight but statistically significant differences in longevity of males despite their likely genetic similarity. Considering our knowledge of how different geographic populations of this species can be from each other and how widely this species is distributed (e.g., Pease 1968), we can expect to find an even greater variability in longevity when we start considering this species as a whole. The present study however had an objective to estimate how phenotypic plasticity of size induced through variation in caterpillar diet would affect longevity. Hence, it will be up to future studies to characterize the role that overall genetic variation plays in the longevity of this species, the range of which spans two continents. As for our primary

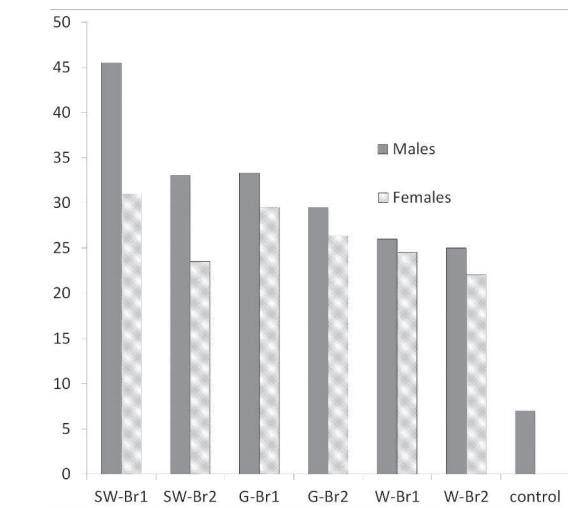


FIG. 1. Survival time (days) of a quarter of the *Utetheisa ornatrix* moths by brood, sex and diet. Males lived longer than females in every instance (SW-Sugar water, G- Gatorade®, W-Water).

objective, if we consider all diet groups and two broods as a subset of natural population, we can conclude that based on a sample of 112 males and 102 females, there exists a positive correlation between the pupal weight, induced through caterpillar diet, and adult moth longevity. Hence, we can speculate that oviposition choice by a maternal female, and subsequent caterpillar feeding and dispersal behaviors will have an effect on the longevity of the next generation of adult moths.

Regardless of diet, the males of this species tended to live longer than the females, which is the reverse of most species, but corresponds to the other ways in which this is an unusual moth. Male *U. ornatrix* are both larger than females and develop longer as caterpillars because they are tasked with sequestering alkaloids from their hostplants, not only for their own defense but also for nuptial gifts and the production of pheromones. For males, in addition to increased dispersal potential, which reduces inbreeding, extended longevity should lead to increase in mating success. In the lab, females of any given brood raised under similar conditions, will always emerge 2–3 days earlier than males because male caterpillars take longer to develop (Sourakov, 2015). However, the development of caterpillars is not synchronized in any given natural *U. ornatrix* population that we observed, and thus the longer a male lives, the higher chance he has to find a receptive mate.

It has been demonstrated previously that *U. ornatrix* females mate preferentially with larger males, and that this mating preference is inherited through the father rather than the mother, and that females with larger fathers have a stronger preference for larger males

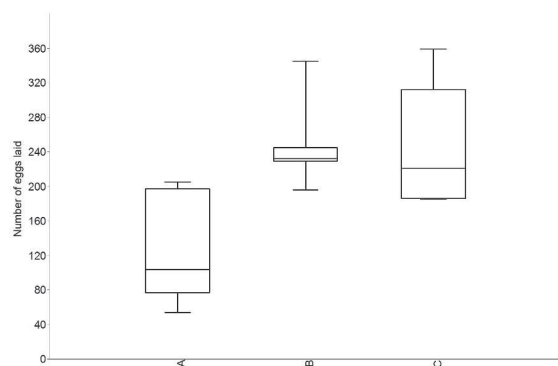


FIG. 2. Fecundity of *Utetheisa ornatrix* females maintained on (A)-Water; (B)-Sugar-water; (C)-Gatorade®.

(Iyengar et al. 2002). The fact that male pupal weight, which is as much a function of a caterpillar's performance and maternal oviposition choice as of the underlying genetics, has, as demonstrated above, a positive correlation with longevity, adds another layer of complexity to the story of how intimately the natural history, sexual selection, and evolution of *U. ornatrix* is intertwined with its hostplants.

We think, however, that the main reasons why *U. ornatrix* evolved the ability to survive 3–4 times longer than other moth species for which data is available is that the predation is less of a factor for *U. ornatrix*, as they are chemically defended (e.g., Eisner & Eisner 1991, Martins et al. 2015, Sourakov, pers. obs.). It is therefore realistic to expect that in nature *U. ornatrix* frequently live out their full physiological potential. While a female *U. ornatrix* can occasionally lay larger clusters of eggs, in natural conditions this is unusual. For observations for which we have the photographic evidence, the common size of egg clusters in nature is around 20, though it is quite variable: Mean \pm SD = 31 ± 34 eggs, N=8, Sourakov (pers. obs.). Based on the present study, a female that has access to nectar can lay upward of 300 eggs and therefore, in nature, lays numerous egg clusters. The increased longevity combined with this gradual oviposition can be highly adaptive for *U. ornatrix*, which is thought to also have high rates of dispersal (Cogni et al. 2011, Pease, 1968), and therefore can spread its eggs far and wide.

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