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EXOTIC *CROTALARIA* SPECIES (FABALES: FABACEAE) AS HOST PLANTS OF THE ORNATE BELLA MOTH, *UTETHEISA ORNATRIX* (LEPIDOPTERA: EREBIDAE), IN FLORIDA: LABORATORY BIOLOGY

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Abstract

The caterpillars of *Utetheisa ornatrix*, the ornate bella moth, feed on host plants in the genus *Crotalaria* (Fabales: Fabaceae), which, in Florida, encompasses 4 native and 10 introduced species. In the laboratory, *Utetheisa ornatrix* male larvae developed faster and resulted in larger adults, when raised on *Crotalaria incana* vs. *Crotalaria lanceolata* (2 species native to Africa). In the wild, this can potentially give a selective advantage to individuals that develop on *C. incana*. The presence of these and other exotic host plants, some of which are quite common (e.g. *C. pallida*, *C. spectabilis*, *C. retusa*), may be skewing the evolution of *U. ornatrix*, as well as its phenology and distribution. A constant temperature of 60 °F (15.6 °C) caused *U. ornatrix* to develop twice as slowly as it did at 72 °F (22.2 °C), but it was sufficiently high for successful development. Sentinel larvae placed in cages in the field during Oct-Dec, when temperatures averaged ≈ 62 °F, developed successfully. Regardless of the rearing conditions and the host plants used in the laboratory, male larvae developed slightly more slowly than female larvae. This translated in their emerging from the pupae later than the females, which is supported by field observations.

Key Words: herbivore, arthropod-plant interactions, invasive exotics, community ecology

Resumen

Las orugas de *Utetheisa ornatrix*, también conocida como la polilla bella ornamentada, se alimentan de plantas del género *Crotalaria* (Fabales: Fabaceae), las cuales en la Florida, abarcan cuatro especies nativas y 10 especies introducidas. En el laboratorio, las larvas de los machos de *Utetheisa ornatrix* se desarrollan más rápidamente y resultan en adultos mas grandes cuando son criados sobre *Crotalaria incana* versus *Crotalaria lanceolata* (dos especies nativas de África). En la naturaleza, esta puede potencialmente dar ventaja selectiva a los individuos que se desarrollan sobre *C. incana*. La presencia de estas y otras plantas exóticas, algunas de las cuales son bastante comunes (por ejemplo *C. pallida, C. spectabilis, C. retusa*) puede sesgar la evolución de *U. ornatrix*, así como su fenología y distribución. Una temperatura constante de 60 °F (15.6° C) causó que *U. ornatrix* se desarrollara dos veces mas lentamente que a los 72° F (22.2° C), pero fue lo suficientemente alta para un desarrollo exitoso. Larvas sentinales (indicadoras) colocadas simultáneamente en jaulas en el campo durante octubre-diciembre, cuando el promedio de la temperatura fue de ≈ 62° F, se desarrollaron con éxito. Independientemente de las condiciones de cría y las plantas hospedera utilizadas en el laboratorio, las larvas de los machos se desarrollaron un poco más lentamente que las larvas de las hembras. Esto resultó en la emergencia de los machos adultos de sus pupas más tarde que las hembras, lo que corresponde a las observaciones de campo.

Palabras Clave: selección sexual, herbívoro, interacciones de plantas-artrópodos, aposematism, especies exóticas invasoras, ecología de la comunidad

The ornate moth, *Utetheisa ornatrix* L., is found in the eastern and midwestern regions of the United States and throughout the Neotropics. Its caterpillars feed on host plants in the genus *Crotalaria* (rattlebox plants) (Fabales: Fabaceae). These moths are brightly, aposematically colored, with shades of yellow, red, pink, orange, and white adorning their wings, and white, spotted heads, thoraxes, and abdomens - a coloration that advertises their demonstrated distastefulness to predators (Eisner & Eisner 1991). The chemical ecology of this species has been studied

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in depth (Conner 2008 and references therein). For instance, pheromone production in males has been determined to directly depend on their diet as caterpillars, and only occurs when the diet contains *Crotalaria* pyrrolizidine alkaloids (PAs) (Conner et al. 1981). This is important, because the genetic quality of males correlates with the pheromone signal (Kelly et al. 2012), larger males contain more PAs than the smaller males (Conner et al. 1990), and evidence suggests that larger ones may be favored by sexual selection (LaMunyon & Eisner 1993; Iyengar et al 2002). The complex interactions between PA-containing plants and Lepidoptera in general are summarized by Boppré (1990) and will not be reviewed here. Additionally, a large body of knowledge also exists on the interaction of *U. ornatrix* specifically with dietary PAs extracted from plants and fed to the larvae (e.g., Cogni et al. 2012).

The main focus of the present paper is to report the observed differences between 2 introduced host plants of the genus *Crotalaria*, which have become naturalized diets of *U. ornatrix* in the southeastern United States, and to discuss how these differences may be important in the evolution of this species.

Many species of *Crotalaria* have been intentionally introduced to North America for use as green manure and soil improvement. Some of these species are considered invasive and have even been proven to be toxic to cattle, with their toxicity varying depending on their PA content (Williams & Molyneux 1987). In Florida, there are 14 different species of *Crotalaria*, 10 of which are introduced (Wunderlin & Hansen 2011) (Table 1). *Utetheisa ornatrix*, which formerly fed on just 4 host plant species native to Florida, presumably is now using all of these *Crotalaria*, some of which are more abundant than the native ones. For instance, the local population of *U. ornatrix* larvae used in the present study naturally feeds on 3 species that are native to Africa (*Crotalaria incana* L., *C. pallida* Ait. and *C. lanceolata* E. Mey.) and one species native to Asia (*C. spectabilis* Roth), and native *C. pumila* Ortega; of these *C. lanceolata* is the most prevalent. Other populations that we observed in north-central Florida may have only a single (native or exotic) *Crotalaria* species available to them.

In the present study, we compared *Crotalaria incana* and *C. lanceolata* as host plants for *U. ornatrix* during laboratory rearing. Specifically, we determined how the growth rate of larvae and the size of the resulting adult moths would vary when raised on one plant vs. the other. *Utetheisa ornatrix*, though mostly a tropical species, is also found in climates where it becomes relatively cold, so we tested how larval and pupal development are affected by temperature.

Materials and Methods

Even though *U. ornatrix* females can mate multiple times, eggs are mostly fertilized by the sperm of a single male (LaMunyon & Eisner 1993). Thus, to reduce genetic variability within a sample group, offspring of a single wild-collected female were used for each of the 2 experiments. Two female moths were netted behind the Florida Museum of Natural History, Gainesville, Florida. The first female, whose offspring were used in the temperature-dependence experiment, was caught on 15 May 2012, while the host plant-quality experiment was conducted with eggs from a female caught on 1 Oct 2012. Females were fed 5% sugar solution twice per wk. They laid eggs in the cups in which they were held, and, when the neonates hatched, they were provided with host plant leaves.

During the temperature-dependence experiment, larvae were initially raised gregariously in 16 oz. plastic cups at a room temperature of approximately 72 ± 2 °F (22.2 °C). Leaves of *Crotalaria lanceolata* were replaced 3 times per wk at which time the cups were also cleaned. During molting into the ultimate instar, larvae were randomly removed and divided into 2 groups. One group was raised further with only one larva to a cup at ≈ 72 °F (22.2 °C), and the second group was raised with one larva per cup at approximately 60° ± 2 °F (15.6 °C) (in the collections room, McGuire Center, Florida Museum of Natural History).

To test whether the results of our laboratory rearing at a constant temperature of ≈60 °F (15.6 °C) translate to the environmental conditions of Oct-Dec in north-central Florida, where temperatures fluctuated between the low 30's °F and low 80's °F and averaged at ≈ 62°F (NOAA 2012), we placed a dozen penultimate instars in 2 mesh cages outside and supplied them with plant material of *C. lanceolata*. Cages were placed in a partially shaded area in the habitat of *U. ornatrix* and were restocked weekly with either green seed pods (cage 1) or stems with leaves (cage 2).

For the experiment that involved raising larvae on *Crotalaria incana* and *C. lanceolata*, neonate larvae were split randomly into 2 groups. At first, larvae in both groups were raised gregariously in 16 oz. cups, but beginning with the penultimate instar, they were kept individually in 2 oz. plastic cups. Three times per week, the leaves and the cups were replaced and the progress of larval development was recorded. This experiment (Trial 1) was repeated using another egg batch laid by the same female starting 2 wk later (Trial 2) with a slight modification: larvae that were raised on *C. incana* were switched for a period of 5 days (while in their penultimate instar) to *C. lanceolata* and then returned to feeding on *C. incana*. A sample of host plant leaves was dried, ground-up

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TABLE 1. SPECIES OF *CROTALARIA* FOUND IN FLORIDA.

Species name	Common name	Origin	Current approximate distribution in U.S.A.	Status (in Florida)	Natural History
*C. incana**	Shakeshake	Africa	AL, FL, HI, OK, SC, TX, PR, VI	Occasional	bushy perenn., up to 2 m
*C. lanceolata**	Lanceleaf Rattlebox	Africa	AL, FL, GA, HI, LA, NC, SC	Frequent	ann. or short-lived perenn. herb, up to 1.7 m
*C. ochroleuca**	Slenderleaf Rattlebox	Africa	AL, FL, GA, LA, MS, NC, SC	Occasional	ann. or short-lived perenn. herb, up to 2.5 m
*C. pallida**	Smooth Rattlebox	Africa	AL, FL, GA, HI, MS, NC, SC, PR, VI	Frequent	robust herb, often well-branched and shrubby, up to 2 m
*C. trichotoma**	West Indian Rattlebox	Africa	FL, PR	Rare	ann., perenn., herb, up to 2 m
*C. virgulata**	Grant's Rattlebox	Africa	FL	Rare	ann., herbs, up to 1 m
*C. retusa**	Rattleweed	Asia	FL, GA, HI, KY, LA, MS, NC, NJ, SC, TX, PR, VI	Occasional	ann., herb, up to 1 m
*C. spectabilis**	Showy rattlebox	Asia	AL, AR, FL, GA, HI, IL, LA, MO, MS, NC, OK, SC, TN, TX, VA, PR	Frequent	ann., herb, up to 1 m
*C. verrucosa**	Blue Rattlebox	Asia	FL	Rare	ann., herb, up to 1 m
*C. juncea**	Sunn Hemp	India	FL	Rare	ann., up to 2.5 m
C. avonensis	Avon Park Rattlebox	Native	FL	Rare	perenn. herb 0.1 m above surface
C. pumila	Low Rattlebox	Native	AZ, FL, HI, MD, NM, OK, TX, UT	Frequent	ann., perenn., shrub or herb, up to 1 m
C. purshii	Pursh's Rattlebox	Native	AL, FL, GA, LA, MS, NC, SC, TN, TX, VA	Occasional	perenn., herb, up to 1 m
C. rotundifolia	Rabbitbells	Native	AL, AR, FL, GA, LA, MD, MS, NC, SC, VA, PR	Common	perenn., herb, trailing, or mat forming, up to 1 m

"*" indicates exotic species.

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into powder, and analyzed for nitrogen content using an Eager 200 CHN analyzer.

Adult moths resulting from all trials were frozen upon emergence and then mounted on spreading boards. Their forewing length (from the base of the wing to the tip) was measured with electronic calipers. All voucher specimens were labeled and deposited in the collection of the McGuire Center for Lepidoptera Research, Florida Museum of Natural History, Gainesville. Statistical analyses comparing the duration of larval and pupal development and forewing length of the different groups were conducted by a two-way ANOVA and an unpaired t-test.

Results

Hostplant Experiments

The 2 groups of larvae that were raised on different host plants developed at different rates (Table 2; Fig. 1). The larvae raised on *C. lanceolata* took significantly longer to reach maturity. In the second trial, where larvae feeding on *C. incana* were switched during their penultimate instar for 5 days to feeding on *C. lanceolata* and then were switched back to feeding on *C. incana*, the larvae pupated with a 5-7-day delay in comparison with the larvae on *C. incana* in the first trial. The larvae raised on *C. lanceolata* in trial 2, developed at about the same rate. There was a difference in the nitrogen content of the 2 host plants (*C. incana*: 3.4-3.6%, *C. lanceolata*: 2.8-2.9%).

In the first trial, the mean size (forewing length (FW)) of male adult moths that resulted from feeding on *C. incana* significantly exceeded that of male moths raised on *C. lanceolata* ($P < 0.03$), while the sizes of females raised on *C. incana* were not significantly different from females raised on *C. lanceolata* (Fig. 2). In the second trial, caterpillars raised on *C. incana*/*C. lanceolata*/*C. incana* also resulted in males which were significantly larger than those raised on *C. lanceolata* ($P < 0.03$). Similarly to Trial 1, the difference observed between females was not statistically significant ($P < 0.098$).

Temperature Experiments

During laboratory rearing at different temperatures, the last instars' and pupal developments were twice as fast at ≈ 72 °F (22.2 °C) than at ≈60 °F (15.6 °C) (Table 2). Low temperature in this study led to development of smaller adult moths, however this study had small sample size and the latter results need to be confirmed by additional replications. The sentinel larvae in the outdoor cages successfully developed into adult moths that emerged between 31 Dec and 7 Jan, developing at approximately the same rate as the laboratory population held at ≈ 60 °F (15.6 °C).

Male vs. Female Rate of Development

In all of our experiments, male larvae developed more slowly than their female counterparts. This statistically significant difference in development time varied from 1 to 5 days depending on the trial (e.g., $P < 0.05$—individually reared moths ≈72 °F (22.2 °C); $P < 0.04$—moths reared on *C. incana* in Trial 1). The difference was quite obvious because females were always the first to emerge. This corresponds to our observations in the wild, where females were observed to initially be the more numerous sex present when the fall generation appeared in late Sep.

Discussion

The observed difference between the rates of development on *C. incana* and *C. lanceolata* cannot be explained just by the slight differences that we found in the nitrogen content of the 2 host plants. Based on preliminary data produced by similar experiments, *C. pallida*, which had an even higher nitrogen content (3.8-4.2%), did not spur larval growth the way that *C. incana* did (Sourakov, unpublished). Because it has been shown that arctiid larvae do not directly absorb plant toxic alkaloids and utilize them for defense, but rather deactivate them first in the gut, which requires energy (Hartman 2008), it is possible that feeding on *C. incana* leads to faster larval development as a result of its lower toxicity. Analyses of seeds from many species of the genus (Williams & Molyneux 1987) indicate that *C. incana* has 3-times lower PA content (0.07%) than *C. lanceolata* (0.21%). This theory is supported by a recent laboratory study that showed that increased PAs in the artificial diet lead to slower larval development in *U. ornatrix* (Cogni et al. 2012). It would be interesting to assess if moths that developed on *C. incana* are more palatable to predators due to their lower alkaloid content. If such variation in adult moth toxicity (and consequently, in palatability) exists, it can be a potential source for automimicry (Bowers 2008) under which condition, the individuals within a population that develop on more toxic plants may serve as models for the ones that developed on less toxic plants. Testing the PA contents and palatability of the *U. ornatrix* adults raised on different *Crotalaria* species is the next logical step in determining if this is the case.

Unlike the larvae of many Lepidoptera, which stay on a single individual plant throughout their development, woolly bears (arctiid larvae) are known to travel between host plants, and *U. ornatrix* larvae are no exception. In the wild, a single larva may travel between host plants of different species, which is now not only possible, thanks to the introduction of many *Crotalaria* species to Florida habitats, but is also likely, because they

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TABLE 2. LABORATORY BIOLOGY OF *UTETHEISA ORNATRIX*: DEVELOPMENT TIME AND WING SIZE OF RESULTING MOTHS REARED ON DIFFERENT HOST PLANS AND UNDER DIFFERENT TEMPERATURES.

Experimental settings: host plants used to feed larvae and rearing conditions		Males			Females		
		Dev. Time (days): neonate to pupa	FW size (mm)	*n*	Dev. Time. (days): neonate to pupa	FW size (mm)	*n*
Trial 1	*Crotalaria incana*	24 ± 1.1	21.2 ± 0.7	15	22.9 ± 1.5	20.6 ± 0.8	16
	Crotalaria lanceolata	45 ± 2.6	20.4 ± 0.8	6	38.7 ± 2.8	20.3 ± 0.8	17
Trial 2	*C. incana*/*C. lanc.*/*C. inc.*	31.5 ± 1.7	22.1 ± 1.0	4	28.5 ± 1.7	21.6 ± 0.5	4
	C. lanceolata	44.3 ± 4.3	20.4 ± 0.9	7	41.2 ± 2.0	20.0 ± 1.6	5
		Dev. Time (days): last instar	FW size (mm)	n	Dev. Time (days): last instar	FW size (mm)	*n*
Trial 3	≈ 72 °F (22.2 °C)/solitary	12.0 ± 0.0	20.9 ± 0.2	3	11.0 ± 0.9	20.7 ± 0.5	9
	≈ 60 °F (15.6 °C)/solitary	24.8 ± 1.8	20.2 ± 0.5	5	23.0 ± 1.6	19.9 ± 0.6	6

Pupal development (Trial 3)		
Temperature	Time (days)	*n*
≈ 72 °F (22.2 °C)	13.6 ± 0.6	12
≈ 60 °F (15.6 °C)	30.8 ± 1.4	11

Results of Two-way ANOVA

	Experimental design	Forewing size	Development time	n
Trial 1	Host plant fed to larvae: *Crotalaria incana* vs. *C. lanceolata*	$P = 0.012$	$P < 0.0001$	54
	Sex of resulting moths: males vs. females	Not significant	$P < 0.0001$	
	interaction: host plant/sex	No	Yes, $P < 0.0001$	
Trial 2	Host plant fed to larvae: *C.incana*/*C.lanc*/*C. inc.*vs. *C. lanceolata*	$P = 0.006$	$P < 0.0001$	19
	Sex of resulting moths: males vs. females	Not significant	$P = 0.044$	
	interaction: host plant/sex	No	No	
Trial 3	Temp. of larval development 72 °F (22.2 °C) vs. 60 °F (15.6 °C)	$P = 0.0035$	$P < 0.0001$	23
	Sex of resulting moths: males vs. females	Not significant	$P = 0.025$	
	interaction: temperature/sex	No	No	

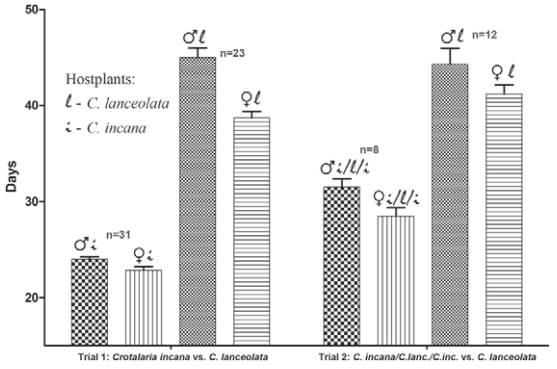


Fig. 1. Effect of host plant choice on the development time (mean ± SEM) from neonate larva to pupa in *Utetheisa ornatrix* in north-central Florida. Trial one was conducted with leaves of *Crotalaria lanceolata* vs. leaves of *C. incana*. Trial 2 was a replication of Trial 1, except that the *C. incana* group was switched to *C. lanceolata* for a period of 5 days during the penultimate instar.

may grow in close proximity, as in the case of our source population. Development was slower for larvae fed on *C. incana*/*C. lanceolata*/*C. incana* compared with that of larvae reared exclusively on *C. incana*. It may be that larvae that were first adapted to feeding on a host plant with lower toxicity may have a difficult time adapting to a more toxic host plant. Alternatively, feeding on a higher PA-level plant without growth could have been a sign of larvae trying to satisfy their PA requirements: in recent laboratory experiments (Hoina et al. 2012), *U. ornatrix* larvae first fed an artificial low-PA diet later preferred a high-PA diet when offered the choice, even though it led to prolonged development.

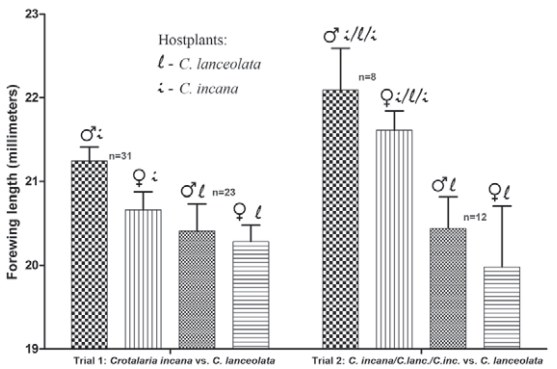


Fig. 2. Effect of the type of host plant fed to the larvae on the size (mean ± SEM) of the resulting *Utetheisa ornatrix* adults. Trial one was conducted with *Crotalaria lanceolata* vs. *C. incana*; Trial 2 was a replication of Trial 1, except that the *C. incana* group was switched to *C. lanceolata* for a period of 5 days during the penultimate instar.

Males that resulted from feeding on *C. incana* exceeded in size males raised on *C. lanceolata.* Being larger can indicate a higher PA load carried by a male (Conner et al. 1990). This can potentially give these males an advantage during sexual selection, as was shown by LaMunyon & Eisner (1993), and can give advantages to the offspring in the form of accelerated oviposition by the female they mate and by the larger eggs she lays (Iyengar & Eisner 2002). However, elaborate experiments, similar to those described by these authors, are required to test whether larger males developed on one host plant would be preferred over smaller males developed on another.

The various plants of the genus *Crotalaria*, appear to have different phenologies in north central Florida. As we observed in 2012, by Dec-Jan, *C. spectabilis* and *C. pallida* in some of the sites were greatly affected by the lightest freezing, *C. incana* showed yellowing and loss of leaves, while *C. lanceolata* and the native *C. pumila*, on the contrary, appeared to be present in all stages (from young sprouts, to flowering and seeding plants). As late as the end of January, we found on them eggs and larvae of *U. ornatrix*. It is possible to speculate, based on these observations and on our laboratory rearing described above, that the phenology and the evolution of *U. ornatrix* in southeastern U.S. have and will be affected by the introduction of so many diverse host plants.

It is noteworthy that male larvae developed more slowly than female larvae. In most other species of Lepidoptera, the reverse is normally the case, with males being both smaller than females and emerging earlier. In most butterfly populations, for example, males are usually on the wing for a few days before females emerge and actively compete for mating opportunities by patrolling the area or even visiting female pupae. It has been shown by other studies that during sexual selection in *U. ornatrix*, males have a lot to lose by mating to a "substandard" female, since they become less desirable by females after the first mating (Bezzerides et al 2005). Conner et al. (1980, 1981) described in detail the courtship in which females call the males, and it was shown that males transfer ca. 10% of their body weight together with the spermatophore to females, during mating (LaMunyon & Eisner 1993). These alkaloids and other nutrients that males lose during mating are collected by the feeding larvae and are, therefore, irreplaceable. Even though that the males must choose carefully to whom they transmit these "nuptial gifts" (González et al. 1999), it has been suggested that the benefits are accrued by females, as males mate on an opportunistic basis (Iyengar & Eisener 2004). Females of *U. ornatrix* are capable of mating multiple times to increase their fecundity (LaMunyon 1997; Iy-

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engar & Reeve 2010), and therefore have less at stake when choosing a mate and more at stake in doing so as early as possible and as many times as possible. Perhaps their faster development and early emergence is a mechanism for them to compete for males rather than not vice versa.

Conclusions

Utetheisa ornatrix is capable of developing on both *Crotalaria lanceolata* (a species distributed in the USA from Louisiana to North Carolina and south to Florida) and *C. incana* (found from Oklahoma to North Carolina to Florida) (USDA plant database) both of which have been introduced to the United States as exotic plants that are native to Africa.

The biology of *U. ornatrix* in the laboratory was markedly affected by the choice of the host plant. Larvae developed faster and resulted in larger adults (males only) when raised on *Crotalaria incana* rather than on *Crotalaria lanceolata*.

Constant temperatures of as low as ≈ 60 °F (15.6 °C) are not an obstacle to the successful development of these moths, even though it takes them twice as long to develop as they do at ≈ 72 °F (22.2 °C). The rate of laboratory development at ≈ 60 °F (15.6 °C) corresponds to that of these moths in the wild in north-central Florida during Oct-Jan.

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