

SYSTEMATICS

A New Look at Adaptive Body Coloration and Color Change in “Common Green Lacewings” of the Genus *Chrysoperla* (Neuroptera: Chrysopidae)

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ABSTRACT Green lacewings in the genus *Chrysoperla* are not always green. They can be yellow (autosomal recessive mutant); change from whitish-yellow to green as young adults; or temporarily turn yellowish, reddish, or brown during diapause. New findings on a yellow mutant in a natural population in southern California and on species-specific diapause coloration are presented, old findings are reviewed, and the adaptive value of color variability and color change in the genus is discussed.

KEY WORDS *carnea*-group, *pubida*-group, winter color, crypsis, cryptic species

The larvae of green lacewings, family Chrysopidae, feed on aphids and other soft-bodied arthropods, and thus are reared commercially for biological control in many countries and on different continents (McEwen et al. 2001). The adults of most of the agriculturally important species feed on honeydew from sternorhynchous hemipteran insects such as aphids, the favorite prey of their larvae. Most green lacewings may look very similar, but some species are not always green. Body coloration and color change were the topics of a review paper published >20 yr ago (Duelli 1992). Since then new findings have expanded our knowledge considerably and require a reassessment of the often-cited coloration variability within the “common green lacewings” of the genus *Chrysoperla* Steinmann. Three types of intraspecific color variation have been observed in this genus.

1. Intraspecific Genetic Variation of Body Color: Here we mean a major difference in overall body color and not the minor variation in color patterns that can be found in many widespread lacewing species (e.g., *Chrysoperla mediterranea* (Hölzel), Henry et al. 1999). For example, a dramatically distinctive autosomal mutant “blue” was detected in a lab culture of *Chrysopa* (= *Chrysoperla*) *carnea* Stephens (Tauber and Tauber 1971), derived from a popu-

lation in eastern North America now assigned to *Chrysoperla plorabunda* (Fitch).

2. Obligatory Ontogenetic Color Change: In the genus *Chrysoperla*, this is known only for *Chrysoperla congrua* (Walker) in the Old World tropics (Brettell 1982, Duelli 1992, Winterton 1999). We consider this to be a distinctive category of change, not comparable to the transition to mature color patterns that can occur, for example, in teneral adults of damselflies (Ueda 1989) and owlflies (Henry 1977), nor to the gradual, life-long increase in markings on the wings of the Hawaiian chrysopid *Anomalochrysa hepatica* McLachlan as the adults age (C. A. Tauber and M. J. Tauber, personal communication).
3. Diapause-Associated Color Change: For the family Chrysopidae, such changes are known only in the genus *Chrysoperla* and are associated with overwintering as adults, a synapomorphy of that genus (Séméria 1977). In this context, color change is hypothesized to increase the probability of survival through crypsis in species associated with deciduous vegetation (MacLeod 1967). Enhanced crypsis is likely to be particularly important in *Chrysoperla* because these species lack the defensive secretions of many other genera that earned green lacewings their common name “stinkflies” (e.g., *Chrysopa* Leach, *Ceraeochrysa* Adams, and *Plesiochrysa* Adams; see Aldrich et al. 2009 and references therein). Diapause-associated color changes have been best studied in *Chrysoperla carnea* s. l., typically called *Chrysopa carnea* in older publications. For >100 yr, this abundant, agriculturally important Holarctic “species” has dominated the scientific literature on lacewings (Canard et al. 1984, Bay et al. 1993, McEwen et al. 2001). To accommodate all the regional differences in life cycles, diapause induction, and color change, it was considered to be a highly

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polymorphic and polytypic taxon (Duelli 1992, Tauber and Tauber 1992, Tauber et al. 2000). In agricultural landscapes of both Eurasia and North America, researchers observed that at least a portion of the adult lacewing population assigned to this species changed body coloration in synchrony with the changing color of the leaves of deciduous plants (references in Bay et al. 1993). Such color change invariably accompanied a reproductive diapause. However, we now understand that *C. carnea* s. l. is actually a large, diverse species group comprising at least 21 cryptic, sibling species (Henry et al. 2013). Because previous observations assumed a single widespread species (Duelli 1992), it is necessary to revisit the nature of color and diapause variation in the *C. carnea*-group (Brooks 1994) of green lacewings.

Here, we review recent contributions to our knowledge of these three types of color change in *Chrysoperla*. In specific, we document a new example of a genetic color polymorphism in *Chrysoperla comanche* (Banks), evaluate an adaptive explanation of ontogenetic color change in *C. congrua*, and reinterpret diapause-associated color change in the *C. carnea*-group within a modern taxonomic framework.

Materials and Methods

The identification of all *Chrysoperla* species treated here was based on morphological and acoustical traits. The *carnea*-group of species within the genus *Chrysoperla* is characterized by obligatory duetting of the two sexes before mating (Henry 1983). Each species shows a specific, distinctive tremulation pattern of the abdomen, which can be made visible on an oscilloscope or computer (for details on all known song phenotypes see references in Henry et al. 2013). Living specimens of lacewings were sorted to species by eliciting a duetting response from each individual using substrate-borne playback signals (methods described in Henry et al. 2012).

The yellow adults of *C. comanche*, which initially inspired the present review, were collected at the following two sites: Pine Valley, San Bernardino Mountains, CA, 7-Sept-2010; and Mount Baldy, San Gabriel Mountains, CA, 8-Sept-2010.

Field collected lacewings were reared in plastic containers (9 cm in diameter, 7 cm in height) provided with a moist cotton pad. The adults were fed a mixture of brewers' yeast, honey, sugar, and water (Hagen and Tassan 1970). The larvae were fed moth eggs (*Ephesia kuehniella* (Zeller)) and in later stages pea aphids (*Acyrtosiphon pisum* (Harris)). The light regimen was either long day (a photoperiod of 16:8 [L:D] h) or short day (a photoperiod of 10:14 [L:D] h). Temperature was maintained at 20–25°C.

To test for diapause color change, larvae entering the third instar were isolated in glass vials with cotton stoppers, kept under short day conditions below 22°C, and fed either moth eggs or pea aphids until pupation. The emerging adults were maintained under short day

conditions for at least 4 wk to check for changed body coloration. If eggs were deposited, the adults were considered nondiapausing and no color change was expected. Vouchers for all specimens used in this study have been placed in the collection of Peter Duelli, Zürich, Switzerland.

Results

Intraspecific Genetic Variability of Body Coloration. In September 2010, on a field trip to the San Bernardino Mountains of southern California in search of a new song morph in the *C. carnea*-group (Henry et al. 2012), several different *Chrysoperla* species were collected. Most of the captured specimens were green, while others showed yellow or reddish-brown body coloration. Later in the laboratory, all were identified morphologically and acoustically, and found to include the following species: *Chrysoperla johnsoni* Henry et al., *Chrysoperla adamsi* Henry et al., *Chrysoperla calocedrii* Henry et al., *C. comanche*, *Chrysoperla downesi* (Smith), and *Chrysoperla downesi* "mohave" (a distinct ecotype of *C. downesi*; see Henry 1993).

Some of the collected specimens were plain yellow, without the characteristic reddish or brown patches known from diapausing adults in the *carnea*-group of species. Those few plain yellow specimens, among many green specimens of the same species, were determined to be *C. comanche*. The other variably yellow-reddish-brown specimens were diapausing *C. downesi* "mohave," which is a member of the *carnea*-group (Tauber and Tauber 1973a, Henry 1993). *C. comanche* belongs to the 15-species *pudica*-group of *Chrysoperla* (Brooks 1994), for which diapause coloration change is known only in *Chrysoperla rufilabris* (Burmeister) (Smith 1922, p. 1336). The two color forms of *C. comanche* are shown in Fig. 1.

Yellow and green *C. comanche* adults were examined for their song phenotype, which has been described previously (Henry 1989). Tremulation patterns were indistinguishable in the two color morphs, confirming that they were the same species. When rearing the offspring of the mix of yellow and green adults of *C. comanche* under short day conditions to encourage acquisition of diapause coloration, most individuals were green, but a few were yellow. Intermediate color morphs, which are expected in diapausing adults of *Chrysoperla*, were not present among the progeny of *C. comanche*.

Pairings of yellow specimens yielded yellow offspring only, whereas green couples produced mostly green offspring mixed with a few yellow individuals. Yellow females deposited yellow eggs and green females green eggs.

To test the hypothesis of an autosomal recessive color allele "yellow," analogous to the mutant blue allele discovered by Tauber and Tauber (1971), yellow females and males, hypothesized to be homozygous *yy*, were crossed with green males or females, hypothesized to be either homozygous *gg* or heterozygous *yg*. All green offspring of those crosses would

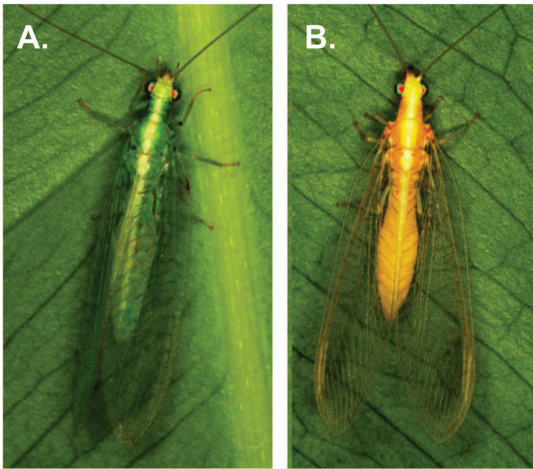
Chrysoperla comanche (southern California)

Fig. 1. Genetic color polymorphism in *Chrysoperla comanche*, found in southern California. The more common green morph, labeled (A) expresses the dominant allele "g" at a locus, whereas the less common yellow morph, labeled (B) expresses a recessive allele "y" at that locus. Both color forms may occur together at the same site.

then be heterozygous *yg* and all yellow offspring homozygous *yy*. Twenty pairs of green (heterozygous) offspring from that cross were then mated and allowed to reproduce. Table 1 shows that on average 24.4% of the next generation were yellow, supporting the idea of an autosomal recessive allele yellow. The hypothesis of 25% yellow homozygous offspring was strongly supported by a χ^2 test ($\chi^2 = 0.069$; $df = 1$; $Q = 0.79$).

In a parallel experiment, three females of green offspring (heterozygous *yg*) were crossed with three

yellow males (*yy*) and vice versa. Table 2 shows a mean of 46.5% yellow offspring, substantiating the results presented in Table 1. A χ^2 test supported the hypothesis of 50% yellow homozygous offspring ($\chi^2 = 0.694$; $df = 1$; $Q = 0.40$). Thus, the allele yellow is a naturally occurring genetic component of the *C. comanche* population in southern California.

The fact that the average percentage of yellow offspring in both experiments was slightly (Table 1) or clearly (Table 2) lower than the expected 25 or 50% suggested a weak negative effect of the yellow allele on preimaginal fitness, at least under laboratory conditions.

Obligatory Ontogenetic Color Change. In the genus *Chrysoperla*, an obligatory and major ontogenetic color change is known so far only in *C. congrua* (Brettell 1982, Duelli 1992, Winterton 1999), a species, like *C. comanche*, belonging to the *pubica*-group (Brooks 1994). With a distribution from sub-Saharan Africa and Madagascar to Australia, *C. congrua* has long been known to occur as two color morphs, a green form and a form variously described as whitish-yellow, pale brown, or reddish-yellow (Tjeder 1966, Hölzel 1989). Emerging adults of this species are always whitish-yellow, soon acquiring some darker hues. After about 4 d they turn green. To investigate the connection between the color change and diapause-inducing mechanisms in *C. comanche*, Duelli (1992) reared individuals under various light and temperature regimens. Neither short or long days nor changing day-lengths before pupation induced a reproductive diapause, and there was no change in color other than the permanent one from yellowish to green.

Diapause-Induced Color Change. With the possibility of detecting and delineating cryptic sibling species in the *carnea*-group by song analysis during the

Table 1. Average percentage of yellow offspring from 18 containers with pairs of supposedly heterozygous (*yg* × *gy*) *C. comanche* parents

Container	Yellow ♀	Yellow ♂	Yellow total	Green ♀	Green ♂	Green total	Total	% yellow
1	3	3	6	8	12	20	26	23.1
2	2	2	4	6	10	16	20	20.0
3	1	2	3	8	7	15	18	16.7
4	3	3	6	8	7	15	21	28.6
5	2	2	4	7	8	15	19	21.1
6	3	2	5	9	7	16	21	23.8
7	4	2	6	9	5	14	20	30.0
8	2	4	6	7	7	14	20	30.0
9	3	1	4	7	11	18	22	18.2
10	1	3	4	5	9	14	18	22.2
11	3	5	8	10	11	21	29	27.6
12	4	4	8	12	9	21	29	27.6
13	3	3	6	8	10	18	24	25.0
14	3	2	5	10	7	17	22	22.7
15	1	3	4	6	5	11	15	26.7
16	3	3	6	6	11	17	23	26.1
17	3	2	5	9	7	16	21	23.8
19	2	3	5	7	9	16	21	23.8
	46	49	95	142	152	294	389	24.4
18	0	0	0	8	11	19	19	0

One couple did not produce any eggs; one couple produced only green offspring (Container 18). The latter was excluded from the calculation, assuming that one of the parents was not *yg*, but *gg*.

Table 2. Average percentage of yellow offspring from six containers with pairs of one supposedly heterozygous (*yg*) green parent and one homozygous (*yy*) yellow parent

Container	Yellow ♀	Yellow ♂	Yellow total	Green ♀	Green ♂	Green total	Total	% yellow
1	5	4	9	6	5	11	20	45.0
2	4	6	10	4	8	12	22	45.5
3	6	8	14	6	7	13	27	51.9
4	6	5	11	7	6	13	24	45.8
5	8	4	12	7	6	13	25	48.0
6	6	5	11	8	7	15	26	42.3
	35	32	67	38	39	77	144	46.5

In Containers 1-3 the female was yellow; in the other three the male was yellow.

last 30 yr (see recent review in Henry et al. 2013), our understanding of the variability of diapause coloration in *Chrysoperla* has changed significantly. What had in the past been interpreted as intraspecific variability may instead be the presence of guilds of reproductively isolated, often sympatric cryptic species.

Some of the cryptic species in the *carnea*-group change color in winter, while others do not. Approximately half of the species change (Table 3), including the following three most important species of agricultural landscapes in temperate climates: *C. plorabunda* in North America, *Chrysoperla nipponensis* (Okamoto) in China and Japan, and *C. carnea* s. str. in Europe and western Asia. Some species may change color more quickly and completely in colder climates than in warmer regions. Tauber et al. (1970) documented wide variation in the intensity of color change depending on the life stage and speed of the transition from long days to short days.

In general (Table 3), we can state that species with an affinity for evergreen foliage or coniferous trees do not change color in fall and winter. Conifer-associated permanently green *carnea*-group species include

North American *C. downesi*, *C. calocedrii*, and *C. "downesi-2,"* as well as Eurasian *C. mediterranea* and *C. "downesi-Kyrgyzstan."* However, winter color change is not necessarily found in all species associated with deciduous vegetation or agricultural environments, for example, *C. adamsi* and *C. johnsoni* from North America and *C. lucasina* (Lacroix) and *C. "adamsi-Kyrgyzstan"* from Eurasia remain green permanently, despite their preference for deciduous habitats. *C. rufilabris*, the only chrysoperlan species outside the *carnea*-group that is known to exhibit seasonal color dimorphism, conforms to the rule that color change is most prevalent in species that occupy deciduous vegetation.

Discussion

Adaptive Significance of Color Variability and Color Change. MacLeod (1967) noted that lacewings of the genus *Chrysoperla* in deciduous forests changed color in winter, whereas those in evergreen and coniferous forests remained green. He concluded that always matching the color of the vegetation was an

Table 3. Diapause coloration and habitat preferences of song-identified species of the *carnea*-group

<i>Chrysoperla</i> species	Change?	Diapause color	Habitat preferences
<i>C. plorabunda</i>	Yes	Reddish brown	Fields, herbs, bushes, trees
<i>C. adamsi</i>	No	Green	Mixed woodlands, bushes
<i>C. johnsoni</i>	No	Green	Mixed woodlands, bushes
<i>C. johnsoni</i> "mohave"	No	Yellowish green w/red	Mixed woodlands, bushes
<i>C. downesi</i>	No	Dark green	Coniferous forest
<i>C. "downesi-2"</i>	No	Green	Coniferous forest
<i>C. downesi</i> "mohave"	No	Yellowish green w/red	Mixed woodlands, bushes
<i>C. calocedrii</i>	No/slight	Dark green w/brown	Coniferous forest
<i>C. heidarii</i>	Yes	Yellowish or reddish brown	Fields, herbs, bushes, trees
<i>C. "adamsi-Kyrg"</i>	No	Green	Mixed woodlands, bushes
<i>C. "downesi-Kyrg"</i>	No	Dark green	Coniferous forest
<i>C. "carnea-Kyrg"</i>	Yes	Yellowish or reddish brown	Fields, herbs, bushes, trees
<i>C. zastrovi zastrovi</i>	Yes	Yellowish green w/purple	Fields, low herbs, bushes
<i>C. zastrovi sillemi</i>	Yes	Yellowish green w/purple	Fields, low herbs, bushes
<i>C. carnea</i>	Yes	Reddish brown w/purple	Fields, herbs, bushes, trees
<i>C. pallida</i>	Yes	Yellowish brown	Deciduous forest
<i>C. agilis</i>	Yes	Yellowish or reddish brown	Fields, herbs, bushes, trees
<i>C. lucasina</i>	No	Green	Fields, herbs, bushes, trees
<i>C. mediterranea</i>	No/slight	Dark green w/brown	Coniferous forest
<i>C. nipponensis</i>	Yes	Reddish brown	Fields, herbs, bushes, trees
<i>C. "nipponensis-B"</i>	Yes	Yellowish or reddish brown	Fields, herbs, bushes, trees

Kyrg is contraction of Kyrgyzstan (Asia); mohave is a distinct ecotype that has evolved convergently in both *C. johnsoni* and *C. downesi*. Informal names of distinct but as yet undescribed species are shown without italics and within quotation marks.

adaptation for avoiding detection and consumption by predators. The same can be assumed for other color changes or color variation in the genus *Chrysoperla*.

We can only speculate on the adaptive significance of an obligatory ontogenetic color change. *C. congrua* always emerges from the cocoon as a whitish-yellow adult, but after several days turns green. Because acquisition of the green color coincides with sexual maturation and reproduction, Winterton (1999) proposed that color might serve as a signal of sexual receptivity, preventing wasteful courtship of immature individuals by mature ones. However, *Chrysoperla* males and females show no evidence of using visual cues during courtship (Henry 1979). A more likely explanation for color change is enhancement of crypsis (Duelli 1992). *C. congrua* is abundant in African savannah habitats, where the larvae feed on sternorrhynchan hemipteran prey on lush green grasses during the rainy season, before they pupate. After the rainy season, the grass turns light yellowish-brown and the surrounding vegetation dries out. With the grass turning yellow, the hemipterans that had produced honeydew either emigrate or die. That is the time when the adults of *C. congrua* emerge from the cocoons. The yellowish adult lacewings stay in the dry vegetation until the ovaries of the females are mature. In search of oviposition sites, the females of all lacewing species investigated for their searching behavior are attracted to the scent of honeydew from hemipteran insects (e.g., Hagen et al. 1976; Duelli 1984, 2001). Assuming that *C. congrua* does the same, the females will have to search for green grass where the food of their future larval offspring can be found. For that phase in life, the adults turn green to afford protection from visually orienting predators. Here, it is worth noting that ontogenetic color change very similar to that in *C. congrua* has been observed in Indian populations of a nonchrysoperlan tropical lacewing, *Plesiochrysa lacciperda* (Kimmins) (P. D., unpublished data). However, its adaptive value in *P. lacciperda*, if any, is unknown.

Cryptic coloration as a protection against diurnal predators can also be postulated for the persistence of the color genotype yellow of *C. comanche* in drier regions of southern California. Blending in with dry vegetation is an option with high adaptive value during much of the year there. Other instances of discrete color forms in Chrysopidae support the notion that these genetic polymorphisms have adaptive value. For example, a "yellow" variant among green adults has been found in *Pseudomallada clathratus* (Schneider), initially on the stony Mediterranean island of Malta (Duelli 1992), but more recently also in seasonally dry habitats in southern Greece (P. D., unpublished data). Laboratory experiments showed that the yellow color was caused by an autosomal recessive allele (Duelli 1992), as in *C. comanche*. A yellow individual was also identified among the progeny of a field-collected green *Chrysopa oculata* Say female in western North America (Tauber et al. 1976). This was shown to be a sex-linked recessive mutation and not an allele normally present in field populations.

Unlike the mutant blue of Tauber and Tauber (1971), which was observed only in a laboratory culture, our mutant yellow for *C. comanche* has been found in nature in two populations in southern California and in several specimens. At the time of collection, they were mistaken for *C. downesi* "mohave," or diapausing adults of other species in the *carnea*-group. In contrast to African *C. congrua*, but similar to *P. clathratus*, the genotype yellow of *C. comanche* keeps its yellow color for the entire adult life.

Diapause Induction, Color Change, and Other Seasonal Effects. In *C. carnea* s. lat. of central Europe, Honek (1973) observed in the field that color change develops in September or early October, ≈ 1 mo after induction of reproductive diapause in August. Reproductive diapause ends in December or January, independently of the light or temperature regimen, but most adults retain their brownish coloration awhile. In comparison, color change in North American *C. plorabunda* (synonymous with *C. carnea* s. l. before the 1990s; see Tjeder 1960) begins as little as 2 wk after diapause induction (P. D., unpublished data). Reproductive diapause ends in January, but diapause coloration remains in effect until mean temperature rises above 4°C (Tauber and Tauber 1973b). Thus, reddish specimens brought into the laboratory in February or March will nevertheless copulate and produce eggs, becoming green again in about a week.

The effect on diapause of almost constant nighttime illumination in and around cities and villages is not known, but constant light is likely to weaken diapause induction and color change. Many eggs will be deposited too late in the season to allow all instars to complete development before the first killing frost occurs.

There is some evidence that temperature is much more important for color change than for initiation, intensity, and termination of reproductive diapause (Tauber et al. 1970). However, all published accounts on diapause coloration in field populations from both North America and Eurasia, for example, on the percentage of individuals remaining green in winter (Tauber and Tauber 1972, Honek 1973, Honek and Hodek 1973), suffer from uncertain identification of what are now known to be distinct cryptic species (Duelli 2001). Consequently, no general conclusions can be drawn from earlier experiments on the influence of temperature and light regimen on diapause coloration.

The change of diapause coloration in *C. rufilabris* of North America illustrates the adaptive significance of color change in temperate climates dominated by deciduous vegetation. *C. rufilabris*, one of only two members of the *pudica*-group found mainly in temperate regions, changes color in late fall and winter and prefers deciduous vegetation. The other temperate-zone species in the group is *Chrysoperla harrisi* (Fitch), which lives on conifers and remains dark green all year, consistent with the crypsis hypothesis. A third primarily subtropical and tropical member of the *pudica*-group, *Chrysoperla externa* (Hagen), has been shown to enter winter diapause at higher latitudes in South America, but it apparently does not change

color (Albuquerque et al. 1994, 2001). The remaining 12 species of the *pudica*-group tend to be limited to tropical, subtropical, or sclerophyll-dominated Mediterranean climates, where evergreen vegetation prevails; none exhibits diapause-related color change. Thus, either the possibility to change color in synchrony with vegetation evolved independently in the two *Chrysoperla* species-groups, or it is an ancestral trait of the genus *Chrysoperla* that has been lost in many species that live or overwinter in evergreen forests.

Chrysoperla green lacewings are very rare among insects in their capacity to change color dramatically during a single individual's adult lifespan, that is, without requiring a transitional molt. It is far more usual for hues and color patterns to be fixed in the cuticle shortly after or within several days of the pupal-adult molt. However, a few species of Pentatomidae (Hemiptera), notably in the genera *Thyanta* Stål and *Nezara* Amyot & Serville, also change color with the seasons (McPherson 1977, Musolin 2012). Like *Chrysoperla*, these stink bugs overwinter as adults and individuals respond to long days versus short days by gradually turning green or brown, respectively. The mechanism in *Nezara viridula* (L.) involves phase changes in the pigment erythropterin, located in the epidermis (Harris et al. 1984). It is an intriguing notion that a similar mechanism might also be responsible for seasonal color change in *Chrysoperla* green lacewings.

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