

CHRYSOPERLA MOHAVE (BANKS) (NEUROPTERA:
CHRYSOPIDAE): TWO FAMILIAR SPECIES IN AN
UNEXPECTED DISGUISE

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ABSTRACT

The vibrational courtship song of *Chrysoperla mohave* (Banks) from several widely separated sites in California is described and compared to *C. downesi* (Smith) and to a *C. mohave*-like population of the recently described species, *C. johnsoni* Henry, Wells, and Pupedis. Unexpectedly, *C. mohave* is shown to have a song very much like that of *C. downesi*, in contrast to the very different song of *mohave*-like *C. johnsoni*. Yet the *C. downesi* and *C. johnsoni* versions of "*C. mohave*" are physically indistinguishable. Therefore, *C. mohave* is not a monophyletic taxon, but instead it is a color morph that has arisen independently at least twice in separate lineages of *Chrysoperla*. Both *C. downesi* and *C. johnsoni* are thus highly variable species, encompassing populations that range from solid dark green or bright green with no markings to light yellowish-green with tergal spotting and dark crossveins. It is argued that *C. downesi* should be taken from synonymy with *C. carnea* (Stephens) and recognized as a valid biological species or species complex, defined by a unique type of courtship song.

Key Words: systematics, song, sibling species, courtship, reproductive isolation

My interest in green lacewings began in the fall of 1968. The preceding year, as a Junior in college, I had enrolled in an exciting undergraduate course on the biology of insects, taught by Professor Frank M. Carpenter. Carpenter had been approachable and encouraging, so I asked him to support an undergraduate honors thesis

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project in biology. He agreed to serve as my advisor, and suggested that I talk to his graduate student, Lee Miller, for some additional ideas. Miller was studying the structure and physiology of the unique ultrasound detector in the forewing of the common green lacewing, known then as *Chrysopa carnea* Stephens (Miller 1970). He proposed a trade: if I took over the care of his lacewing colonies, he would let me use his lacewing stocks and some of his laboratory space and equipment for my project. Before long, I was deeply involved in a study of courtship and mating behavior in this insect. By the end of the academic year, my undergraduate project was completed. It included the first description of the vibrational courtship songs that are now known to be typical of the lacewing genus *Chrysoperla*. Although years would pass before I returned to acoustical communication in insects, this study set the stage for all of my later research on songs, systematics and speciation.

In those days, the taxonomy of the common North American chrysopids seemed relatively straightforward. *Chrysoperla* (formerly *Chrysopa*) *carnea* was considered to be a widespread, holarctic species: Tjeder had recently synonymized nearctic *C. plorabunda* (Fitch) with palearctic *C. carnea*, unable to find consistent anatomical differences between the two (Tjeder 1960). Thereafter, it was assumed that the results of studies on American populations would apply equally to European or Asian populations—and vice versa. Thus, findings within local populations of *C. carnea sensu lato* were broadly generalized to the entire species in investigations of photoperiod and diapause (Honek and Hodek 1973, Sheldon and MacLeod 1974; Tauber and Tauber 1969, 1970), dispersal flight (Duelli 1980, 1981), defensive responses to bat sonar (Miller 1975), and resistance to common insecticides (Bartlett 1964, Plapp and Bull 1978). In addition, lacewings identified as *C. carnea* were shipped freely all over the world in commercial and government-sponsored programs of biological control (Jones and Ridgway 1976, Ridgway and Jones 1969, Tulisalo and Korpela 1973, Tulisalo and Tuovinen 1975, Zeleny 1965). However, those most familiar with the species were acutely aware that this unified view of *C. carnea* was a reflection more of ignorance than of cogent empirical data (Adams 1983, Bickley and MacLeod 1956, Bram and Bickley 1963; Adams, pers. comm.).

Recognition of taxonomic diversity within *C. carnea* of North America (= *C. plorabunda s. lat.*) actually began years earlier, with

the description of several species from local geographical areas that were later synonymized with or included as varieties of *C. plorabunda*. These have included *C. robertsonii* (Fitch), *C. californica* (Coquillet), *C. vegata* (Navás), *C. downesi* (Smith), and *C. mohave* (Banks), among others (Bickley and MacLeod 1956). Each was thought to be distinguishable from "true *C. plorabunda*" (or *C. carnea*) by different shades of green or by unique markings on the body and wings. Of these taxa, only *C. downesi* and *C. mohave* are commonly recognized and discussed today, although neither has official species status anymore (see below). Unfortunately, colors fade badly in lacewings no matter how they are preserved, so museum holotypes and paratypes have been of little use in resolving taxonomic questions that concern the closely related taxa of the *Chrysoperla carnea/plorabunda/downesi* complex. Even in living specimens, ground color and markings, setation, body size, wing shape, and venation have been shown to vary markedly within single presumed species across relatively small geographical areas (Tauber and Tauber 1986a; Tauber and Tauber 1975, 1981).

Increasing awareness of songs produced by *Chrysoperla* green lacewings has completely changed how we perceive species boundaries within the genus. These songs are vibrational tremulation signals, produced by rapid vertical oscillations of the insect's abdomen, and are transmitted between individuals through compliant substrates such as leaves, grass blades, or conifer needles (Henry 1979, 1980b, 1983a). No drumming is involved. Both sexes sing, and copulation depends upon a male and a female successfully establishing a duet in which each partner alternately produces the same song phrase. Because the songs of each partner must exactly match for this to happen, populations which differ acoustically from one another will be unable to interbreed and should be considered separate biological species. By this criterion, *C. carnea* is not holarctic and monolithic, but instead consists of distinctive complexes of several species each, in both Europe and North America (Henry 1983a). The *C. carnea* complex of Europe remains to be analyzed (Henry 1985b), but extensive song analysis and behavioral tests of North America's equivalent *C. plorabunda* complex have supported the recognition of three sibling, cryptic species within it: *C. plorabunda*, *C. adamsi* Henry, Wells, and Pupedis, and *C. johnsoni* Henry, Wells, and Pupedis (Henry 1993,

Henry, Wells, and Pupedis 1993, Wells and Henry 1992). These newly defined species are not clearly comparable to any of the species, subspecies, races or varieties of nearctic *Chrysoperla* previously described in the literature. A very different type of song characterizes *C. downesi*, strongly supporting its taxonomic validity and arguing against Garland's decision to synonymize it with *C. carnea/plorabunda* (Garland 1985). In fact, variation on the *C. downesi* song theme in different parts of North America suggests that this taxon may itself turn out to be a complex of cryptic biological species (Henry 1985a).

C. mohave is a special case. It appears to be closely allied to the three described species of the *C. plorabunda* complex, but it is uniquely characterized by numerous darkly pigmented crossveins and gradate veins in the wings (Banks 1938, Tauber and Tauber 1973). Also, the body is usually light yellowish-green, with more or less numerous brownish or reddish-brown spots on the thoracic and abdominal terga (Henry 1993). This suite of features is unknown in the *C. plorabunda* or *C. downesi* complex outside of the American southwest. Other traits that have been associated with some populations of *C. mohave* include semi-predaceous adult food habits and prey-mediated control of reproductive diapause (Tauber and Tauber 1981). Although it was finally reduced to the rank of a variety or ecotype of *C. plorabunda* (Tauber and Tauber 1973), it has enough distinctive traits to suggest that it might constitute a cohesive genetic unit. Certainly *C. mohave* is a candidate for careful analysis of courtship songs across its known geographical range.

The present study examines the songs of *C. mohave* collected from widely separated parts of California and identified as that species (or ecotype) by Phillip Adams, California State University, Fullerton. Results are compared to song data collected earlier on a special population of *mohave*-like insects from the San Francisco Bay area (Henry 1993), and to the songs of *C. downesi*, *C. plorabunda*, *C. adamsi* and *C. johnsoni*. The systematic status of *C. mohave* is then discussed and assessed, based on these comparisons.

MATERIALS AND METHODS

Collection and Rearing: Living adults of *C. mohave* were collected 20–28 September, 1987, from three relatively hot, dry sites in California, covering a north-south range of nearly 1000 km (Fig. 1). Those referred to as “Garberville” were found on the evening of 20 September in mixed stands of young Douglasfir and scrub live oak along a side street of Garberville, California, elevation ≈ 280 m, about 22 km southeast of the Humboldt Redwoods. “Bartlett” specimens were obtained 21 September near the transition from desert to forest, elevation ≈ 1000 m, in an open area of



Figure 1. Collecting sites in California of the “*C. mohave*” yellow-green color variant of *Chrysoperla johnsoni* and *C. downesi*. Claremont, marked with a triangle, is the type locale of *C. mohave* (Banks).

mixed Douglasfir and pine, along a dirt road from Route 20 to Bartlett Springs, California, ten km northeast of Clear Lake. "Forest Home" insects were taken 26–28 September in an open, diverse forest at the Forest Home Campground, California, elevation ≈ 1650 m, in the San Bernardino Mountains. Collecting data for other *mohave*-like lacewings, obtained in Strawberry Canyon, Berkeley, California and assigned to *C. johnsoni*, can be found in another paper (Henry 1993).

Adults of *C. downesi* were procured in September and October, 1977–1983, from a second-growth forest of red spruce and from a young, open stand of red pine at the Huyck Nature Preserve, Rensselaerville, New York, elevation ≈ 650 m, about 32 km southwest of Albany. Other specimens identified as *C. downesi* were collected in 1987 at various locations in western North America, including the Bartlett and Forest Home sites described above.

All insects were returned to Storrs, Connecticut for maintenance, rearing and song analysis. Sexes were kept apart and supplied with water and a WheatTM-based diet. In the laboratory, long day photoperiods (17:7 hr L:D) terminated reproductive diapause in field-collected individuals and brought on sexual receptivity and spontaneous singing after 1–6 weeks. Progeny of selected mated pairs were raised under short day conditions (10:14 hr L:D) using established methods (Henry 1979, 1983b, 1991). Upon eclosion, all adults were maintained under a long day photoperiod regime. This rearing protocol was designed to satisfy any obligatory diapause requirements of the insects (Nechols, Tauber, and Tauber 1987, Tauber and Tauber 1973b) and to facilitate rapid acquisition of sexual receptivity.

Analysis of Songs: At least five complete courtship songs (shortest repeated units or SRUs) of each presumed member of *C. mohave* from each locality were recorded on cassette tape and then digitized and analyzed with *MS-DOS*-based computer hardware and software, using methods described in previous papers (Henry 1979, 1980b, 1990; Henry and Johnson 1989, Henry and Wells 1990). Males and females were induced to sing by playing back previously recorded or artificially synthesized songs through a loudspeaker (Henry 1989). A similar protocol was applied to at least five SRUs of each individual of *C. downesi*. Comparisons to other species and populations used the results of analyses performed previously and tabulated in earlier papers.

The songs of *Chrysoperla* green lacewings consist of frequency-modulated volleys of abdominal vibration repeated at regular intervals. Some taxa, such as *C. plorabunda* and *C. adamsi*, are characterized by relatively simple songs, composed of single-volley SRUs repeated many times (Henry, Wells, and Pupedis 1993). Other species, such as *C. downesi* and *C. johnsoni*, produce more complex songs that consist of much longer, multisyllabic (multi-volley) SRUs and perhaps even two or more distinctly different types of volleys (Henry 1980a, Henry, Wells, and Pupedis 1993). The populations of *C. mohave* analyzed here have complex songs, very similar to those of *C. downesi*; I defined and measured ten song features, chosen for maximum compatibility with the song measurements published for other species (Table 1, Fig. 2). The following measurements were taken for each of the two types of volleys, long and short, found in these songs: (1) duration of each volley, (2) interval between the start of one volley and the start of the next, (3) frequency (pitch) of each volley, and (4) number of volleys per SRU. In addition, it was necessary to measure frequency (3, above) separately for beginning versus terminal short volleys in each SRU. Total length of the SRU (5) was also tabulated.

In total, comprehensive analyses were performed on the songs of 18 *C. mohave* individuals from California (13 from Garberville, 3 from Bartlett, and 2 from Forest Home). The sex ratio (male:female) of the total sample was 0.44. For *C. downesi* from New York State, the songs of 19 individuals were analyzed (sex ratio = 0.47). Comparisons were made to 31 additional *mohave*-like individuals of *C. johnsoni* from Strawberry Canyon, described in another paper (Henry 1993).

Temperature strongly influences song characteristics, and data must be treated in some way to compensate for this if they are collected at different temperatures. Fortunately, all measurements of *C. mohave* were taken within half a degree of 25°C. However, data for *C. downesi* were obtained over several years, at temperatures ranging from 19–31°C. Therefore, for that species, all individual means at different temperatures were transformed (normalized) to a standard temperature (25°C). This was done by regressing temperature against each song feature. When the temperature effect was significant ($P \leq 0.05$), as it was for most features, the slopes of the resulting regression equations were used to modify the original

Table 1. Means and standard errors of song features of *Chrysoperla downesi* (eastern U.S.A.) and *mohave*-like *C. downesi* (California). Unless otherwise noted, time is in milliseconds and frequency is in Hertz. Also shown are the results of a *T*-test to determine significant differences between the populations.

	<i>C. downesi</i> (N=19)	<i>C. "mohave"</i> (N=18)	<i>T</i> -Value	<i>P</i> -Value
Duration, long volleys	311.66 ±14.91	485.47 ±8.96	9.86	0.000
Interval, long volleys	633.50 ±10.23	675.63 ±16.52	2.19	0.035
Duration, short volleys	126.35 ±5.34	155.45 ±4.32	4.13	0.000
Interval, short volleys	290.88 ±5.81	241.88 ±7.50	-5.20	0.000
Frequency, long volleys	82.50 ±2.02	80.02 ±0.66	-1.44	0.163
Frequency, 1st short volleys	74.41 ±1.59	73.56 ±0.73	-0.56	0.583
Frequency, last short volleys	64.81 ±1.27	64.20 ±0.78	-0.44	0.664
Number of long volleys	4.52 ±0.21	5.75 ±0.28	3.54	0.001
Number of short volleys	13.36 ±0.99	23.90 ±1.26	6.52	0.000
Song Duration (total, in seconds)	6.23 ±0.28	9.66 ±0.52	5.91	0.000

values; otherwise, data were left unchanged. Calculations of basic statistics and Student's *T*-tests were then performed on the new data set of temperature-compensated and raw values. When appropriate, tabulation of the residuals from the linear regression analysis was used to predict the mean and standard error at 25°C for each song feature (Table 1).

I used the PC software package *CSS: Statistica 3.1* (StatSoft Inc., Tulsa, OK) for statistical analyses. Acquisition, display, tem-

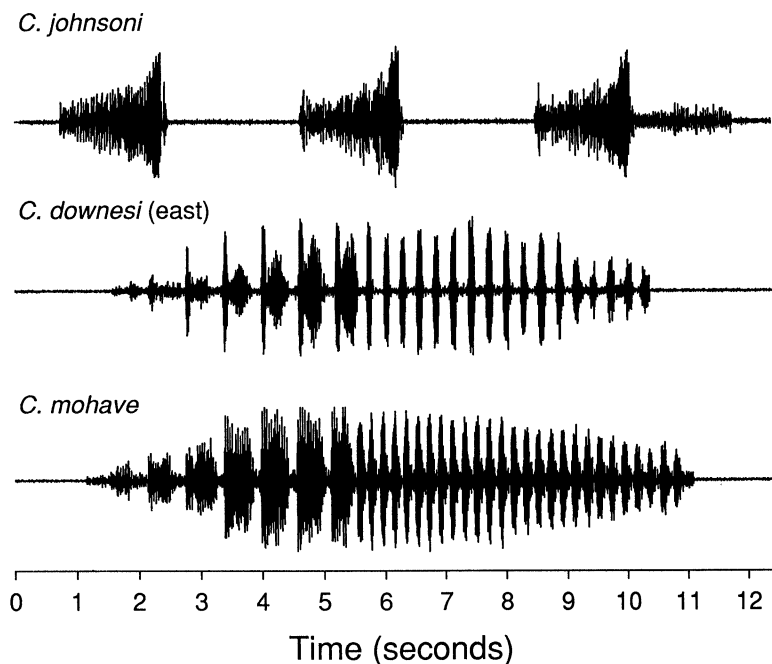


Figure 2. Digitized oscillographs of the shortest repeated unit (SRU) of the vibrational song of *mohave*-like *C. johnsoni* from Strawberry Canyon, California, dark green *C. downesi* from New York State, and *mohave*-like *C. downesi* from Garberville, California. All were recorded at 25°C.

poral and spectral analysis, and artificial synthesis of songs were executed using *Waterfall 3.18* and *Spike2 4.0* (Cambridge Electronic Design, Cambridge, U.K.) and *DADiSP 2.00B* (DSP Development Corp., Cambridge, MA). The graphs and other figures were produced in *SigmaPlot 5.0* (Jandel Scientific, Corte Madera, CA) and *CoreIDRAW 3.0* (Corel Systems Corp., Ottawa, Canada). All programs ran under *MS-DOS* on an 80286 computer.

Analysis of Morphology: All living, field-collected individuals of *C. mohave* were examined under a dissecting microscope, to identify external morphological features that might vary among geographical populations or between morphs. The genitalia of two preserved *C. mohave* males from Garberville and two more from

Forest Home were prepared for closer study by clearing the last few segments of the abdomen in hot 10% KOH for 15–30 min, as described by Bram and Bickley (1963). Sclerotized regions were enhanced by staining for two minutes in 5% Chlorazol Black E aqueous solution. The genitalic structures were then everted using a small pipette and placed in a drop of glycerin for examination under a compound microscope. These preparations were compared to those of eastern *C. downesi* and *mohave*-like *C. johnsoni* genitalia made earlier (Henry, Wells, and Pupedis 1993).

Voucher specimens, pinned or in 70% ethanol, have been deposited in the personal collection of Charles S. Henry or in the collection of the Connecticut State Museum of Natural History, the University of Connecticut, Storrs.

RESULTS

Oscillographs of the vibrational songs (SRUs) of a *mohave*-like *C. johnsoni* from Strawberry Canyon, a *C. downesi* from New York State, and a *C. mohave* from Garberville, California are shown in Fig. 2. Each exhibits the volley duration, interval, and amplitude structure typical of its population at 25°C. The songs of *C. downesi* and Garberville *C. mohave* are compared further in Fig. 3, which shows the frequency (pitch) structure of the songs as computer-generated sonographs. The figures establish that the song of *C. mohave* from sites outside of Strawberry Canyon is very similar to that of classic *C. downesi*, and bears no resemblance to the song of its closest look-alike, *C. johnsoni* from Strawberry Canyon. When the temperature-corrected means of each song feature were compared between *C. mohave* and *C. downesi*, the striking similarity of the two populations was confirmed. Even though the comparison was between populations on opposite sides of the continent, *T*-tests revealed only minor differences (Table 1). Basically, *C. mohave* has a lengthier song than *C. downesi*, distinguished by more and longer volleys of both kinds, and the interval between its short volleys is less. But without seeing the striking color differences that separate them, it would be easy to consider *C. mohave* and *C. downesi* a single, homogeneous species. In a parallel manner, *mohave*-like *C. johnsoni* from the Berkeley area is acoustically indistinguishable from other, more typically pigmented *C. johnsoni* from the Pacific Northwest, central and southern California, and southwestern Arizona (Henry 1993). Its song is

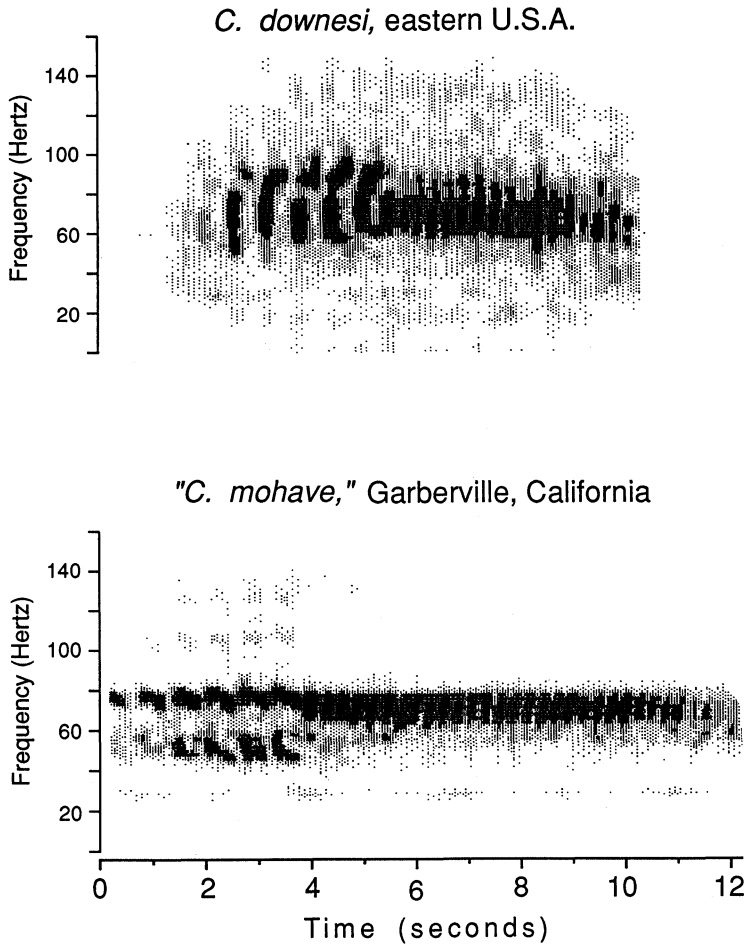


Figure 3. Computer-generated sonographs of the SRU of typical dark green *C. downesi* from New York State and *mohave*-like *C. downesi* from Garberville, California, at 25°C. The sonograph shows frequency (tonal or pitch) changes with time, for the duration of each song.

so different from that of *C. mohave/downesi* that it is not clear how to begin any comparison. Two other sibling species, *C. plorabunda* (*sensu stricto*) and *C. adamsi*, were not considered further in this study, because neither exhibits *mohave*-type morphology. Also, they are even less similar to *C. mohave/downesi* in the structure of their songs than is *C. johnsoni* (Henry 1993).

Externally, all *C. mohave* featured some degree of yellowish ground color, tergal spotting, and darkening of crossveins. So also did all individuals of *mohave*-like *C. johnsoni* from Strawberry Canyon, and in fact the latter could not be distinguished from the former using external morphology. More detailed studies of the male genitalia of several specimens from each taxon failed to reveal any uniquely different character states that could be of systematic use.

DISCUSSION

The results clearly show that *C. mohave*, collected over a wide geographical range in California, shares its song with *C. downesi* and is almost certainly a member of that species. However, earlier results just as emphatically placed similarly defined "*C. mohave*" in the new species *C. johnsoni*, again based on song structure (Henry 1993). Yet there is little resemblance between *C. downesi* and *C. johnsoni* in any other way: not only are their songs completely dissimilar, but the former is typically a much deeper green color than the latter. Two conclusions emerge from this. Neither conclusion is new or original at first glance, but each demands an important revision in the way we should approach the systematics, ecology, population genetics, and general biology of *Chrysoperla* in the future.

First, *C. mohave* is not a valid clade, and therefore should not be recognized, even as a variety or ecotype. It is polyphyletic, having arisen in two independent (though very closely related) lineages. Of course, *C. mohave* even now has no official validity, having been synonymized with *C. carnea* (= *C. plorabunda* *s. lat.*) some years ago (Tauber and Tauber 1973). However, it continues to figure in detailed models of nutritional and photoperiodic control of seasonal diapause, evolution of seasonal adaptations and life history traits, geographic polymorphism in ecophysiological responses, and sympatric speciation (Tauber and Tauber 1982,

1987, 1989; Tauber and Tauber 1973a). Without sure knowledge of the species affiliation of the particular "mohave" being investigated, even the most careful, elegant experiments will generate misleading or meaningless results. Thus, much of the Taubers' work on Strawberry Canyon *C. mohave* probably applies to *C. johnsoni*, in the *C. plorabunda* species complex, but is not at all applicable to other California populations of *C. mohave* belonging to the *C. downesi* complex. Nor is it certain that *C. mohave* collected at any given site is the same entity from year to year or even from individual to individual: *Chrysoperla* spp. are renowned for their dispersal capabilities (Duelli 1980), and several different species are often sympatric or syntopic at western North American sites (Henry 1991). Every field-collected individual must be placed in its correct species, based on courtship song, before any other work can be done.

The second conclusion is that acoustically defined species such as *C. johnsoni* and *C. downesi* are not necessarily homogeneous in their external appearance or biology. Again, the polymorphic nature of several species within *Chrysoperla* has already been recognized and described, but that was when many different forms were still included within a monolithic, holarctic *C. carnea* (Tauber and Tauber 1986b) and *C. downesi* was defined by color alone (Tauber and Tauber 1981). It is now known that *C. johnsoni*, formerly considered part of *C. plorabunda* s. lat., encompasses populations whose colors vary from light yellowish-green to bright green, some of which remain green in winter diapause and others of which turn brown while hibernating or aestivating (Henry 1993). More surprisingly, the present study shows that *C. downesi* is also extremely variable in color. It is no longer acceptable to assign all dark green, nearctic *Chrysoperla* with *carnea*-type male genitalia to *C. downesi*. In fact, some are among the yellowest populations yet encountered in the genus.

Throughout this paper, I have assumed that *C. downesi* is a valid species, even though it is presently in synonymy with *C. carnea*—and therefore, presumably, with some unspecifiable member of the *C. plorabunda* species complex. Support for its validity comes from the unique structure of its courtship song (Henry 1980a), which is so different from the songs of the three species in the *C. plorabunda* complex. The *C. downesi* song varies regionally, but is always recognizable in populations across the entire

width and breadth of the North American continent. Based on what we know of the songs of hybrids produced between eastern *C. downesi* and *C. plorabunda* in the laboratory (Henry 1985b), *C. downesi* seems not to hybridize with other species in nature: individuals with hybrid songs have not been found in the field, in spite of extensive collecting. Thus, all evidence indicates that *C. downesi* is a monophyletic clade, and that it should have its species status reinstated. But as in *C. johnsoni*, distinctive color forms like "*C. mohave*" probably do not respect species boundaries within the *C. downesi* species complex. Instead, single biological species may show a wide range of color patterns and life-history traits in different regions, perhaps through adaptation to local conditions.

The reasons for the parallel evolution of *mohave*-like morphology in at least two lineages of lacewings are unknown. One can speculate that these morphs are restricted to dry areas with highly seasonal precipitation patterns, and that the yellow-green ground color and dark crossveins camouflage the insects against desiccated vegetation. Yet one of the driest regions collected, the Kofa Mountains of southwestern Arizona, supports a bright green population of *C. johnsoni* that remains green even during the winter (Henry 1993). Also, *mohave*-type individuals of *C. downesi* at the dry Bartlett Spring site coexist with typical dark green *C. downesi*, which seems contrary to the camouflage hypotheses (C.S.H., unpublished data). Clearly, much hard work remains to be done on the systematics and ecology of the *C. downesi* complex. Recognizing the true, biologically-defined species boundaries within this and the other sibling species complexes of *Chrysoperla* will greatly facilitate our understanding of all aspects of their biology and prevent potentially costly scientific mistakes.

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