Larval Coloration in Lophocampa maculata Harris 1841: Instar-Specific Partial Depigmentation in Captive and Wild Populations

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LARVAL COLORATION IN *LOPHOCAMPA MACULATA* HARRIS 1841: INSTAR-SPECIFIC PARTIAL DEPIGMENTATION IN CAPTIVE AND WILD POPULATIONS

Additional Key Words: melanin

The Spotted Tussock Moth, *Lophocampa maculata* Harris 1841, (Erebidae, Arctiinae (Lafontaine & Schmidt 2010)), is found across North America on both sides of the US/Canadian border, along the Pacific coast, and in both the Appalachian and Western mountains of the US (Powell & Opler 2009). Eastern and western larvae show differences in coloration, which are most noticeable in the final, 5th instar. The Eastern form, found from Newfoundland to the Southern Appalachians and west to Saskatchewan, as a 5th instar (Fig. 1l), is characterized by black setae at both ends and a yellow central region with black dorsal spots. In addition, there are longer white setae at both ends. The Western form, found from the Rocky Mountains to the Pacific coast, is similar in the 5th instar, except that the central region is orange and there are no dorsal spots (Fig. 1d). California coastal populations show additional color variation, which is under investigation. This note describes a previously unreported instar-specific, partial loss of pigmentation discovered during a larger study of the natural history of this species.

In the course of captive rearing to investigate the larval development of the species, I observed an unusual partial loss of pigmentation in two individuals from two widely separated locations. Eggs were obtained from each of two gravid females having normal coloration, collected at two California locations: the San Bernardino Mountains and the Sierra Nevada Mountains, near Bishop, California. The two locations are approximately 380 km apart and separated by about 100 km of the Mojave Desert, which is unlikely to provide suitable habitat for this species. They are, thus, likely to be genetically isolated. The San Bernardino (SB) and Bishop (B) groups, were reared under identical conditions of temperature, daylight and humidity. They were both fed vine maple, *Acer circinatum* Pursh. The SB group consisted of 62 siblings at the 4th instar stage, when the depigmented individual was found. The B group consisted of 41 siblings at the 3rd instar stage, when the second depigmented individual was found. At the time of discovery, each depigmented individual was removed from the group and reared separately, but under conditions identical to the rest of the population. Except for coloration, these two individuals appeared no different from the rest of their respective siblings. They fed and developed normally. Further observations of these two individuals are presented below.

San Bernardino Individual

All members of the SB group appeared normal until the 3rd to 4th instar molt. Figure 1a-d shows typical 2nd to 5th instar individuals of the Western form. These photos show the "normal" appearance of both the SB and B groups. Figure 1e shows the depigmented individual as a 4th instar. All of the setae are white except for a series of dorsal tufts, of which the most posterior two are black and the remaining six are red-orange. In addition, the head is brown in contrast to the normal black color. The appearance of this individual remained constant through the 4th instar. On molting to the 5th instar, however (Fig. 1f), it reverted to the normal 5th instar appearance (compare Fig. 1d and f). This individual continued to thrive and eventually formed a cocoon.

Bishop Individual

All individuals in the B group developed normally until the 2nd to 3rd instar molt. One individual emerged as a 3rd instar with coloration similar to the 4th instar of the SB individual (Fig. 1g). The setae were all white except for some of the dorsal tufts, which showed the same coloration as the SB individual. In addition, its head was the same brown color as the SB specimen. This individual developed normally and molted to a 4th instar with no change in coloration (Fig. 1h). The 4th instar continued normal development and molted to give a typical 5th instar (Fig. 1i). This individual also eventually formed a cocoon.

Wild Populations

Subsequent to the discovery of these individuals in the two California populations, I conducted a search to see if other photographic documentation of this phenomenon existed. Three cases were discovered: two from Vancouver Island, BC, Canada, which arose within the Western larval phenotype, and another from Bailey's Harbor, WI, which arose in the Eastern phenotype.

The Vancouver Island photos (Fig. 1j,k) show two likely 4th instar individuals. The pattern of coloration, white setae except for the dorsal spots and brown head, match that of the California specimens. The number of dorsal spots and the distribution between two black

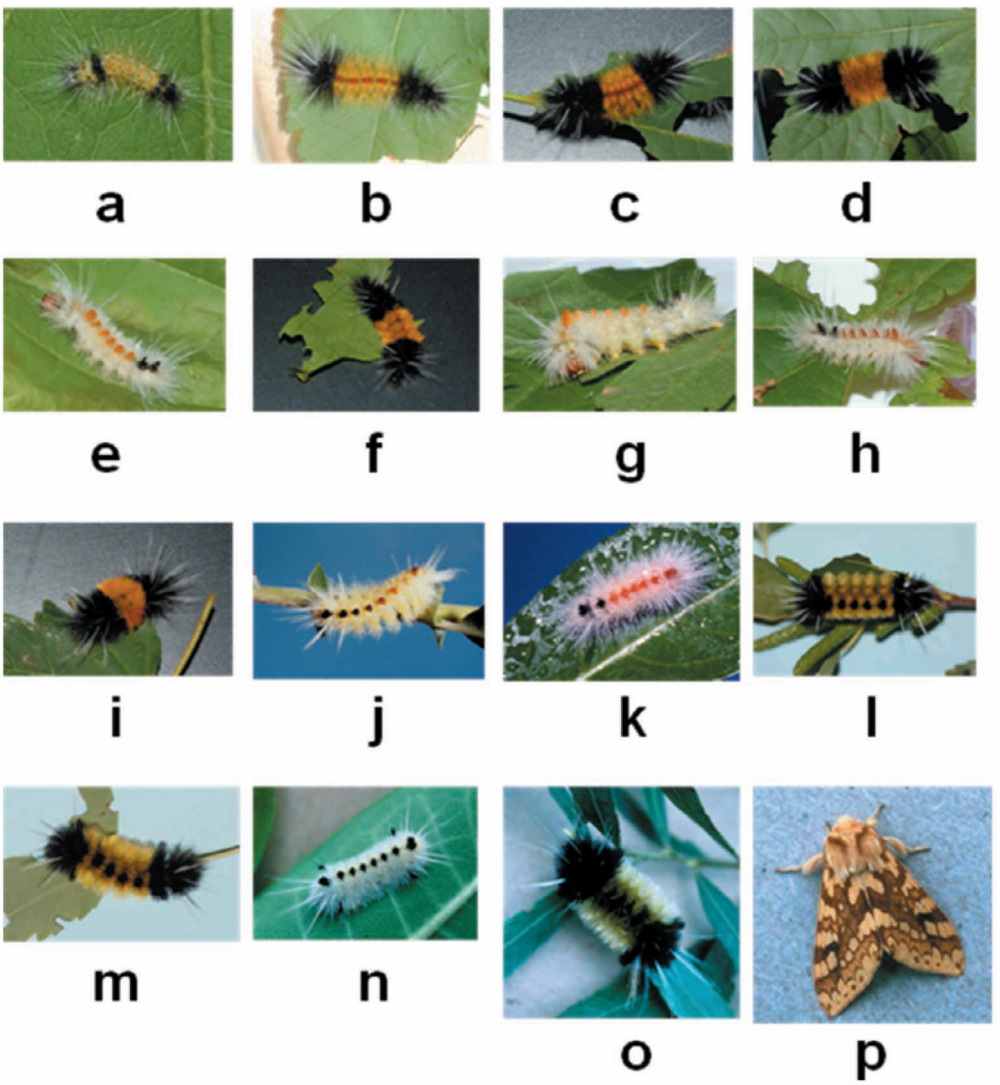

FIG. 1. Normal and instar-specific, partially depigmented individuals of Lophocampa maculata from both captive and wild populations. **a-d**, normal 2nd to 5th instar larvae of the western form of L. maculata (San Bernardino Mtns., CA) raised in captivity; **e**, 4th instar larva from the same female parent as a-d, showing partial depigmentation; **f**, same individual as e, as a 5th instar larva; **g-i**, 3rd, 4th, and 5th instar larva of a single individual from Bishop, CA, raised in captivity, showing depigmentation in the 3rd and 4th instars and reversion to normal phenotype in the 5th instar; **j-k**, two 4th instar individuals found in the wild (Vancouver Island, BC) showing depigmentation similar to that seen in the captive CA populations (j-k courtesy Jeremy B. Tatum); **l-m**, normal pigmentation in typical 4th and 5th instar larvae of the eastern form of *L. maculata* (Prince Edward Island, Canada) raised in captivity; **n-o**, 4th and 5th instar larva of an individual found in the wild (Bailey's Harbor, WI); **p**, adult of the individual shown in o after emergence the following year (n-p courtesy Janice Stiefel).

posterior and four orange anterior spots in Figure 1k match also. In Figure 1j, there appears to be a transition zone between the two black posterior spots and the orange anterior ones where several tufts are a mixture of black and orange setae. Because these individuals were not collected, there is no record of reversion to normal appearance in the 5th instar.

The larval phenotype in Wisconsin is the yellow variety. Figure 1l,m shows the normal 4th and 5th instar Eastern larval appearance, as documented in a captive reared population from Prince Edward Island, Canada. Both 4th and 5th instars have a yellow central area with a series of black dorsal spots, which distinguish them from the Western phenotype. The black regions at both

ends of the body and long white setae are similar to the Western phenotype. Figures 1n–p document the appearance of a single individual from Wisconsin. It was discovered in the wild as a 4th instar (Fig. 1n), showing a depigmentation pattern similar to that of the Western phenotype: white setae over the entire body except for black dorsal spots and, uniquely, a pair of lateral black tufts at both ends of the body. The lateral black tufts do not appear in the Western individuals. This individual was collected and observed to molt into a normal appearing Eastern 5th instar larva (Fig. 1o). The 5th instar larva eventually formed a cocoon and eclosed the following spring. The male adult (Fig. 1p) has the normal coloration of *L. maculata*. This is the only depigmented larval individual for which the adult form has been observed. The reversion to normal coloration in the 5th instar larva leads to a normally pigmented adult.

Comparison of Individuals

Comparison of the depigmented individuals documented here reveals a number of similarities. In both the Western and Eastern depigmented forms, the body is covered with white setae except for the dorsal spots. These spots appear to have the normal pigmentation for the specific instar stage of the individual. The coloration of the dorsal spots appears to follow the normal Western or Eastern phenotype. The lone Eastern individual also has single black tufts laterally at both ends of the body. In all documented cases, the depigmentation was observed in the 3rd or 4th instars with reversion to normal pigmentation in the final, 5th, instar.

Normal individuals of both Western and Eastern phenotypes of *Lophocampa maculata* show an instar-specific pattern of pigmentation. This is shown for the Western phenotype in Figure 1 a-d. The chemical nature of the pigments in this species, and the regulatory mechanisms responsible for the normal patterns of coloration, are unknown, but all of the observed colors could result from various types of melanin (see Wittkopp & Beldade 2009 for a recent review). In the depigmented individuals, the dorsal spots are pigmented in the normal black or red-orange colors, indicating the biochemical pathways necessary for pigment production are intact in these individuals. Regulation of the dorsal spot pigmentation appears to be controlled independently of that of the rest of the body, since they retain normal pigmentation. Thus, some disruption of the regulation of pigment production in particular regions of the body must have occurred. The depigmented areas are normally black and either orange in the western form or yellow in the Eastern form. Therefore, the loss of pigmentation affects more than one pigment production pathway. This suggests a complex situation where different regulatory elements control pigmentation over different regions of the body. The absence of pigment production is likely to result from disruption of a regulatory element that acts as an on/off switch rather than loss of an enzyme in one of the biochemical pathways producing a specific pigment since all affected individuals have some pigmented setae. Thus, each individual transitions from normal pigmentation to the depigmented form for one or two instars and then reverts back to normal pigmentation in the 5th instar. The single case where the resulting adult was documented demonstrates that adult pigmentation is not affected by larval loss of pigmentation.

Larval pigmentation in Lepidoptera is known to be affected by environmental conditions. There are many reports in the literature of changes in larval coloration in response to temperature (Solensky & Larkin 2003; Suzuki & Nijhout 2006), diet (Green 1989; Akino et al. 2004), population density (Fescemyer & Hammond 1986; Lee & Wilson 2006), and color of perceived light (Green 1996) among others. All of these effects were observed throughout the larval period. The present observation differs in two significant ways from these previously reported environmental effects. First, although environmental conditions were identical for each group of siblings from California being raised in captivity, only a single individual in each group exhibited the depigmentation effect. Second, the depigmentation affected only one or, in one case, two of the instar stages, and all individuals reverted to normal pigmentation in the final instar. In addition, the discovery of similar depigmented individuals in wild populations argues against the effect being some consequence of captive rearing. I have been unable to find any mention in the literature of an instar-specific loss of pigmentation.

Some arctiine genera show variations in pigmentation that are believed to be genetic in origin. These include polymorphisms among individuals (Wagner 2009) and, in the case of some species of Acronictinae, within-individual color changes both between instars and within a single instar (Wagner 2005). *Lophocampa maculata* exhibits both inter-instar color changes as well as geographic pigmentation polymorphism.

The depigmentation reported here appears to be genetic in origin. It could result from a particular allele, or combination of alleles of one or more genes. These alleles, although occurring in low frequency, may nevertheless persist in populations over wide geographic areas for long periods of time. This would explain the similarity of the depigmented larvae from

widely separated regions. An alternative explanation is that the depigmented individuals resulted from a spontaneous mutation that affected an instar-specific regulator of pigmentation. However, this would require an unusually mutation-prone site to account for the number of individuals observed.

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