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A HOSTPLANT-INDUCED LARVAL POLYPHENISM IN *HYALOPHORA EURYALUS* (SATURNIIDAE)

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ABSTRACT. A hostplant-induced larval polyphenism is described in *Hyalophora euryalus*. Larvae reared on madrone (*Arbutus menziesii*) and manzanita (*Arctostaphylos patula*) have greatly reduced or no lateral nor abdominal scoli; sibs reared on the conifer Douglas-fir (*Pseudotsuga menziesii*) possess fully expressed scoli. Other native hosts (*Ceanothus integerrimus* and *Prunus emarginata*) do not induce the polyphenism. The third instar appears to be the critical stage during which the polyphenism is determined. Size and fecundity of adults reared on madrone and Douglas-fir are comparable. The evolutionary basis of this polyphenism is discussed in terms of increased crypsis on the appropriate host. Madrone may be an ancestral host, a member of the Madro-Tertiary flora with which *H. euryalus* is closely associated. Douglas-fir may have been important during the re-invasion of northern and boreal regions following the Pleistocene. Mature larvae of the allied *Callosamia* also have a similar "nude" larval phenotype, suggesting a possible ancestral genetic potential to evolve the polyphenism.

Additional key words: caterpillar, crypsis, developmental plasticity, life cycle, phenotypic plasticity, polymorphism.

Although known as the "Ceanothus silk moth", *Hyalophora euryalus* (Boisduval) is polyphagous and occupies an unusual range of West Coast plant communities including the deserts of Baja California, Coast Range and Sierran chaparral, Central Valley riparian habitat, Great Basin scrub, and conifer forests in the Sierra Nevada and the Cascades (Tuskes et al. 1996). In the central Sierra Nevada the larvae feed on at least eight genera of shrubs and trees, representing six plant families, including the conifer Douglas-fir (*Pseudotsuga menziesii* Mirb. [Franco]). By dispersing their populations over a range of plant communities, hostplant generalists may benefit from reduced search time for ovipositing females, and partially escape from predators and parasitoids associated with specific plant species or plant communities (Janzen 1984a). Nevertheless, a large, palatable larva like *H. euryalus* must also depend on crypsis to survive. Its larval phenotype inevitably represents a compromise in camouflage value among such a wide variety of foliage shapes, colors, and lighting regimes. The host-induced larval polyphenism reported here appears to represent an evolutionary response to this dilemma.

The larvae of *H. euryalus* differ from congeners in the last two instars in the tendency of scoli to be smaller relative to total larval size, and in being armed with fewer and smaller spines on their scoli (Fig. 1) (Collins 1997, Tuskes et al. 1996). This trend reaches its extreme expression in a "nude" fifth instar larval phenotype in which all but the two pairs of dorsal thoracic scoli, the first dorsal abdominal pair, and the caudal scolus are very reduced or absent. I have observed this phenotype in approximately a third of wild collected larvae in the central Sierra Nevada, and have recorded it in populations from as far north as Victoria, British Columbia and as far south as Baja California. No other *Hyalophora* taxon expresses this reduction in scoli.

The environmental control of scoli expression was discovered fortuitously when I divided a batch of *H. euryalus* ova laid by a single female into two lots, one of which I reared on *Arbutus menziesii* Pursh (madrone; Ericaceae) and the other on *Pseudotsuga menziesii* (Douglas-fir; Pinaceae). Both are common hosts for *H. euryalus* throughout the Sierra Nevada and Cascade Range. All larvae on madrone developed into the nude morph (Fig. 2), while their sibs on Douglas-fir all expressed fully developed scoli (Fig. 3). In this paper I report the results of a controlled breeding program to verify these findings and to further investigate the genetic basis for this host-induced polyphenism. In the discussion I offer the interpretation that the nude larval morph is especially cryptic on madrone and the full expression of scoli is cryptic on Douglas-fir.

MATERIALS AND METHODS

Stock of *Hyalophora euryalus* from northern California was derived from a female collected as a cocoon near Donner Lake, Placer Co., and mated to a wild male from Nevada Co. Subsequent generations were produced by mating reared females to wild Nevada Co. males. One other brood resulted from mating a reared female from Victoria, British Columbia, Canada, stock to a wild male from Nevada Co., California. Ova were obtained by confining females in paper bags and cutting out sections with clusters of ova attached. Ova were incubated during May in a screened-in insectary at 1000 meters in Nevada Co., California. Newly eclosed larvae were confined with twigs of hostplant in 15 cm × 4 cm plastic petri dishes. After 2 to 3 days larvae were transferred to nylon mesh sleeves placed on *Arbutus menziesii*, *Pseudotsuga menziesii*, and other indigenous hosts. Larval growth

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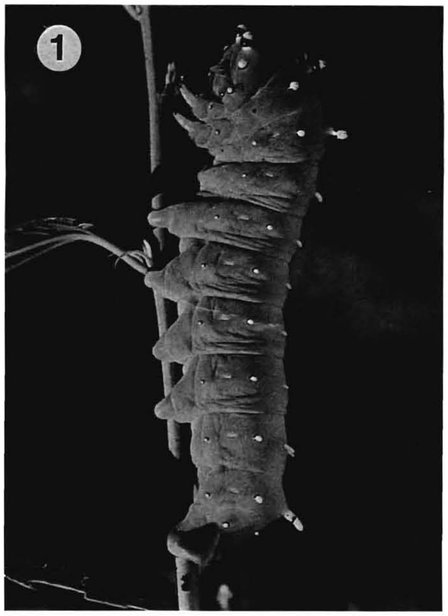

FIG. 1. *Hyalophora euryalus* fifth instar reared on *Ceanothus integerrimus*; most common phenotype in mid-latitude California Sierra Nevada, with reduced, but entire, scoli. FIG. 2. Fifth instar *H. euryalus* of the "nude" phenotype reared on *Arbutus menziesii* (madrone). Dorsal and lateral abdominal scoli reduced to near absence. FIG. 3. Fifth instar *H. euryalus* reared on *Pseudotsuga menziesii* (Douglas-fir) with fully developed scoli, induced by feeding on this host. FIG. 4. Fifth instar *H. euryalus* reared on *Arctostaphylos patula* (manzanita), which induces the "nude" phenotype. Siblings of larva in Fig. 3.

and phenotypes expressed were monitored periodically under these natural conditions. Fifth instar larval phenotypes were scored as a presence or absence of abdominal scoli. For larvae reared on *Arbutus* or *Arctostaphylos* (manzanita) compared to *Pseudotsuga* this was virtually a qualitative trait, although some larvae expressed much reduced button-like scoli. Larval morph scores were analyzed using a Chi-square test, assuming a null hypothesis that a simple polymorphism existed based on a single major genetic locus, independent of hostplant.

The possible effect of the maternal hostplant was tested by mating a female reared on *Pseudotsuga* and another on *Arbutus* each to wild males, and rearing larvae from both matings as split broods on both hosts as before.

TABLE 1. Effect of hostplant on expression of fifth instar larval scoli in *Hyalophora euryalus*.

Brood	*Pseudotsuga*		*Arbutus*	
♀×♂	scoli	nude	scoli	nude
Victoria, B.C. × Nevada Co., Calif. 1994	26	0	0	25
Donner L., Placer Co. × Nevada Co., Calif. 1996	23	0	1	22
Sib above × Nevada Co. 1997a	7	0	0	2
As above 1997b	9	0	0	13
Total:	65	0	1	63

Chi^2 for pooled data = 128.0 .0005 >> p.

To assess the possible effect of hostplant species on reproductive fitness, fecundity of females was recorded for *Pseudotsuga* vs. *Arbutus* and compared to published data for other hosts. Since saturniid females eclose with a full complement of mature ova and oviposit virtually all their ova, the total number of eggs laid yields a direct index of fecundity when divided by forewing length to standardize for variation in adult size (Collins 1997). Unmated females were dissected to determine fecundity.

In an attempt to determine the critical instar in which induction of larval morph occurs, I initially switched one batch of 20 third instar larvae from *Arbutus* to *Pseudotsuga*. All larvae died within a few days of transfer, apparently from either refusing to feed on or an inability to metabolize this new host. This test was repeated in 1998 with lots of ten sibling larvae each reared in cages on either *Pseudotsuga* or *Arbutus*, then switched to the other hostplant of the pair during the third instar. A control lot was reared continuously on the common foothill host, *Ceanothus integerrimus*. In addition, a fourth lot was reared on *Ceanothus* until the third instar, and then switched to *Pseudotsuga*. Individuals from a different brood were reared on *Pruaus emarginata* (Rosaceae).

TABLE 2. Effect of maternal parental hostplant on induction of larval morph in *Hyalophora euryalus*. Siblings of 1997 broods in Table 1.

	Female parental host			
	Pseudotsuga		*Arbutus*	
Host	scoli	nude	scoli	nude
Arbutus	0	13	0	2
Arctostaphylos	0	14	0	9
Pseudotsuga	7	0	9	0

TABLE 3. Phenotype and survival of *Hyalophora euryalus* sibling larvae switched to new host as third instars.

			Fifth instar phenotype		
Host switch	No. switched as 3rd instar	Number survived	full scoli	intermediate*	nude
1998a: ♀ progeny of 1997a × wild Nevada Co. ♂					
Arbutus - *Pseudotsuga*	4	4	4	0	0
Ceanothus - *Pseudotsuga*	5	4	2	1	1
Pseudotsuga - *Arbutus*	8	3	0	1	2
Ceanothus integerrimus (Control, not switched)	7	7	3	0	4
1998b: ♀ progeny 1997a × sib. Sleeved as ova on live hostplant, not switched.					
Prunus emarginata			2	9	13
Arctostaphylos patula			0	0	13
Pseudotsuga menzeisii			6	0	0

* Larvae with the intermediate phenotype possessed entire but reduced lateral scoli, and no or only remnant dorsal abdominal scoli.

RESULTS

Larval phenotypes for broods reared on *Pseudotsuga* vs. *Arbutus* are shown in Table 1. A nearly complete dichotomy in phenotypes for both broods was seen in relation to hostplant, disproving the null hypothesis that the expression of scoli reduction is due to a simple genetic polymorphism independent of hostplant.

During the first two rearing seasons, survival on both hostplants was nearly 100%. In 1997 larvae in some sleeves suffered heavy parasitism by the braconid *Cotesia*. Although exact data were not collected, I observed that larval growth rates on *Arbutus* were consistently faster in all broods than those for larvae reared on *Pseudotsuga*. Notes on approximate average time to cocoon spinning show that larvae on madrone matured about one week to 10 days faster than on Douglas-fir.

No effect of maternal hostplant on larval phenotype was seen (Table 2), as larval morphs showed the expected dichotomy regardless of the hostplant of the female parent. In addition, larvae reared on *Arctostaphylos* completely expressed the nude phenotype in the last instar (Table 2, Fig. 4). Observation of larvae showed that the reduction of scoli was nearly as pronounced in the fourth instar on *Arbutus* and *Arctostaphylos*, although the majority possessed scoli as small knobs, especially the lateral rows. In all broods, third instars possessed fully developed scoli. However, of six third instar larvae reared in 1997 on *Pseudotsuga*, three had all scoli heavily pigmented with black,

TABLE 4. Effect of hostplant on fecundity. Index = no. ova/forewing length.

No. ova	Forewing length	Index
	Arbutus	
California: Placer Co. × Nevada Co.		
228	55	4.15
130	57	2.28
151	57	2.65
Canada, Victoria B.C. × California, Nevada Co.		
143	57	2.51
Avg.		
163.0	56.5	2.90
	Pseudotsuga	
California: Placer Co. × Nevada Co.		
247	60	4.12
192	62	3.10
154	55	2.80
Canada, Victoria B.C. × California, Nevada Co.		
178	57	3.12
209	59	3.54
Avg.		
196.0	58.6	3.34
	Prunus emarginata	
California, Nevada Co.; avg. 12 pairings (Collins 1997)		
175	58.3	2.99
	Ceanothus integerrimus	
California, Nevada Co.		
179	57	3.14

as is seen in *Hyalophora columbia columbia* and *Hyalophora columbia gloveri*, while the remaining three possessed yellow dorsal and light blue lateral scoli as is typical of *H. euryalus* (Tuskes et al. 1996). Of 15 third instars examined in madrone broods, none possessed black scoli, nor were such dark forms seen among madrone broods in previous seasons, although careful notes were not made previously on third instar coloration. In 1998 among third instar larvae on *Pseudotsuga* two possessed black lateral scoli with yellow dorsal scoli, three had blue tipped with black lateral scoli and yellow dorsal scoli, none were all black, and two had the normal blue lateral and yellow dorsal scoli coloration. All ten third instar larvae on madrone possessed the yellow and blue pattern.

The effects of host-switching on survival and larval phenotype are shown in Table 3. Initial losses from the lots of 10 neonates were highest in the lot begun on *Arbutus*, due apparently to wandering off the hostplant. Only 2 larvae were lost before the third instar for those begun on *Pseudotsuga*. None of the controls on *Ceanothus* was lost. After host switching, the lot switched from *Pseudotsuga* to *Arbutus* suffered the greatest loss with only 3 of 8 surviving. Larvae switched from *Arbutus* to *Pseudotsuga* expressed fully developed scoli. However, larvae switched from *Ceanothus* to *Pseudotsuga* showed different phenotypes: one larva was intermediate with small but distinct lateral scoli and very reduced or absent dorsal scoli; two other fifth instar larvae had large scoli and one was of the nude phenotype. Of the larvae switched from *Pseudotsuga* to *Arbutus* two expressed the nude phenotype but one other was intermediate. Control larvae reared continuously on *Ceanothus* displayed both morphs; some had fully developed scoli, while others had the nude morph.

The brood reared on *Prunus emarginata* (Table 3) also expressed all three larval morphs in the final instar, while siblings reared on *Arctostaphylos* and *Pseudotsuga* expressed the expected nude vs. scoli phenotypes. These results suggest that *Prunus emarginata* and *Ceanothus integerrimus* are neutral with respect to the host-induced polyphenism.

The host switching experiments suggest that the third instar is the stage that is responsive to host cues, thus controlling final instar phenotype, because exposure during the first two instars can be counteracted by subsequent exposure to other hostplant taxa. Although I did not attempt to subject fourth instars to host switching, casual observations showed that the fourth instar phenotype was usually an accurate predictor of final instar phenotype. Fourth instars with very reduced scoli often produced nude fifth instars. However, two fourth instars reared on *Prunus* and possessing fully developed scoli changed to the nude phenotype in the fifth instar.

Sibling females reared on *Pseudotsuga* or *Arbutus* did not differ in fecundity (Table 4). Average number of ova laid, forewing length, and fecundity index were larger for those reared on *Pseudotsuga*, although the sample size was too small to justify calculating statistical significance. Collins (1997) reported an average and SD for these parameters, respectively, of 175.5 ± 36.8, 58.3 ± 4.6, 2.99 ± 0.48 for a sample of 12 *H. euryalus* reared on *Prunus emarginata*.

DISCUSSION

In discussing the evolutionary significance of larval phenotypic plasticity in *H. euryalus*, it is important to distinguish between the terms polymorphism and polyphenism. In a polymorphism, genetic differences among individuals produce discrete phenotypes. A polymorphism is a population phenomenon; the frequency of alternate morphs in the population reflects the frequency of those genes controlling the expression of each morph, and the phenotype of a given individual is dependent on its genotype. A polyphenism is the expression of a specific phenotype in response to environmental cues, which regulate gene action through a neural-molecular pathway. ("Phenotypic plasticity" is also a widely used term (Stearns 1989), although Williams (1992) objects to its non-genetic connotation). Every individual in a polyphenic population theoretically could be genetically identical for the loci in question, and phenotypic variation within the population then would be a consequence of individual exposure to variable environmental cues. In a seasonal polyphenism, immatures in the population respond to a reliable seasonal cue, such as photoperiod, to produce "spring" and "summer" adult phenotypes in pierids (Shapiro 1989) or in the saturniid genus *Actias* (Miyata 1974, 1986); or the "wet" and "dry" seasonal forms of the neotropical saturniid *Rothschildia lebeau* (Janzen 1984b), and in the African butterfly *Bicyclus* (Windig et al. 1994).

Fewer cases of larval polyphenism in Lepidoptera have been carefully documented. Greene (1989) showed that strikingly different cryptic phenotypes are produced in the geometrid *Nemoris* when larvae feed on oak flower buds in the spring versus leaves during the summer rainy season in southeast Arizona. Fink (1995) demonstrated that hostplant partly controls a color polyphenism in *Eumorpha* (Sphingidae) larvae, but was unable to do controlled breeding experiments due to the difficulty of pairing these moths in the lab. The number and spacing of the large, silvery, lancet-shaped scoli of certain Southwestern *Sphingicampa* (Saturniidae) appear to be influenced by hostplant leaflet size and number (Tuskes et al. 1996; P. Tuskes, pers. comm.). Plant secondary compounds may act as cues in controlling these polyphenisms, although a pupal color polyphenism in certain *Papilio* is controlled by light level and other environmental cues (West 1995, Sims & Shapiro 1983).

My interpretation of the nude larval morph in *H. euryalus* is that this phenotype is more cryptic on madrone than the morph with fully developed scoli. The leaves of madrone are large, typically 10–14 cm in length, with entire margins, and light grey-green below. Especially when viewed from below, even the mature larva of *H. euryalus* is inconspicuous in the nude morph as it rests or feeds underneath the large, similarly colored madrone leaf. The same argument can be applied to the association with *Arctostaphylos*; the leaves of most species are also glaucus with smooth, entire margins, but smaller than the foliage of *Arbutus*. By contrast, the larval morph with fully developed scoli appears more cryptic against the foliage of Douglas-fir because the numerous scoli break up the solid mass and match the visual effect of spots of light shining through a matrix of small needles. In both cases, the cryptic appearance is lost when each morph is viewed against the foliage of the "inappropriate" hostplant. The trend in early instars of darkening of scoli seen in broods reared on Douglas-fir would seem to camouflage these larvae against the dark twigs and foliage of Douglas-fir. The early instars of the *Larix* feeder, *H. c. columbia*, are always black.

The larvae of the related *Callosamia* also have very reduced scoli in later instars (Tuskes et al. 1996). This condition is most pronounced in the Magnoliaceae specialists, *C. angulifera* and *C. securifera*, whose larvae are very cryptic hidden under the large leaves of their hostplants.

The foliage of *Pseudotsuga*, in common with other conifers, is rich in terpenes and so presents a metabolic barrier against some insect herbivores (Smith 1989, Gershenzon & Croteau 1991, Harborne 1997). In a study of Lepidoptera diversity associated with *Abies* and *Pseudotsuga*, Powell and De Benedictis (1995) list 40 species, of which 73% are conifer specialists. Conifer feeding is not common within the three North American saturniid subfamilies. The few known examples, with the exception of *Hyalophora euryalus*, are generally feeders on *Pinus* spp., whose congeners feed on leafy shrubs and trees (Lemaire 1988, Tuskes et al. 1996, Wolfe 1993). *Hyalophora euryalus* is exceptional because it is primarily a generalist on shrubs and trees, and also because it was the only species found on Douglas-fir that preferred older needles (Powell & De Benedictis 1995). My work confirms this preference. First year conifer needles have been shown to contain up to ten times the diterpene acids of older needles (Ohigashi et al. 1981), so feeding on older needles may be due to an avoidance of high levels of these diterpene acids.

Adaptation to a new host involves many complex fitness tradeoffs affecting the evolution of life history traits (Fox & Morrow 1981; Krainacker et al. 1987; Fox & Caldwell 1994; Leclaire & Brandl 1994). Although it is difficult to measure the metabolic and other "costs" of conifer feeding in *H. euryalus*, larvae on *Pseudotsuga* consistently matured more slowly than sibs reared on *Arbutus* and one larval brood begun on *Arbutus* could not switch to *Pseudotsuga* in the third instar. It is not known if this result was due to a refusal to initiate feeding, or perhaps due to the failure of induction of the synthesis of a critical enzyme (cf

Brattsten et al. 1977, Brattsten 1983; Moldenke et al. 1983). No reduction in adult size nor female fecundity was found in broods reared on *Pseudotsuga*.

The foliage of *Arbutus menziesii* may also contain secondary compounds exacting a metabolic cost from insect herbivores. Ezcurra et al. (1987) list cardiac glycosides, quinones, and tannins among others in leaves of the Mexican madrone species, *Arbutus xalapensis*. Larvae of *H. euryalus* switched from Douglas-fir to madrone were reluctant to accept madrone (Table 3).

Larvae feeding in the Douglas-fir canopy may partially escape those predators and parasites normally associated with the smaller trees and shrubs that serve as *Hyalophora* hosts. The majority of the Lepidoptera fauna feeding on Douglas-fir are microlepidoptera (Powell & De Benedictis 1995), which could attract a different set of predators and parasites than those attacking *Hyalophora*.

Danks (1994) asserts that genetic polymorphisms tend to evolve in predictable environments, while polyphenisms are associated with unpredictable environments. An example of a polymorphism in a predictable environment would be the various color forms of *Saturnia mendocino* larvae, which match the living green foliage and persistent yellow and mauve dead leaves all reliably present on manzanita (Tuskes et al. 1996). The array of hosts utilized by populations of *H. euryalus* represent an unpredictable environment. One can theorize that if a *H. euryalus* population were genetically polymorphic for larval scoli size, females ovipositing on both madrone and Douglas-fir would produce many larvae of the inappropriate phenotype, stranded on large trees against a non-cryptic background.

Collins (1997) proposes that conifer feeding in *Hyalophora* arose as an adaptation to post-Pleistocene environments, in which pioneer populations of *H. euryalus* fed on *Pseudotsuga* as they reinvaded northern and montane portions of the moth's current range, and *H. columbia columbia* similarly adapted to *Larix* (tamarack) as it spread north and east where it currently occurs in tamarack bogs. Even coastal populations of *H. euryalus* in southern California may accept and mature on *Pseudotsuga*, but the Rocky Mountain subspecies *H. c. gloveri* lacks this adaptation (Tuskes et al. 1996). Madrone and manzanita are members of the Madro-Tertiary flora, and probably represent ancestral *Hyalophora* hosts, based on comparative biogeographical evidence and the close association of *H. euryalus* with modern derivatives of this ancient flora (Collins 1997).

Fully developed fifth instar scoli appears to be the primitive condition in the Saturniidae (Ferguson 1971, Minet 1994), and fifth instar scoli are prominently expressed in all *Hyalophora* taxa except *H. euryalus*. The neutral condition in *H. euryalus* is one of variable but reduced scoli in later instars. The evolution of the larval polyphenism in *H. euryalus* may best be described as the host-induced shift in this neutral developmental state toward either suppression of scoli when larvae feed on certain Ericaceae, or a shift in the opposite direction toward full scoli expression in larvae feeding on *Pseudotsuga*. Certain other hosts, such as *Ceanothus integerrimus* and *Prunus emarginata*, appear neutral in inducing the scoli polyphenism and a range of developmental variation in scoli expression occurs among siblings reared on these hosts. It is difficult to determine to what extent this represents genetic variation in loci controlling scoli development, given the environmental influence seen in this study, but I have observed larvae with fully developed scoli on *Arctostaphylos* (fig. 1d in Collins 1997).

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