Can What We Don't Know About Lacewing Systematics Hurt Us?

A Cautionary Tale About Mass Rearing and Release of *"Chrysoperla carnea"* (Neuroptera: Chrysopidae)

Charles S. Henry and Marta M. Wells

Predaceous green lacewings, family Chrysopidae, have a long history of use in the biological control of soft-bodied arthropod pests of field crops, vineyard grapes, fruit trees, and other important cultivated plants (Fitch 1856, Duelli 2001). Within this large neuropteran family, members of the genus *Chrysoperla* Steinmann have proven to be among the most effective larval predators of phytophagous arthropods (Lingren et al. 1968, Ridgway and Jones 1968).

Consequently, several species of the genus are grown by commercial North American, European, Australian, and Asian insectaries for mass release into agricultural ecosystems. Recently, the industry has expanded to include hundreds of such operations around the world (van Lenteren et al. 1997). Interest in the subject has even spawned a major book on lacewings in the crop environment (McEwen et al. 2001). Here, we explore the uncomfortable partnership that exists between systematics and economics in the *Chrysoperla* biocontrol industry. New data are presented that illustrate inattentiveness by some insectaries to important issues of taxonomy, conservation biology, and, ironically, self-interest. We then propose inexpensive, but critical solutions to these problems.

The *Chrysoperla carnea* Problem

Foremost among the species raised commercially for augmentative biological control is *"Chrysoperla carnea* (Stephens)." Although once considered a single species with a Holarctic distribution (Tjeder 1960), the recent trend among specialists in biological control is to consider it a species complex of uncertain makeup (Chang et al. 2000, Daane 2001). Morphological variation is simultaneously slight and inconsistent within this *"carnea* group," rendering taxonomic decisions very difficult. In fact, some years ago, the late Phil Adams, at that time the foremost lacewing systematist in North America, confided to one of us (CSH) that variation within the complex made no sense to him. For that reason, he always turned away outside requests to identify *C. carnea* "biotypes."

Fortunately, the many species masquerading as *"C. carnea"* can be distinguished by their vibrational songs—as long as living specimens are available. Before copulation, heterosexual pairs vibrate their abdomens, producing substrate-borne low frequency signals that the courting individuals exchange in precise, often lengthy duets.

The vibrational song of each species is unique, exhibiting little or no sexual dimorphism. Our previous work has shown that songs have a powerful reproductive isolating effect among species. In addition, forced interspecific hybridizations in the laboratory yield progeny
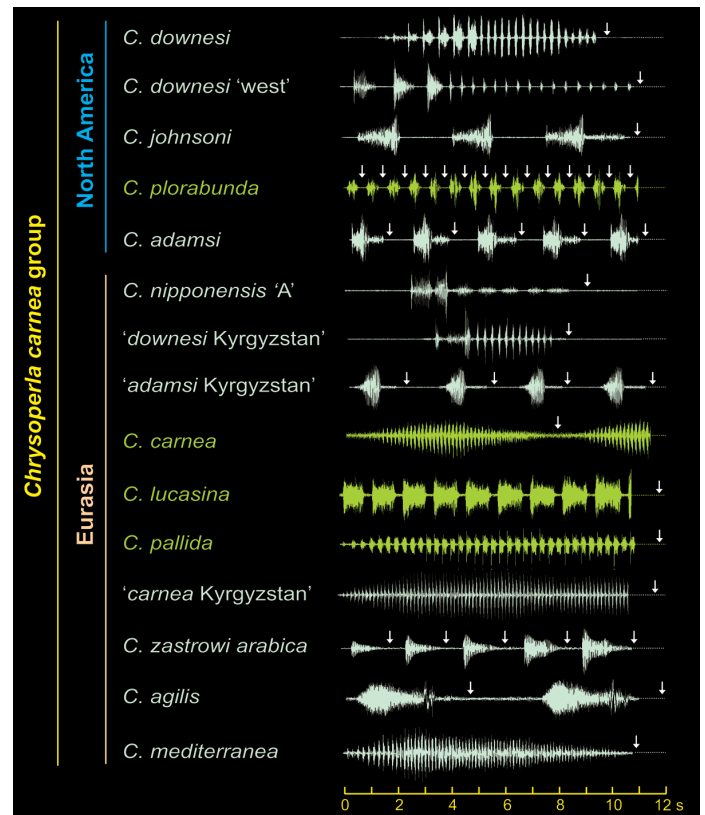

Fig. 1. A list of 15 cryptic "song species" of the *Chrysoperla carnea* group from North America and Eurasia. On the right is a twelve-second amplitude recording (oscillogram) of the typical male or female vibrational song of each taxon, showing the volley components and the points at which a partner inserts its song during a heterosexual duet (white arrows). The four species discussed in the text are shown in green.

whose hybrid songs are never found in the wild (Wells and Henry 1998). Thus, the "song types" constitute valid biological species, and more than 15 such species have been described to date within the original Holarctic range of *C. carnea* (Fig. 1). In some parts of the world, such as the Swiss Alps or the Sierra Nevada of California, one can collect as many as three distinct species of the *carnea* group from the same shrub or tree branch (Henry 2006). Figure 2 illustrates the striking song differences between two such species, *C. carnea* (Stephens) s. str. and *C. lucasina* (Lacroix), which occur intermixed in field-edge shrubbery across much of Europe.

On the negative side, identifying biological species within the *carnea* group requires a combination of living insects, electronic equipment, and special training. It is perhaps those obstacles that have dissuaded students of biological control from using any other name than *"C. carnea"* for various members of the *carnea* group around the world. Such a reaction is certainly understandable in Europe, where *C. carnea* was first described and coexists with several cryptic relatives. However, it cannot excuse continued use of *"C. carnea"* in North America (e.g. see Chang et al. 2000, Tauber et al. 2000; Dutton et al. 2003), because on that continent, the names *C. plorabunda* (Fitch), *C. adamsi* Henry et al. 1993, and *C. johnsoni* Henry 1993 officially replaced *C. carnea* years ago (Henry 1993a; Henry et al. 1993). Today, the taxonomic name *C. carnea* (Stephens) is correctly applied only to one of six species found in Eurasia (Henry et al. 2002). Yet very few papers, and none by North American authors, demonstrate awareness of these formal changes to the systematics of the *carnea* group (e.g., Naka et al. 2005). As we shall see shortly, "Ignorance is not bliss; what we do not know can indeed hurt us" (Schaefer 1998).

The Importance of Systematics

Viewed within the context of programs for biological control, it is more than an arcane academic exercise to get the systematics of the *carnea* group right. In an influential paper, it is correctly asserted that "...systematics forms the framework for virtually all biological control procedures" (Tauber et al. 2000, p. 27). However, in the same paper, the authors reject the need to recognize valid (but cryptic) species within the *carnea* group (p. 28). The U. S. government assumes that the systematics of a taxon is well known before it can be exempted—as are all families of Neuroptera—from rules governing international import and export of biological control agents (New 2001). Yet by ignoring existing systematic work within the *carnea* group, the principal advocates and practitioners of biological control have violated that assumption.

More significantly, we must pay attention to the reasons behind these assertions and regulations. Import/export rules, for example, specify accurate systematic knowledge of an organism because with such knowledge presumably comes an understanding of its basic biology, behavior, and ecology (Coulson et al. 1991). That kind of understanding also confers upon the bearer a considerable ability to predict the future (Schaefer 1998). Thus, in an ideal situation, one can be confident that an introduced organism will live where and eat what we expect it to, without outcompeting and eliminating native species or becoming an invasive element. For lacewings destined for mass release, those goals have immediate economic consequences as well: we want the insects to eat and control target pests, without dispersing too quickly from the chosen agricultural ecosystem.

It is certain that future economic benefits depend upon the application of accurate, detailed knowledge of *carnea*-group systematics. The results of several studies by laboratories in western Europe already support this assertion. For example, at a site in Switzerland studied by Peter Duelli and his colleagues (2002), three cryptic species are common: *C. carnea* (Fig. 2A), *C. pallida* Henry et al. 2002, and *C. lucasina* (Fig. 2B). The authors demonstrate that important,
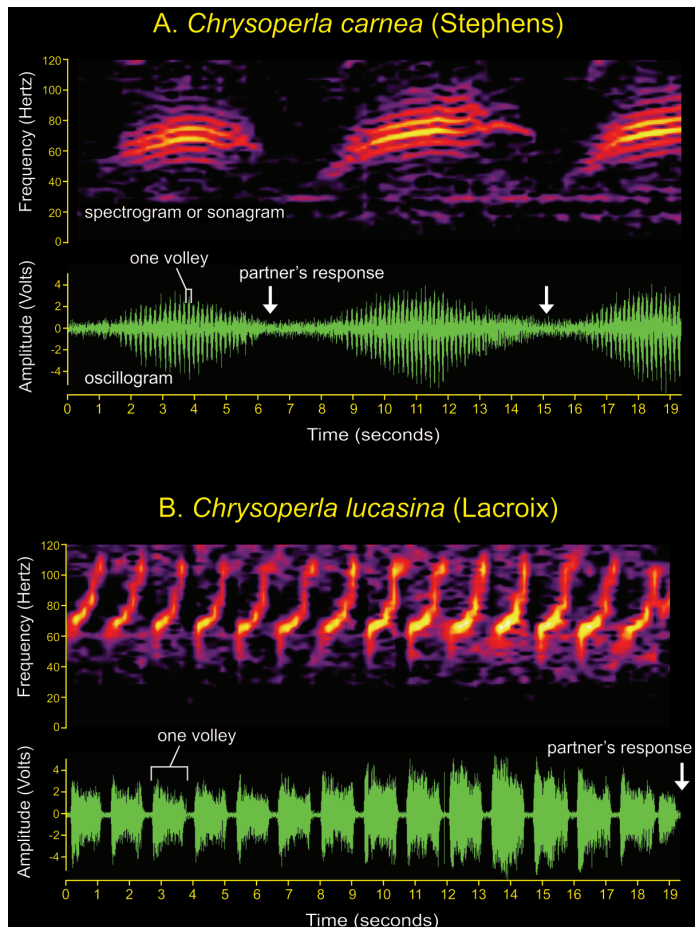

Fig. 2. Amplitude oscillograms (green) and frequency spectrograms (multicolored) of the songs of *C. carnea* (A) and *C. lucasina* (B), two cryptic species with overlapping distributions across much of Europe. Song units exchanged during duets are delimited by arrows. Note the obvious differences in volley duration, volley period, and carrier frequency between the songs of the two species.

repeatable differences exist among the three species with respect to habitat choice, flight activity, migratory behavior, and overwintering sites. Other studies document contrasting hibernation ecology among several cryptic species at a site near Angers, France (Thierry et al. 1995, 2002). Nor are these differences limited to European members of the complex. Although Nearctic species remain less studied in this respect, it is clear that the herb- and shrub-associated species *C. plorabunda* turns brown during winter diapause, while its tree-associated close relatives *C. adamsi, C. johnsoni,* and *C. downesi* (Smith) do not (Henry 1980; Henry et al. 1993). Furthermore, different types of seasonality, including voltinism and response to photoperiod, have often been found to be partitioned among distinct song species rather than among "biotypes" within a single species (Tauber et al. 1977; but see also Henry 1993b).

Lacewing biologists have long known about such variation in the *carnea* group, but have not understood it. Now we have the knowledge required to assign suites of physiological and ecological traits to individual species, based on song type. These recently revealed taxon-specific differences will influence the effectiveness of a particular control agent in a given agricultural context, thus requiring the user to choose wisely among the species in order to secure the best economic return. But are commercial insectaries making such wise decisions possible?

Sampling the Wares of Commercial Insectaries

Previous surveys comparing promised versus delivered goods ordered from major commercial insectaries have shown that the latter often ship the wrong quantity, life stage, and/or species of lacewings (Wang and Nordlund 1994, O'Neil et al. 1998). The most common error was substituting *Chrysoperla rufilabris* (Burmeister) for *"C. carnea,"* despite the fact that *C. rufilabris* does not even belong to the *carnea* species group.

We conducted a similar survey, but among fewer distributors and with somewhat different goals. Those goals were (1) to order and raise to adulthood typical shipments of *"C. carnea"* from all the North American companies that claimed to grow their own lacewing stocks of that "species;" (2) to determine the actual species received, using all available phenotypic traits including courtship song; and (3) to record and analyze several songs from every reared individual of each species belonging to the *carnea* group, in order to make acoustical comparisons between and among natural and insectary populations. Ultimately, we predicted that the song analyses would reveal song differences among populations of each species, perhaps caused by inbreeding, laboratory directional selection, interspecific hybridization, or geographic origin.

Methods. By contacting more than 40 North American retail outlets for *"C. carnea,"* we determined that only 4 grew their own insects. We then ordered once to several times over a period of six years from each of those four companies (Table 1, A–D), rearing the larvae and maintaining the adults using established protocols (Henry et al. 1996). Two additional shipments were received through different channels and in separate years from a fifth European company labeled E (Belgium). Those extra populations were sent unsolicited to one of us (CSH) for species identification.

At least 10 courtship songs from each of several adults *(N)* from each shipment were recorded and analyzed, using methods described previously (Henry et al. 1996). Song phenotype unambiguously assigned each lacewing to a known species. Population sizes <10 (Table 1) reflected inherently high levels of mortality in the stocks received, rather than inadequate care.

We performed acoustical analyses on the songs of the most prevalent species in the shipments, *C. plorabunda* and *C. lucasina.* For *C. plorabunda,* five features of each simple, single-volley song were measured (Fig. 3): the duration of each volley, the volley period (from the start of one volley to the start of the next), and the carrier (fundamental) frequency at the start, middle, and end of each volley. For *C. lucasina,* the duration of each multivolley song was also measured, because in *C. lucasina,* it is the multivolley sequence rather than the single volley that serves as the unit of exchange or "shortest repeated unit" (SRU) between dueting individuals (Figs. 1, 2B; arrows show dueting partner's response). Analyses of variance (ANOVAs) were performed on individual averages using population (i.e. field and various insectary shipments) as the independent variable (Tables 1 and 2). Principal components analyses (PCAs), with factors extracted from the five or six measured song features, were used to summarize and visualize the song differences among the different populations of *C. plorabunda* and *C. lucasina* (Fig. 4). All statistical analyses were calculated using *Statistica* version 6.1 (StatSoft 2003).

Results. Insectaries A, B, D, and E sent shipments made up entirely or partly of *C. plorabunda* (Table 1; Fig. 3). Receipt of *C. plorabunda* in two separate shipments from Belgium a year apart (E) was a surprise because *C. plorabunda* is a strictly North American species. Insectary C shipped only *C. rufilabris,* which had been correctly labeled by the growers. Insectary D advertized mixed stock specified as *"C. carnea* plus *C. rufilabris."* That insectary's shipment from Arizona was dominated by *C. rufilabris;* however, its two shipments from Texas in June 2000 and April 2006 consisted entirely of *C. lucasina,* a species of the *carnea* group normally found only in Europe and northern Africa (Fig. 2B). All lacewing stocks seemed healthy and vigorous except those received from D (both locations), which were characterized by high mortality of first-instars and abnormal spinning behavior of prepupae.

There were no statistically significant differences among insectary populations A–E for any of the five measured song features of *C. plorabunda* (Table 1). When comparisons were extended to include a larger transcontinental population of field-collected individuals, significant differences became detectable for measures of volley period and initial volley frequency, but only between the field population and the "A" insectary population from California. Even those differences were very small, as demonstrated by the PCA plot (Fig.

Table 1. Values at 25 ± 1°C of five song features of populations of *Chrysoperla plorabunda.* **First row: North American field-collected from the Pacific Northwest, central California, and Connecticut. Other rows: raised from eggs or larvae shipped as** *"C. carnea"* **by different insectaries, specified by capital letters A–E. Each value is the mean of the means of** *N* **individuals in the population, ± one standard deviation.**

	Frequency of volleys, Hz			Time measures of volleys, ms	
	Start	Middle	End	Duration	Period
Field, North America	87.86[a]	58.69	31.13	629.00	1207.68[b]
(N = 71) 1985–2004	± 5.96	± 3.89	± 2.99	± 75.70	± 118.63
A. California 1	83.30[a]	57.58	31.15	615.15	1110.40[b]
(N = 8, 20) vi-2003, vi-2005	± 3.51	± 3.66	± 3.12	± 56.60	± 129.96
B. New Mexico	86.75	59.30	31.15	657.05	1131.41
(N = 16) vi-2005	± 3.64	± 2.80	± 3.79	± 67.02	± 118.31
B. California 2	85.68	59.08	30.17	656.37	1106.07
(N = 9) vi-2005	± 2.37	± 3.52	± 3.81	± 65.55	± 87.17
C. California 3	*Chrysoperla rufilabris (pudica* group, North America)				
(N = 15) vi-2005					
D. Arizona (N = 1) [3]	81.66	56.89	31.73	695.80	1233.29
vi-2000					
D. Texas	*Chrysoperla lucasina* (see Table 2)				
(N = 2, 23) vi-2000, iv-2006					
E. Belgium	84.69	58.45	31.40	597.41	1173.03
(N = 8) vi-2004, vi-2005	± 2.01	± 1.55	± 1.82	± 54.06	± 143.67

[a] ANOVA: $F = 3.90$, $df = 127$, $P = 0.0042$
[b] ANOVA: $F = 3.62$, $df = 139$, $P = 0.0025$
[3] Only one individual of *C. plorabunda* was reared successfully; the rest were *C. rufilabris.*
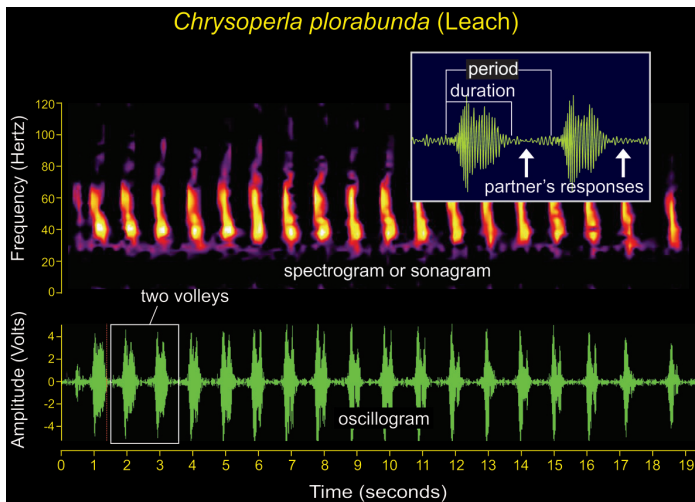
Fig. 3. Amplitude oscillograms (green) and frequency spectrograms (multicolored) of the songs of *C. plorabunda* from North America. A detail of two volleys is provided, showing volley duration, volley period, and song units exchanged during duets. Note the many differences between this song and those of *C. carnea* and *C. lucasina* in Fig. 2.

4A). In that plot, none of the populations occupied an isolated position in "factor space," and variation of the field population encompassed that of all insectary populations combined.

Insectary-reared individuals of *C. lucasina* from Texas differed significantly from field-collected European specimens in only two of the six measured components of their songs (Table 2). Even those differences were likely artifactual because of changes in methods of frequency analysis used over the years. PCA confirmed extensive overlap of the two populations (Fig. 4B).

Overview. The results of this simple study indicate that the major growers of *Chrysoperla* green lacewings in North America, and probably those in Europe as well (based on our single sample), remain unaware of the differences between the principal song species of the *carnea* group. As expected because of its broad distribution, the most usual North American species shipped as *"C. carnea"* is *C. plorabunda,* but occasionally *C. rufilabris* is substituted for *C. plorabunda* without notification. Our results also show that North American *C. plorabunda* has contaminated at least one insectary culture in Europe, and has been sold and distributed from there for more than a year. Similarly, the European species *C. lucasina* has taken over and dominated a commercial insectary population in North America for at least six years. Consequently, the potential exists for the permanent establishment in both global hemispheres

of nonnative members of the *carnea* group, largely because the biological control establishment has remained "blissfully ignorant" of lacewing systematics.

That this problem is not limited to Europe and North America is clear from recent east Asian studies. In Japan, for example, Taki et al. (2005) confirmed acoustically that the lacewing being raised by insectaries in Japan is *C. carnea* (Stephens), introduced from Germany in 1996 and, as of 2001, legally registered for use in pest control. This species has a song (Fig. 2A) that is very different from the songs of either of the two native Japanese species of the *carnea* group, called Type A and Type B *Chrysoperla nipponensis* (Okamoto). Addressing the same issue, Naka et al. (2005) warned of the ecological risks of releasing nonnative European *C. carnea* into natural ecosystems of Japan, where the two variants of *C. nipponensis* are currently established.

Acoustic analyses show that long-term culturing of *C. plorabunda* and *C. lucasina* for mass release has not apparently affected the song phenotype of either species in any measurable way. We anticipated that inbreeding might change certain features of the songs, or alternatively that the presence of a mixture of cryptic species in the source population could result in introgression of alien song elements into the songs of *C. plorabunda* or *C. lucasina* being shipped to customers. Perhaps stabilizing selection or fixation of all song-controlling alleles at the species level has prevented significant song changes from taking place, or, if two or more species were present originally, hybridization between them did not occur.

On the other hand, rearing practices might indeed be affecting viability of insectary-reared stocks, possibly because of inbreeding or other sources of reduced genetic variability. That could explain the high mortality noted in stocks shipped by company D. Alternatively, a disease organism could have infected those lacewings. Our results cannot confirm or reject either hypothesis.

Discussion and Conclusions

Globally distributed insect species are comparatively rare. This is probably because isolation by distance and other aspects of geography and environment act over time to subdivide the majority of widely distributed species into populations, ecotypes or subspecies. Sometimes, a "species" is found to be a complex of cryptic species. As has been true for the lacewings of the *carnea* group, it often takes a while for entomologists to identify existing behavioral, ecological and taxonomic structure within species previously thought to occupy more than one continent.

As outlined earlier, there are three good reasons for making an effort to recognize the cryptic species in the *carnea* group. The first is to maintain taxonomic accuracy: These species represent valid entities based on formal descriptions in the scientific literature.

Table 2. Values at 25 ± 1°C of six song features of populations of *Chrysoperla lucasina,* **a member of the** *carnea* **group native to Europe, northern Africa, and parts of the Middle East. First row: field-collected from the European subcontinent. Second row: raised from eggs or larvae shipped as** *"C. carnea"* **by a North American insectary, but identified by the authors as** *C. lucasina.* **Each value is the mean of the means of** *N* **individuals in the population, ± one standard deviation.**

	Frequency of volleys, Hertz			Time measures of volleys, ms		Time measures of SRUs
	Start	Middle	**End**	Duration	Period	**Duration** (s)
Field, Europe	57.83 ± 4.02	68.90[a] ± 4.14	92.21[b]± 6.81	1052.60	1431.40	15.00 ± 10.69
(N = 118) 1985–2004				±160.46	±232.68	
D. Texas	58.24 ± 3.83	77.80[a] ± 3.71	98.73[b] ± 4.23	1010.51	1369.46	15.04 ± 6.43
(N = 23) iv-2006				±88.49	±140.22	

[a]ANOVA: *F* = 91.74, *df* = 139, *P* = 0.0000
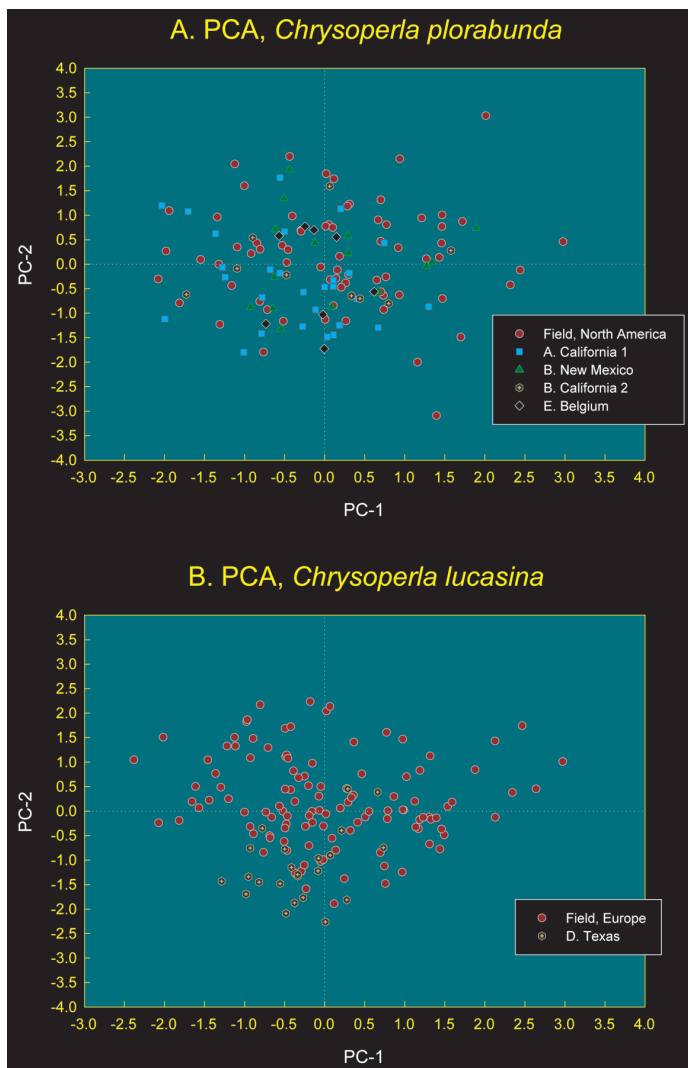[b]ANOVA: *F* = 19.53, *df* = 139, *P* = 0.0000

Fig. 4. Scatterplots of the first two factors of a principal components analysis (PCA) of multiple song features measured in different populations of *C. plorabunda* (A) and *C. lucasina* (B). Each data point represents a single individual, coded by population. The PCA for *C. plorabunda* (A) is based on five song features (see text) measured in five populations, four (A, B, B, E) from commercial insectaries and one (Field) comprising specimens collected across much of North America. The PCA for *C. lucasina* (B) is based on six features (see text) measured in two populations, one (D) from a commercial insectary in North America and one (Field) comprising specimens collected across much of Europe.

The second is to practice good, ethical environmental stewardship: We should not knowingly introduce nonnative species without a compelling rationale and appropriate governmental oversight as required by law.

Simply arguing that an alien lacewing species will be an effective biological control agent is not sufficient if there is a native species that will do the same job just as well. The future history of an introduced species is always uncertain, but common dangers include permanent establishment of the new species and the reduction or extirpation of closely related, native species occupying the same niche.

The third reason to recognize such species is to maximize the impact of each mass release when lacewings of the *carnea* group are used against agricultural pests. It makes good economic sense to select the best species for a particular application. In addition, aug-

mentative biological control can only be effective if endemic species are reared and released. As shown by Duelli and others (e.g., 2002), each cryptic species has a unique set of physiological and ecological characteristics that make it more valuable in some agricultural situations than in others. Only after it was understood that songs delimited species did the consistency of these ecological differences become evident and thus potentially useful for biocontrol.

Knowing species boundaries can lead not only to ecological insights, but also morphological ones. For example, awareness of the song differences segregating the various populations and species of 13- and 17-year periodical cicadas has led to greater understanding of a wide range of additional information about life history, brood membership, molecular markers, and physical appearance (Simon 1979, Williams and Simon 1995, Cooley et al. 2001). In *carnea*-group lacewings as well, subtle but consistent physical differences between the cryptic species have already been discovered, and more are likely to emerge now that we can focus morphological analyses on real biological units. Associating a unique suite of morphological characteristics with each song species is important, because it cannot be expected that nonspecialists will record and categorize the songs of lacewings in order to sort their specimens into species. Traits that have emerged as potentially useful taxonomic indicators within the *carnea* group include the shape of the apex of the male abdomen, the size and shape of the basal dilation of the pretarsal claw, the extent and color of markings on the head, prothorax and abdomen, and the size, distribution and color of hairs found on certain parts of the body (Henry et al. 2002, 2003).

Thanks to these discoveries, accurate morphological keys may eventually allow routine identification of the cryptic species of the *carnea* group, at least within restricted geographical regions (e.g., see Thierry et al. 1998). Until then, songs of living individuals must be observed and categorized before a species diagnosis can be made. However, the gross temporal patterning of the songs is so distinctive among species that it is not hard to learn the differences. Once learned, species identification is as easy as watching a few living individuals in a jar and counting volleys of abdominal vibration while using a stopwatch. In lieu of that, lacewings can be shipped for identification to anyone on a growing list of specialists trained in song recognition. Lacewing suppliers should adopt such procedures for ecological, socially responsible and profit-based reasons. Accurately placing the members of the *carnea* group in a contemporary systematic framework will take some extra effort, but the rewards include scientific integrity, responsible environmental stewardship, and better control of agricultural pests (happier customers).

Acknowledgments

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Charles Henry has been studying the vibrational songs of lacewings since his undergraduate days, when he undertook a senior project under the direction of the renowned insect paleontologist and neuropterist Frank M. Carpenter. His primary interest is in the role that lacewing vibrational signals have played in rapid -- and possibly sympatric -- speciation. He has been a faculty member in the EEB Department at the University of Connecticut since 1975. **Marta Wells** is a native of Colombia and a former Ph.D. student of Henry's. She and the first author have maintained an active research collaboration on many aspects of lacewing behavioral ecology, including mate choice, duetting responsiveness to modified mating signals, and intrasexual selection. She is currently an Instructor in EEB at Yale University and an honorary faculty member at the University of Connecticut.