Journal of Research on the Lepidoptera 25(3): 188-201, 1986 (87)

Chromatic Polymorphism in *Callophrys mossii bayensis* Larvae (Lycaenidae): Spectral Characterization, Short-Term Color Shifts, and Natural Morph Frequencies

Larry Orsak[1]
and
Douglas W. Whitman[2]

Dept. Entomological Sciences, University of California, Berkeley, CA 94720

Abstract. A tristimulus colorimeter and UV-VIS spectrophotometer supplemented visual assessments of color polymorphism in wild fourth instar larvae of the endangered butterfly *Callophrys mossii bayensis*. Wild larvae are of many color hues; this contrasts with the distinct morphs reported from laboratory rearings. Larval color changed over short time periods when fed yellow flowers or red bracts. The preciseness of visual color matching between larvae and plant substrates is higher for red than for yellow larvae. This crypsis does not extend to any precise mimicry of spectral reflectance. Genetic color-determining mechanisms seem to be supplemented by an environment-derived factor in producing the broad range in color hues found in wild larvae. The color-assessment techniques described here could be used to better understand the role of color pattern in thermoregulation, sexual selection and predation-avoidance.

Introduction

Body color is a universal life attribute that influences intraspecific communication, predator avoidance, and/or thermoregulation. Systematists use color patterns to characterize species and subspecies, especially in avian and lepidopteran taxa. Despite these important roles, color patterns are usually qualitatively described, not quantitatively characterized. Partly, this is due to the difficulty in quantifying and standardizing color description. Color standard texts (e.g., Munsell, 1963) are useful, but not widely accessible. Each text uses different descriptors and their value is limited mainly to mono-colored organisms.

An added complexity is the variation in color pattern within populations. This is particularly apparent in the Lepidoptera, with color polymorphism occurring in LARVAE (e.g., Poulton, 1888; Bell & Scott, 1937; Pinhey, 1960; Clarke, Dickson & Sheppard, 1963; Curio, 1965,

[1]Institute of Ecology, University of Georgia, Athens, GA 30602
[2]Dept. Entomology, University of Georgia, Athens, GA 30602

1970a, 1970b, 1970c; Boer, 1971; Emmel & Emmel, 1973; Common & Waterhouse, 1981; see also Edmunds, 1974), PUPAE (Poulton, 1890; Sims & Shapiro, 1983, and citations therein), and ADULTS (Ford, 1955; Kettlewell, 1961; Clarke & Sheppard, 1963, 1972; Owen & Chanter, 1969; and citations in Wickler, 1968 and Rettenmeyer, 1970). Larvae of the federally endangered (U.S. Fish & Wildlife Service, 1976) San Bruno elfin butterfly, *Callophrys mossii bayensis* R. W. Brown exhibit a striking color polymorphism, with chromatic variability of both larvae and foodplant substrates. This provides an ideal situation for comparing color assessment techniques.

Callophyrs mossii bayensis Color Morphs

Brown (1969) first described color morphs in third and fourth instar *C. m. bayensis*. He felt that greenish, fresh-hatched larvae acquired the same color as the *Sedum spathulifolium* Hooker foodplant part they ingested. *Sedum* exhibits diverse colors in late spring when larvae are near maturity: Basal leaf rosettes range from deep green to rosy red. Flowering stalk stems and bracts are initially green, becoming pale to rosy, or deep red; petals are yellow.

Brown's assessment of color determination was disputed by Emmel and Ferris (1972), who described three distinct color morphs from laboratory-reared fourth instars fed only green *Sedum* rosettes: yellow, pale orange, and cherry red. Arnold (1978, 1983), in turn, disputed the concept of three distinct morphs: "Newly eclosed larvae were colored either red or yellow. They remained one color throughout their larval life," and "larvae possess two distinct color morphs, red and yellow, plus an intermediate light orange." Lumping light orange and yellow larvae, Arnold proposed a simple 1:3 allelic expression of yellow:red forms, and equated laboratory and field expression of larval color. Finally, our repeated field observations of an array of color forms conflicts with all previous reports of two or three distinct morphs in nature. Clearly, there are discrepancies regarding the expression of color, its stability, and its derivation in *C. m. bayensis*. This paper seeks to resolve some of them.

Materials and Methods

C. m. bayensis and *Sedum spathulifolium* samples were obtained on north-facing slopes of San Bruno Mountain (San Mateo County) California between Brisbane and Colma Canyon. Larvae occur from about mid-March to very early June. About mid-May, third and fourth instar larvae ascend to budding *Sedum* flower stalks (Emmel & Ferris, 1972; Arnold, 1983). We took food-plant and fourth (penultimate) instar samples after ascent.

COLOR CLASSIFICATION SCHEME: Following a preliminary 1977 field examination, a scheme was developed to quickly color-sort wild larvae: Seven larval "standards" (Fig. 1) divided the visual color range of

wild larvae. These were sequentially numbered; the higher the number, the more red (or less yellow) the larva. These were photographed with Kodachrome 25 film, using two Sunpak 411 flashes. Subsequent Kodak color prints facilitated rapid color classification in the field. Although film color reproduction is inexact, we found no problem placing wild larvae into one of seven color categories. A "color category" represents a range between two points defined by the larval standards, except for Category 7 which had only one larval standard "anchor." A larva whose general color fell anywhere between the discrete point of Standard 1 up to, but not matching Standard 2, was a Category 1 larva and so on.

COLORIMETER ANALYSIS: Live larval and foodplant samples were color-analyzed using a Hunterlab Tristimulus Colorimeter Model D25M-9. This employs a source-photodetector-filter combination to simulate the colormatching response functions of a "normal" human observer. Quantifiable, repeatable results are in the form of the L_1 a_1 b_1 (henceforth, LAB) system (Hunter, 1975). "L" measures brightness (L = 100 for pure white, 0 for pure black). "A" and "B" are chromaticity dimensions. The value of "A" indicates redness (+ value), gray (0 value), and green (− value). "B" measures yellowness (+ value), gray (0 value) and blue (− value). Measurements were made by holding similar-sized samples of *Sedum* flowers and adjacent bracts, secondary bracts, green rosettes, or *C. m. bayensis* penultimate instar larvae against the 1/2-inch diameter port.

SPECTRAL ANALYSIS: A Cary UV-VIS spectrophotometer with spectral capacity of 187−875 nanometers (nm), and equipped with a diffuse reflectance sphere, was used. Larval and foodplant samples were affixed in similar orientation on coal black cards with double-stick tape. Each sample was scanned at 1 nm/second, with a spectral band width of 3.5 nm, allowing resolution of narrow reflectance peaks. To reduce sample orientation effects, all samples were positioned similarly. After scanning, larvae were released unharmed by wetting the double-stick tape.

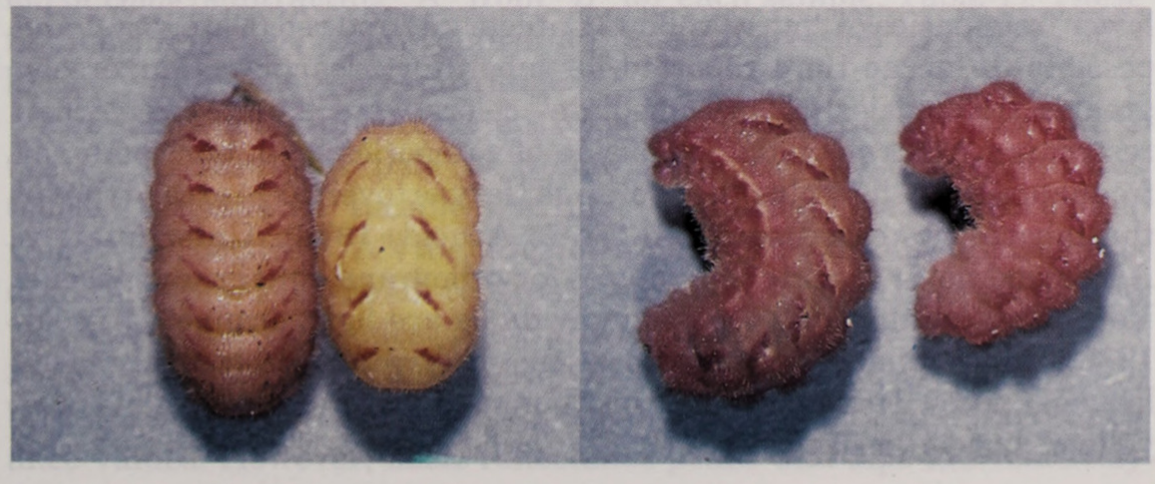
LARVAL COLOR CHANGES: To explore short-term color changes, fourth instar larvae with previous access to all *Sedum* plant parts were segregated into color categories using the seven standards. Free access to all foodplant parts was maintained under low intensity fluorescent lighting. Forty-eight hours later, the larvae were color-reclassified. Only tachinid parasitoid-free larvae (assayed at pupation) were used in the data analysis.

We investigated Brown's (1969) statement that larval and ingested food colors converged: Larvae that had ingested only green rosettes for two days were grouped into pairs of identically colored larvae and color-classified. For the following 48 hours, one member of each pair was provided only yellow *Sedum* flowers; the other was given only very red flower stalk bracts. All experienced the same fluorescent light exposure. Pairs then were reunited and color-compared, using the larval standards. Only parasitoid-free larvae were used in the data analysis.

Fig. 1. Seven larval "standards" used to characterize color polymorphism in wild *Callophrys mossii bayensis*. Standards are labeled sequentially, starting with the most yellow (Top row, 1–4; bottom row, 5–7).

Fig. 7. (LEFT BELOW) Larval color shift from light to dark over a 48-hour period. LEFT: Flower-fed larva now in color Category 3, formerly Category 2; RIGHT: Red bract-fed larva, unchanged in Category 2.

Fig. 8. (RIGHT BELOW) Larval color shift from dark to light over a 48-hour period. LEFT: Flower-fed larva now in color Category 5, formerly Category 6; RIGHT: Red bract-fed larva unchanged in Category 6.



Results

QUALITATIVE DESCRIPTION OF LARVAL COLOR: Nearly 500 wild larvae were color-classified. Virtually none were lighter yellow than Standard 1; some had less pronounced "chevrons," the paired, dorsolateral curved markings occurring on many body segments. Category 7 proved exceptionally restrictive, since few Category 7 larvae were redder than Standard 7.

Larvae within each color category can be generalized as follows:

1 = Yellow, no peach tint; chevron markings generally faint
2 = Yellowish with faint orange tint; distinct chevrons.
3 = Distinctly light orange with slightly darker rosy suffusions; chevrons usually with pale outlines.
4 = Orange with darker peach-colored suffusions on much of the body; chevron outlines and dorsal midline generally pale.
5 = Orange with brownish tinge; dark chevrons and less distinct pale outlines.
6 = Rosy red, with less distinct but noticeable pale chevron outlines. Larvae in this category may be lighter colored than the previous category, but are distinctly redder.
7 = Cherry red throughout; chevrons generally faint.

While color category designation was based upon general background color, ignoring fine-scale pattern differences, we also noted that chevron markings did not intensify in direct relation to increasingly red background coloration (see Emmel & Ferris, 1972).

COLOR DISTRIBUTION IN NATURE: Fig. 2 shows the color distribution of 433 wild larvae, comparing the results to distributions obtained by Emmel and Ferris (1972) for wild larvae, and Arnold (1978) for laboratory-rearings. This alignment easily satisfied the "morph" descriptors provided by each author for his respective sample. Our categories 2 and 3 are the only ones that would fit the definition of "light orange" (*sensu* Arnold, 1978).

Our sample indicates larvae to be broadly distributed across color categories, at these frequencies: 1 = 6.0%; 2 = 10.6%; 3 = 14.6%; 4 = 13.9%; 5 = 12.0%; 6 = 24.7%; 7 = 18.3%. Further, our sample yielded lower frequencies of "pure" yellow (Category 1) and red (Category 7 and possibly 6) larvae than reported for laboratory rearings. Conversely, greater frequencies of "intermediate" colors were found. Even when restricting "intermediates" to larvae of categories 2–3, our combined frequencies of yellow plus "light orange" larvae (over 30%) exceed that of the laboratory-reared sample (24.4%; Arnold, 1978). Unfortunately, Arnold did not segregate frequencies for yellow and light orange larvae. Yet, he states that only "a few individuals are light orange" (Arnold, 1983), which tends to corroborate our observations of rosette-reared larvae, and by deduction, confirms the much rarer occurrence of "pure yellow" larvae in nature.

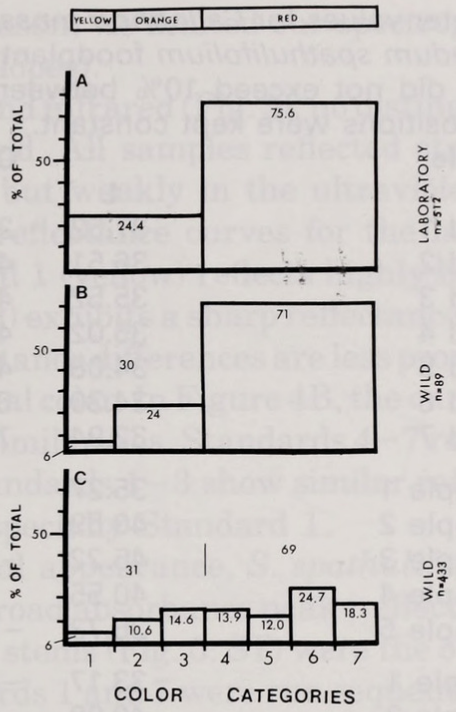


Fig. 2. Color category distribution of *C. m. bayensis* larvae: Comparisons of wild- and laboratory-derived samples, from (A) Arnold, 1978; (B) Emmel & Ferris, 1972; (C) this study. Alignments are based upon each author's color descriptions of cited morphs. Frequency figures within each bar pertain to that study. Above-bar frequencies in (B) and (C) are provided to facilitate cross-sample comparisons.

COLORIMETER VALUE COMPARISONS: Table 1 lists LAB values for *C. m. bayensis* larval standards and foodplant samples. Predictably, "A" values are higher for the "redder" larval standards, although the most yellow standard reflects some red. The "redness" increase, measured by "A," changes little for standards 2–5, increasing for 6 and 7. In contrast, "yellowness," measured by "B," drops in significant increments through standard 5. Thus, while larval standards broadly cover the yellow-to-red spectrum, they do not represent evenly spaced color points for either chromaticity dimension. This is clear in the composite expression of color (subtracting "A" from "B" for each sample; Table 1). These findings, however, again confirm a graded expression of color in wild larvae within their spectral range.

The range in larval LAB values approximates that of foodplant parts (Table 1). However, pale or yellowish flowering stalk substrates (flowers+associated racemes) exhibit significant green colorimeter values (i.e., negative "A") that are not duplicated in any larval standards or in Category 1 larvae. In contrast, there is close matching of "A" and "B" values for the reddest *Sedum* samples and larvae.

SPECTRAL VALUE COMPARISONS: Sample orientation (Fig. 3), brightness, and other features of the sample can affect absolute reflectance values. However, basic reflectance peaks and dips are relatively

Table 1. LAB colorimeter values for *Callophryr mossii bayensis* larval standards and *Sedum spathulifolium* foodplant samples. Variation of each sample did not exceed 10% between readings as long as orientation positions were kept constant.

Sample		Color Values L	A	B	(B-A)
Larva:	Color Standard 1	37.52	2.81	12.17	9.4
	Color Standard 2	36.51	4.01	10.21	6.2
	Color Standard 3	35.52	4.53	8.95	4.4
	Color Standard 4	35.02	4.68	6.65	2.0
	Color Standard 5	34.08	4.91	4.37	−0.5
	Color Standard 6	34.30	6.83	3.98	−2.9
	Color Standard 7	32.94	7.72	3.76	−4.0
Sedum Flowers:	Sample 1	35.27	1.80	24.13	
	Sample 2	40.59	3.45	15.36	
	Sample 3	45.22	−2.05	19.70	
	Sample 4	40.55	.70	17.33	
	Sample 5	36.73	−1.74	18.22	
Sedum Leaves: (green)	Sample 1	33.17	−6.03	13.01	
	Sample 2	40.88	−6.82	12.42	
	Sample 3	47.21	−5.90	13.60	
	Sample 4	38.74	−2.85	5.59	
Sedum Bracts: (reddish)	Sample 1	33.14	9.08	3.56	
	Sample 2	28.23	6.27	3.55	
	Sample 3	35.41	4.33	4.97	
	Sample 4	38.10	7.44	3.34	
	Sample 5	44.20	4.97	2.19	

Cumulative Spectral Ranges:	*L*	*A*	*B*
Larvae	32–37	2.8–7.7	3.8–12.2
Foodplant Rosettes	28–47	−6.0–9.1	2.2–24.1
Flowering Stalk	28–45	−2.1–9.1	2.2–24.1

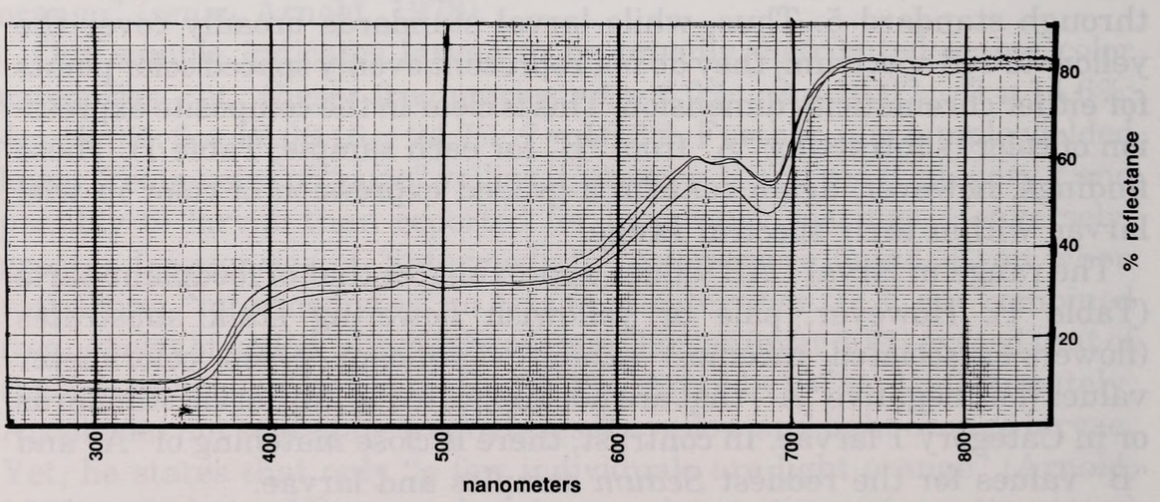


Fig. 3. Reflectance spectra of a *Sedum spathulifolium* leaf sample placed at different angles in the spectrophotometer diffuse reflectance sphere sample port.

constant. For this reason, we limited our spectrograph comparisons to reflectance curves (slopes).

In the ultraviolet and infrared (Fig. 3), no distinguishable intersample differences were found. All samples reflected strongly in the red and near-infrared range but weakly in the ultraviolet.

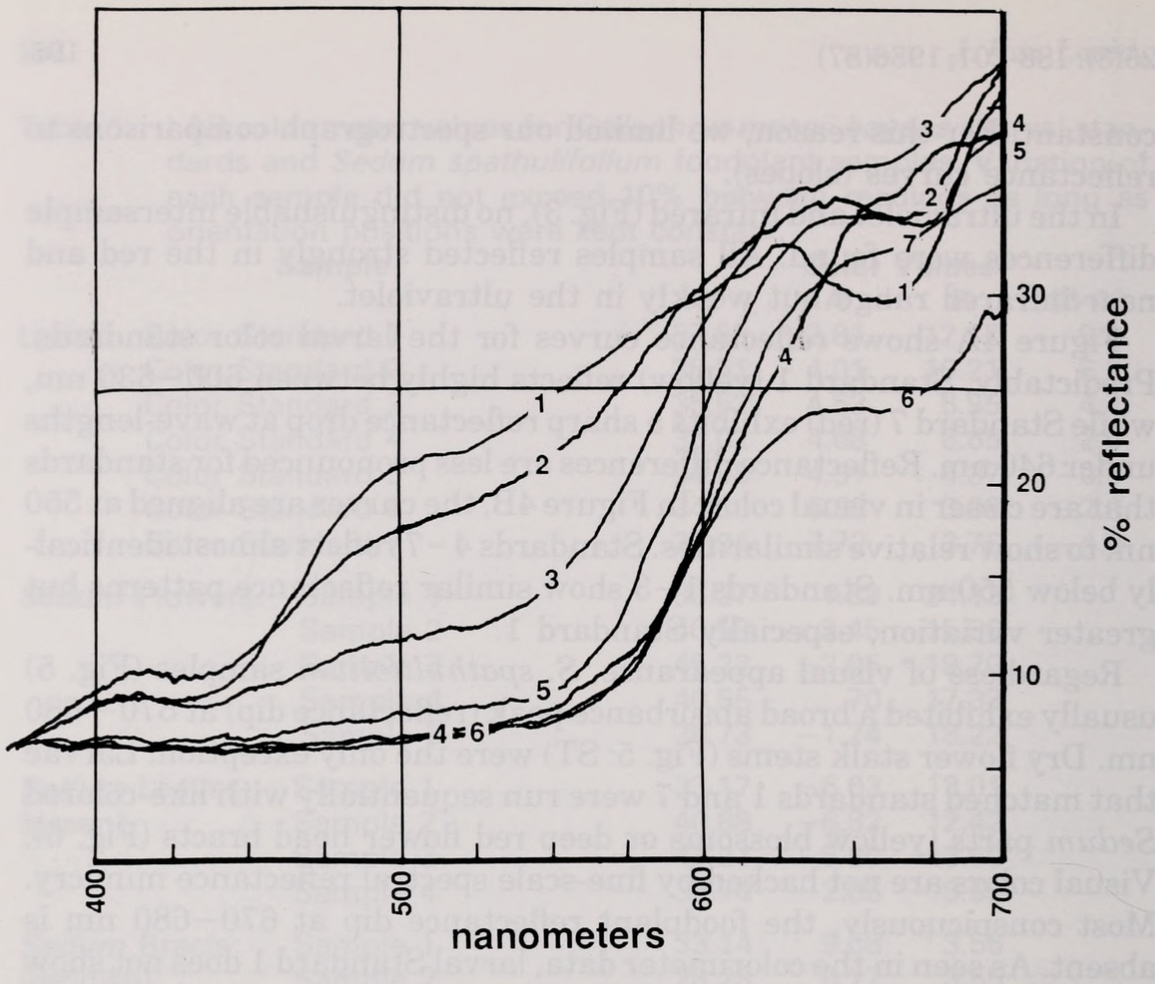
Figure 4A shows reflectance curves for the larval color standards. Predictably, Standard 1 (yellow) reflects highly between 600–630 nm, while Standard 7 (red) exhibits a sharp reflectance drop at wave-lengths under 640 nm. Reflectance differences are less pronounced for standards that are closer in visual color. In Figure 4B, the curves are aligned at 550 nm to show relative similarities. Standards 4–7 reflect almost identically below 550 nm. Standards 1–3 show similar reflectance patterns but greater variation, especially Standard 1.

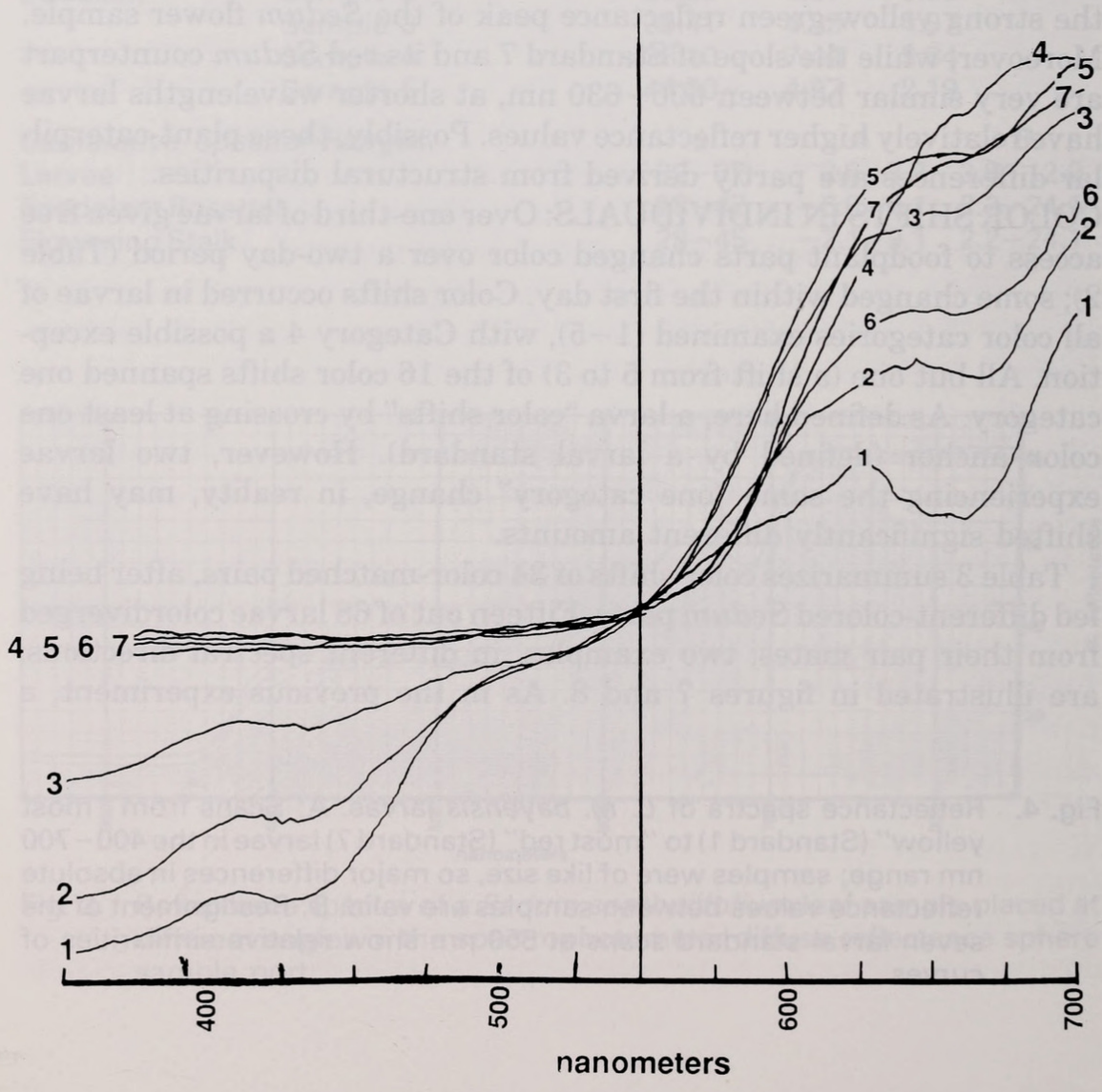
Regardless of visual appearance, *S. spathulifolium* samples (Fig. 5) usually exhibited a broad absorbance peak (reflectance dip) at 670–680 nm. Dry flower stalk stems (Fig. 5: ST) were the only exception. Larvae that matched standards 1 and 7 were run sequentially with like-colored *Sedum* parts (yellow blossoms or deep red flower head bracts (Fig. 6). Visual colors are not backed by fine-scale spectral reflectance mimicry. Most conspicuously, the foodplant reflectance dip at 670–680 nm is absent. As seen in the colorimeter data, larval Standard 1 does not show the strong yellow-green reflectance peak of the *Sedum* flower sample. Moreover, while the slope of Standard 7 and its red *Sedum* counterpart are very similar between 600–630 nm, at shorter wavelengths larvae have relatively higher reflectance values. Possibly, these plant-caterpillar differences are partly derived from structural disparities.

COLOR SHIFTS IN INDIVIDUALS: Over one-third of larvae given free access to foodplant parts changed color over a two-day period (Table 2); some changed within the first day. Color shifts occurred in larvae of all color categories examined (1–5), with Category 4 a possible exception. All but one (a shift from 5 to 3) of the 16 color shifts spanned one category. As defined here, a larva "color shifts" by crossing at least one color anchor (defined by a larval standard). However, two larvae experiencing the same "one category" change, in reality, may have shifted significantly different amounts.

Table 3 summarizes color shifts of 34 color-matched pairs, after being fed different-colored *Sedum* parts. Fifteen out of 68 larvae colordiverged from their pair mates; two examples, in different spectral directions, are illustrated in figures 7 and 8. As in the previous experiment, a

Fig. 4. Reflectance spectra of *C. m. bayensis* larvae. A: Scans from "most yellow" (Standard 1) to "most red" (Standard 7) larvae in the 400–700 nm range; samples were of like size, so major differences in absolute reflectance values between samples are valid. B: Realignment of the seven larval standard scans at 550 nm show relative similarities of curves.


% reflectance
30
20
10
400
500
600
700
nanometers
1
2
3
4=6
5
4
5
2
3
7
1
6


4 5 6 7
3
2
1
400
500
600
700
nanometers
4
5
7
3
5
7
3
4
6
2
1
6
2
1

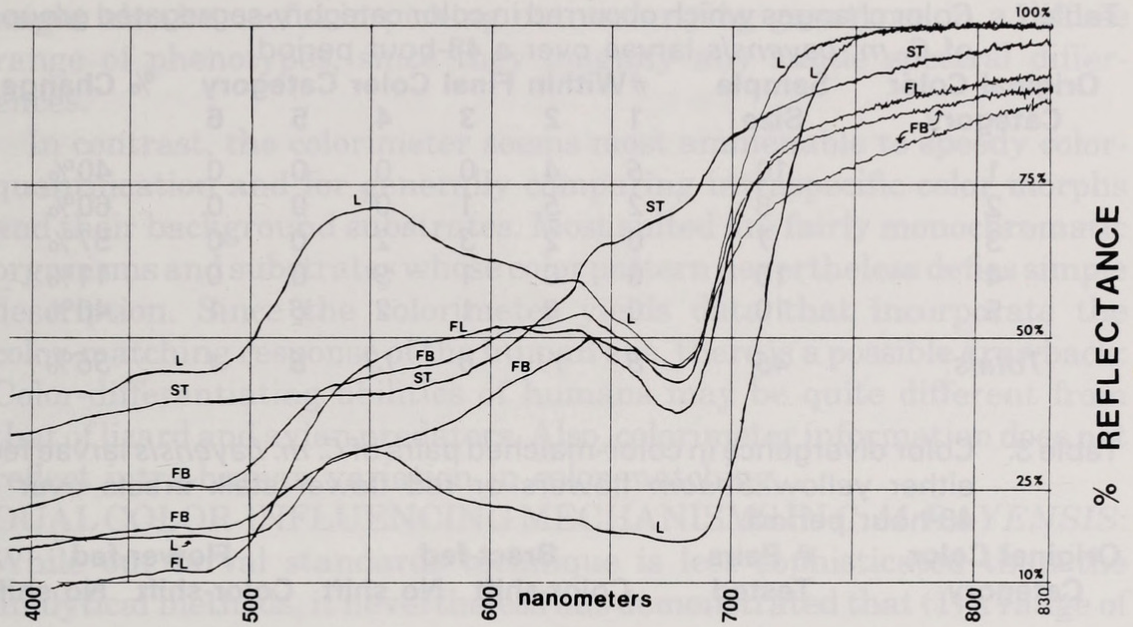


Fig. 5. Reflectance spectra of different *S. spathulifolium* foodplant parts: L = green rosette leaf; ST = dried, reddish flower stalk; F = yellow flowers; FB = yellow flowers and associated green and reddish bracts and stems.

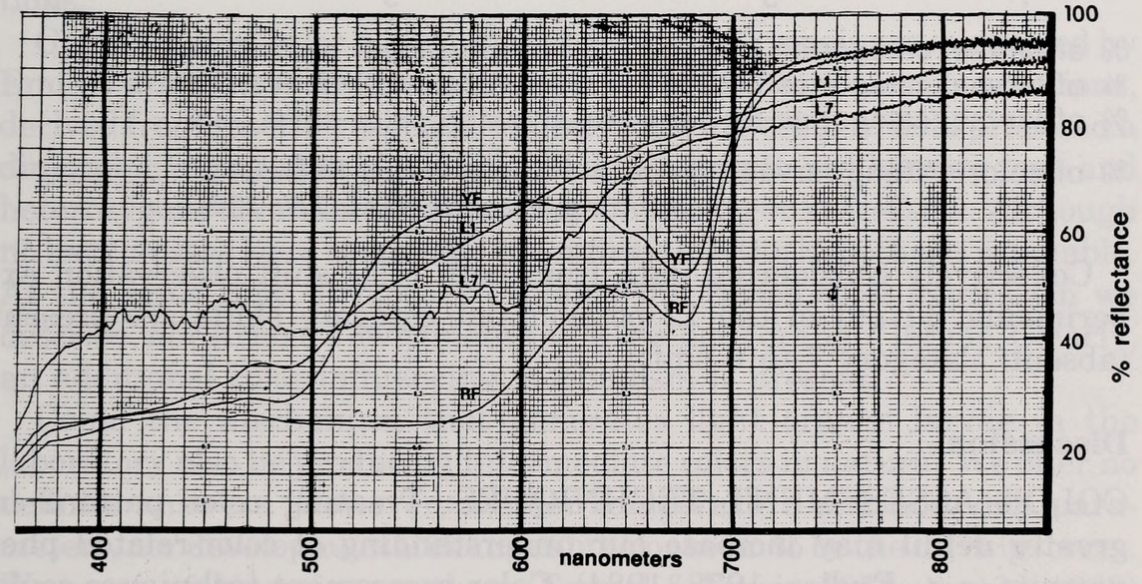


Fig. 6. Comparative reflectance spectra for similar-colored *S. spathulifolium* foodplant and *C. m. bayensis* larval samples. RED: Larva in Category 7 (L7), *Sedum* red flower stalk stem leaf (RL); YELLOW: Larva in Category 1 (L1), *Sedum* flower petals (YF).

slightly higher percentage of Category 1 and 2 "yellow" morphs experienced color shifts, in contrast to redder individuals. However, color shifts were often not in the direction of the foodplant part's color: Six larvae fed yellow flowers color-shifted towards red; only two became more yellow. In total, two-thirds of the 15 recorded color changes involved shifts towards red. As in the previous experiment, a single two-category shift was recorded (from Category 1 to 3).

Table 2. Color changes which occurred in color category-segregated groups of *C. m. bayensis* larvae over a 48-hour period.

Original Color Category	Sample Size	#Within Final Color Category 1	2	3	4	5	6	% Change
1	10	*6*	4	0	0	0	0	40%
2	8	2	*5*	1	0	0	0	60%
3	7	0	2	*3*	2	0	0	57%
4	10	0	0	1	*9*	0	0	11%
5	10	0	0	1	2	*6*	1	40%
Totals:	*45*	*8*	*11*	*6*	*13*	*6*	*1*	*36%*

Table 3. Color divergence in color-matched pairs of *C. m. bayensis* larvae fed either yellow *Sedum* flowers or red flower stalk bracts over a 48-hour period.

Original Color Category	# Pairs Tested	Bract-fed Color-shift	Bract-fed No shift	Flower-fed Color-shift	Flower-fed No shift
1	3	1(#2) 1(#3)	1	1(#2)	2
2	7	1(#3)	6	4(#3)	3
3	4		4		4
4	6		6	1(#5)	5
5	1		1		1
6	8	3(#5) 1(#7)	4	2(#5)	6
7	5		5		5

% of larvae, categories 1–2 (n=20), showing color shift: 40%
% of larvae, categories 3–5 (n=22), showing color shift: 5%
% of larvae, categories 6–7 (n=26), showing color shift: 23%

% of color-shifting larvae (n=15), shifting towards RED: 66%
shifting towards YELLOW: 33%

Collectively considering data from both color shift observation experiments, 11 out of the 12 possible one-category shifts are present (absent: Category 7 to 6 shift).

Discussion

COLOR ASSESSMENT TECHNIQUES: Treating color pattern in greater detail may increase our understanding of color-related phenomena (e.g., Endler, 1978, 1984). Color assessment techniques could be employed more widely in studies of antipredation thermoregulation, sexual selection, and more broadly, in evaluating how how precisely selective pressures operate on elements of a color pattern. Colorimetric and spectrophotometric data are fairly unbiased and repeatable ways of defining color. On the negative side, acquisition of these data may be time-consuming and equipment is not always available.

The most likely application of spectrophotometer data is in assessing the fine degree of color matching between organism and substrate over the spectral absorbance range. This relates to antipredation strategies, and such information could yield useful clues on the parameters that influence prey-substrate matching: predator vision, predative pressure, and the prey's genetic constraints. Spectrographs

might also be useful in picking out underlying genotypes in a diffuse range of phenotypes, since they magnify any subtle spectral differences.

In contrast, the colorimeter seems most ammenable to speedy color-quantification and for generally comparing intraspecific color morphs and their background substrates. Most suited are fairly monochromatic organisms and substrates whose color pattern nevertheless defies simple description. Since the colorimeter yields data that incorporate the color-matching response of the human eye, there is a possible drawback: Color-differentiating abilities of humans may be quite different from that of lizard and avian predators. Also, colorimeter information does not reflect intra-human variation in color-matching.

DUAL COLOR-INFLUENCING MECHANISMS IN *C. M. BAYENSIS*: While our larval standards technique is less sophisticated than the analytical methods, it nevertheless has demonstrated that (1) a range of color patterns exists in nature; (2) color pattern is not static; (3) color pattern can shift towards red or towards yellow; (4) both "red" and "yellow" wild larvae can change color; and (5) color shifts can occur over short time frames. Some of these results obviously counter previously published statements, but we see a possible resolution of the contradictions.

Genetic larval color determinants for *C. m. bayensis* are suggested by Emmel and Ferris (1972) and Arnold (1978, 1983). Their observations, derived from rosette-reared larvae, corroborate ours. Arnold proposed a dimorphic expression of a single allele leading to red homozygous and heterozygous dominants, plus a yellow homozygous recessive. Although no backcrosses were conducted to confirm this, the hypothesis is tenable. At the same time, it neither explains the varied color expression we describe, nor Arnold's own finding of "a few light orange" larvae. Clearly, an additional color-influencing mechanism is present.

Could the mechanism that generates light orange larvae in the laboratory also be producing intermediate colors in nature? We offer no definite answers. However, neither temperature and humidity parameters, nor developmental changes in color seem to be the driving forces. We agree with previous authors (Emmel & Ferris, 1972; Arnold, 1983) that no direct connection exists between the color of ingested plant parts and resultant larval colors. Yet, we do not preclude a less direct relationship. Indeed, the fact that laboratory-maintained larvae allowed access to all *Sedum* parts color-shift — while rosette-reared larvae seemingly do not — is indication that diet does have an influence on color.

Color in larval *C. m. bayensis* probably offers predation-avoidance advantages, but the specifics are unclear. Why, for example, are most full-grown larvae red, while the most frequently occupied substrate is yellow, if crypsis is the antipredator strategy? And does dual-mechanism color determination offer advantages over genetic or environmental

determinants alone? Approaching these questions from both mechanistic and ecological perspectives, using descriptive information as a foundation, may offer answers. All-told, we suggest there is greater value in exploring the subtleties of color expression in this taxon, rather than burying them.

Acknowledgements. The invaluable assistance of David Schooley is gratefully acknowledged, as well as constructive critical comments on the manuscript by Clifford Ferris and Arthur Shapiro. The Permit Branch of the Office of Endangered Species (U.S. Fish & Wildlife Service) and California Department of Fish & Game provided study permit #PRT 2–757.

We appreciate the color plate opportunities of the Journal of Research on the Lepidoptera. When a picture is worth a thousand words, color photographs are beyond value in communicating the details of this topic!

Finally, we salute the many lepidopterists, botanists, biologists, and local citizens to whom *C. m. bayensis* owed its continued existence. Aware of the uniqueness of San Bruno Mountain's habitats and native inhabitants, they have actively worked for the protection of this national resource using their diverse scientific, educational, and political talents.

Literature Cited

ARNOLD, R. A., 1978. Status of six endangered California butterflies. 1977. Contract report for State of California. Department of Fish and Game. 95 pp.

_____, 1983. Ecological studies of six endangered butterflies (Lepidoptera, Lycaenidae): Island biogeography, patch dynamics, and the design of habitat preserves. Univ. Calif. Publ. Entomol. 99: 1–161.

BELL, T. R. D. & F. B. SCOTT, 1937. The Fauna of British India Including Ceylon and Burma. Moths. Vol. 5., Sphingidae. Taylor & Francis, London.

BOER, M. H. DEN, 1971. A colour polymorphism in caterpillars of *Bupalus piniarius* (L.) (Lepidoptera: Geometridae). Neth. J. Zool. 21: 61–116.

BROWN, R. M., 1969. Larva and habitat of *Callophrys fotis bayensis* (Lycaenidae). J. Res. Lep. 8: 49–50.

CLARKE, C. A., DICKSON, C. G. C. & P M. SHEPPARD, 1963. Larval color pattern in *Papilio demodocus*. Evolution 17: 130–137.

CLARKE, C. A. & P. M. SHEPPARD, 1963. Interactions between major genes and polygenes in the determination of the mimetic patterns of *Papilio dardanus*. Evolution 1: 404–413.

_____, 1972. The genetics of the mimetic butterfly *Papilio polytes*. Phil. Trans. R. Soc. London, B 263: 431–458.

COMMON I. G. B. & D. F. WATERHOUSE, 1981. Butterflies of Australia. Angus & Robertson, London.

CURIO, E., 1965. Die Schutzanpassungen dreier Raupen eines Schwärmers (Lepid., Sphingidae) auf Galapagos. Zool. Jb. Sys. 92: 487–522.

_____, 1970a. Die Messung des Selektionswertes einer Verhaltensweise. Verh. dt. zool. Ges. 64: 348–352.

_____, 1970b. Die Selektion drier Raupenformen eines Schwärmers (Lepidop., Sphingidae) durch einen Anolis (Rept., Iguanidae). Z. Tierpsychol. 2: 899–914.

———, 1970c. Validity of the selective coefficient of a behaviour trait in hawkmoth larvae. Nature, Lond. 228: 382.

EDMUNDS, M., 1974. Defence in Animals. Longman, Essex.

EMMEL, J. F. & C. D. FERRIS, 1972. The biology of *Callophrys* (*Incisalia*) *fotis bayensis* (Lycaenidae). J. Lepid. Soc. 26: 237–244.

EMMEL, T. C. & J. F. EMMEL, 1973. The butterflies of southern California. Nat. Hist. Mus. L. A. Co. Science Series 26: 1–148.

ENDLER, J. A., 1978. A predator's view of animal color patterns. IN: Hecht, M. K., Steere, W. C. & B. Wallace (eds.), Evolutionary Biology, Vol. 11, pp. 31–364.

———, 1984. Progressive background in moths, and a quantitative measure of crypsis. Biol. J. Linn. Soc. 22: 187–231.

FORD, E. B., 1955. Moths. Collins, London.

HUNTER, R. S., 1975. The Measurement of Appearance. Wiley, New York.

KETTLEWELL, H. B. D., 1961. The phenomenon of industrial melanism in Lepidopterea. Ann. Rev. Ent. 6: 245–262.

MUNSELL COLOR COMPANY, 1963. The Munsell Book of Color. Munsell Color Company, Baltimore.

OWEN, D. F. & D. O. CHANTER, 1969. Population biology of tropical African butterflies. Sex ratio and genetic variation in *Acraea encedon*. J. Zool. London 157: 345–374.

PINHEY, E., 1960. Hawk Moths of Central and Southern Africa. Longman, Cape Town.

POULTON, E. B., 1888. Notes in 1887 upon lepidopterous larvae, etc., including a complete account of the life history of the larvae of *Sphinx convolvuli* and *Aglia tau*. Trans. Ent. Soc. Lond. (1888) pp. 515–606.

———, 1890. The Colours of Animals. Kegan, Paul, Trench, Trubner, London.

RETTENMEYER, C. W., 1970. Insect mimicry. Ann. Rev. Ent. 15: 43–74.

SIMS, S. R. & A. M. SHAPIRO, 1983. Pupal color dimorphism in California *Battus philenor*: Pupation sites, environmental control and diapause linkage. Ecol. Ent. 8: 95–104.

U. S. FISH & WILDLIFE SERVICE, 1976. Endangered and threatened wildlife and plants — Determination that six species of butterflies are endangered species. Fed. Register 41: 22041-22044. (28 April issue.)

WICKLER, W., 1968. Mimicry in Plants and Animals. McGraw Hill, New York.