LARVAL MORPH VARIATION IN *CHLOSYNE LACINIA* (NYMPHALIDAE)

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Mature larvae of the patch butterfly, *Chlosyne lacinia* (Geyer), exhibit striking color polymorphism. First described by T. D. A. Cockerell in Edwards (1893) and illustrated by Neck et al. (1971), the three morphs are as follows: rufa, an all orange or orange-red form; nigra, an all black form; and bicolor, a form basically black as in nigra but with a prominent mid-dorsal row of orange to orange-red blotches whose proximity to each other gives the impression of a stripe. The black pigment is present in the cuticle while the orange pigment is in a deeper layer (hypodermis) that shows through window-like areas of the cuticle devoid of pigment.

Laboratory crosses utilizing adults of known larval phenotypes revealed that the larval color polymorphism involves two unlinked autosomal loci (Neck et al., 1971). At one locus bicolor (B) is dominant to nigra (b). At the second locus rufa (R) is dominant to non-rufa (r). The rufa allele is epistatic to the first locus; no phenotypic expression of the first locus occurs when the rufa allele is present at the second locus.

Although there are only three major morphs in this species, a variety of subtypes exists which indicate the influence of genetic modifiers and/or environmental factors. The most common variant is a nigra form with circular light yellow-orange spots of varying intensity at the base of each mid-dorsal spine. This phenotype, named dot, is pictured in Plate 1D of Neck et al. (1971). It may be the same form reported by Cockerell (in Edwards, 1893) and Gorodenski (1969) although the description by Cockerell ("with numerous yellow-white spots") could possibly refer to the super-dot form described below.

Nearly all nigra have a small spot at the base of each mid-dorsal spine. (42 of 50 or 84.0% nigra larvae collected 10 September 1972 at Austin were definitely dot; others had very small dot.) In some individuals it is inconspicuous enough to be unnoticed unless critically examined under a dissecting microscope. In other individuals the dot is so large as to create confusion with the bicolor morph. In most cases the dot of the nigra tends towards yellow whereas the block of the stripe in bicolor is more orange. In addition, a black mid-dorsal line present in those larvae is seen in the bicolor larvae only between the orange spots and

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TABLE 1. Parental larval phenotypes: black × black.

	Phenotypes of Progeny		
brood number	black	dot	total
129	84	86	170
272	194	8	202
273	120	11	131
277	92	27	119
301	50	21	71

never in them. In dot nigra this line is seen between and entering the dot, continuing almost to the base of the spine.

Super-dot is also a variant of nigra with a yellow-orange spot at the base of each mid-dorsal, medio-dorsal, supra-spiracular and infra-spiracular spine. Super-dot also has a spot at the base of paired spines just above each proleg, a spot also present in bicolor and nigra. The more heavily yellowish-pigmented dot larvae also have yellow spots at the base of supra-spiracular spines, but they lack yellow at the base of medio-dorsal spines. A relationship between the dot and super-dot varieties may exist. One larva, collected as fourth instar was an extreme form of dot, i.e., very large spots at the bases of the mid-dorsal spines (but not others). This larva subsequently molted into a fifth instar super-dot form. Although dot larvae would thus appear to have a tendency to produce an abundance of yellowish spots, many dot phenotypes occur in fifth instar larvae.

Variation exists in the amount of melanin present in the cuticle. Nigra exhibits definite black and gray forms although intermediates occur that are difficult to place in either category. Dot larvae may be either gray or black, but all super-dot forms observed have been gray. The more evident dot larvae, however, are grays. The more intense pigmentation in the black form tends to cover up the dot, but it can still be observed in most specimens. Therefore, unless the genetic basis involves incomplete dominance or incomplete penetrance of a normally dominant allele, two separate genetic systems are involved. A form of bicolor exists with extensive melanization which obscures most of the orange. This form is sometimes difficult to distinguish from nigra, particularly in third and, sometimes, fourth instar. Inspection of less heavily melanized thoracic segments where the yellow-orange pigment can be seen more readily reveals such larvae as bicolor.

Intense melanization is also observed in rufa. Black pigmentation which is normally restricted to the base of various spines and inter-segmental membranes may be so intense that it is difficult to differentiate

TABLE 2. Parental larval phenotypes: dot × dot.

brood number	Phenotypes of Progeny black	dot	total
455	74	0	74
507B	288	13	301
516	44	15	59
517	72	36	108
559	70	24	94
570	62	0	62

it from nigra. Heavily pigmented rufa may be correctly determined as rufa by orange pigmentation which can be detected in areas around and ventral to spiracles. Also, rufa lacks the mid-dorsal black line present in the non-rufa morphs. A similar darkening appears in *Chlosyne harrisii* (Scudder) as the normally orange larvae of this species have been observed to be "nearly black at maturity, the fulvous being represented merely by a few dots and small spots" (Edwards, 1877). In this case, however, the imago was also strongly melanic; this has not been observed in *C. lacinia.*

Environmental conditions may exert a significant force in production of black, hidden-stripe and heavily melanized rufa forms. These forms are readily seen in laboratory cultures; they are quite rare in field populations. Caterpillars raised under crowded laboratory conditions have been noticed to be generally darker than caterpillars occurring in the wild (see Long, 1952, 1953, and references therein). Cooler temperatures are also known to produce larvae which are more heavily pigmented than larvae reared at warmer temperatures (David & Gardiner, 1962). On the other hand, dot are often seen and super-dot forms have been seen in natural populations. The occurrence of super-dot forms appears to be correlated with large population sizes. Although observations are limited, this may indicate a relaxation of selection pressures as reported for adult phenotype of *Melitaea aurinia* Rott. (Ford & Ford, 1930).

Attempts to determine the genetic basis of these forms have been inconclusive (Tables 1 and 2). Certain black × black crosses yielded black and dot larvae in 1:1 and 3:1 ratios in addition to some broods highly skewed for black, i.e., very few dot. However, several dot × dot crosses yielded broods with both black and dot larvae and some broods with only black larvae! The genetic basis of these forms is vague and may be highly influenced by environmental conditions as previously reported in the larvae of the arctiid moth *Utetheisa pulchella* L. (Kettlewell, 1964). Kettlewell (1944) reported results which he interpreted as being due to the expression of a gene which is normally buffered in natural conditions but is released under artificial laboratory conditions. Major variation within morph classes in some amphibians (Volpe, 1961; Resnick & Jameson, 1963) has been shown to be the result of incomplete penetrance (variable expressivity) of various genes.

CONCLUSION

In *Chlosyne lacinia* genetic modifiers and environmental influences apparently act upon a basic three-phenotype polymorphic system. The result is to modify a genetically discontinuous system of variation into a system of nearly continuous variation. Such continuous variation was described for the larvae of this species by two workers (Koehler, 1927; Comstock, 1927, 1946).

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