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## Courtship song of the South African lacewing *Chrysoperla zastrowi* (Esben-Petersen) (Neuroptera: Chrysopidae): evidence for a trans-equatorial geographic range?

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### Abstract

The taxonomic status of green lacewings of the *Chrysoperla carnea* group from Africa and the Arabian Peninsula is investigated using comparative analyses of substrate-borne vibrational songs, adult morphology, larval morphology and ecology. For the first time, the courtship song of *C. zastrowi* (Esben-Petersen) is described and compared to the songs of other Eurasian taxa. This South African species is the only known representative of the *carnea* group from the Southern Hemisphere, yet both acoustically and morphologically it shows a striking resemblance to a previously undescribed song morph, *Cc5*, from the Arabian Peninsula. In fact, *Cc5* and *C. zastrowi* are so much alike that they are here considered to be a single species, characterized by single-volley songs of relatively long duration and carrier frequencies that lack complex harmonics and that sweep downward during the course of each volley. The two taxa also share several other traits, including nomadic habits, light green colour, identically shaped external genitalia in the male, small basal claw dilation, similar markings on the genae, clypeus and frons of the adult head, and similar larval head markings. However, the taxa are sufficiently different in song, morphology and geographic distribution that they are best considered distinct subspecies. *Cc5* is, therefore, formally described as *C. zastrowi arabica* n. subsp., leaving the nominate species as *C. zastrowi zastrowi*. We surmise that *C. zastrowi* likely originated from *Cc5* or a *Cc5*-like ancestor in the Northern Hemisphere, where all other members of the *carnea* group of cryptic species are presently found.

**Keywords:** Systematics, mating signal, cryptic species, Eurasia, morphology, biogeography, larvae, *arabica*

### Introduction

Without exception, the numerous cryptic song species of the *carnea* group of *Chrysoperla* Steinmann have large and extensively overlapping geographic distributions. For example,

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the common green lacewing *Chrysoperla plorabunda* (Fitch) is found across the entire continent of North America (Henry et al. 1993) and is broadly sympatric with *C. adamsi* Henry et al. 1993, *C. johnsoni* Henry 1993 and *C. downesi* (Smith). Similarly, in Eurasia *C. agilis* Henry et al. 2003 ranges from the Azores Islands eastward at least to northern Iran (Henry et al., 2003), co-occurring at many sites with *C. lucasina* (Lacroix), *C. carnea* (Stephens), *C. pallida* Henry et al. 2002 and *C. mediterranea* (Hölzel). Yet in spite of the extraordinary vagility of its members, the *carnea* group is confined almost completely to the Northern Hemisphere. The single exception to this pattern is *C. zastrowi* (Esben-Petersen). This unique but abundant Southern Hemisphere representative of the group is known principally from the Republic of South Africa (Tjeder 1966), but the species has also been reported from the South Atlantic islands of Ascension and St. Helena (Brooks 1994). Like most *carnea*-group lacewings it is nearly identical to *C. carnea* s. str., whose confusing taxonomic status has been untangled only recently (Henry et al. 2002).

Previous experience with the *carnea* group suggests that hidden taxonomic diversity often exists within morphologically indistinguishable populations (Wells and Henry 1998). Such diversity is parsed along boundaries of mating song phenotype instead of body form or structural features, and is based on the existence of strong premating isolation between populations that sing different substrate-borne vibrational songs (Henry 1994). Moreover, some morphologically different populations have been shown to share the same courtship song (Henry 1993b; Henry et al. 1999). Consequently, one must approach the entity “*C. zastrowi*” with caution, because it might include several cryptic but valid biological species within its morphological limits. Comparative song analysis of field-collected individuals (or their offspring) from populations identified by morphology and location as likely to be *C. zastrowi* is one way to test the hypothesis that the latter is indeed a single species.

Complicating the taxonomic landscape is the existence of an enigmatic taxon of the *carnea* group informally designated *Cc5* “generator” (Henry et al. 2001), found in and around the Arabian peninsula (Figure 1). Compared to other species in the Northern Hemisphere, this taxon has a unique mating song, but one that bears a striking similarity to songs recorded from South African *C. zastrowi*. In addition, specimens that show marked morphological similarity to *Cc5* have been collected across central Africa, even well south of the equator where *C. zastrowi* might exist (Figure 1). The geographic proximity of *Cc5* and its morphological analogues to the northern range limits of *C. zastrowi* suggests either (1) that *C. zastrowi* originated from *Cc5* or a *Cc5*-like ancestor, perhaps by dispersal followed by allopatric speciation, or (2) that the two taxa occupy the northern and southern portions of an unbroken distribution and so constitute a single trans-equatorial species. Again, we might be able to address these alternative hypotheses using comparative song analysis, coupled with careful assessment of morphological and ecological traits of adults and larvae.

Here, we describe the courtship and mating signals of *Cc5* and *C. zastrowi*, recorded from three populations of the former from disparate sites on the Arabian Peninsula and two adjacent populations of the latter from the Republic of South Africa. Analyses of geographic and sexual variation are presented for each taxon, and their songs are compared to assess whether the two taxa are simply close relatives or members of a single biological species. Other important phenotypic traits of *Cc5* and *C. zastrowi* are also characterized and compared, including adult and larval morphology, habitat and ecophysiology. Song features, morphology and ecology of *Cc5* and *C. zastrowi* are then compared and contrasted with those of other song species of the *carnea* group, particularly those with which the two taxa potentially co-occur in nature. In recognition of both the similarities and differences

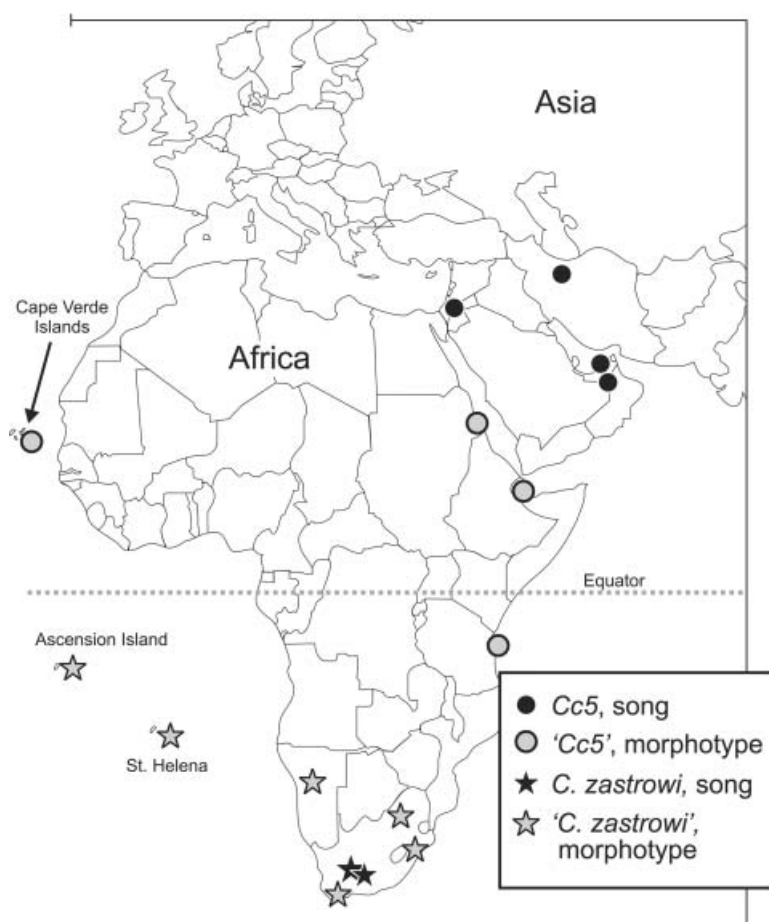


Figure 1. Map of Africa and Middle East showing collecting localities of *Cc5*, *C. zastrowi* and specimens closely resembling those taxa.

between the taxa, a new subspecies of *C. zastrowi* is described, *C. zastrowi arabica* n. subsp., for specimens currently known as *Cc5* from the Arabian Peninsula.

## Materials and methods

### *Collecting, rearing and identification of living lacewings*

Adults of *Cc5* and *C. zastrowi* were collected at three sites in the Middle East and two in the Republic of South Africa between 1993 and 2004 (Table I; Figure 1). An additional *Cc5* male was reared in 2002 from specimens collected in a pistachio field in Iran (Dr. Hossein Heydari). Field-collected and laboratory-reared individuals were shipped to Storrs, Connecticut, USA for maintenance and song analysis. Protocols are described fully in other papers (summarized in Henry et al. 1996, 1999).

Initially, living individuals were identified as *C. zastrowi* by geographic locality, because this species is the only described member of the *carnea* group known from sub-equatorial Africa. Subsequent recordings confirmed that all such specimens from South Africa shared

Table I. Collection sites of *Cc5* and *Chrysoperla zastrowi* used in song analyses and morphological studies 1993–2004.

Local site (with nearest city or region)	Country	Species	Altitude (m)	Latitude	Date
Dāmghān (on Pistachio)	Northern Iran	<i>Cc5</i>	1192	36°44'N	vi.2002
Eilat	Israel	<i>Cc5</i>	0–10	29°34'N	x.1993
Dubai	United Arab Emirates	<i>Cc5</i>	0–10	25°18'N	x.1994
Al Buraymi	Oman	<i>Cc5</i>	285	24°15'N	x.1994
Wolfdrif (Cedarberge)	Republic of South Africa	<i>C. zastrowi</i>	400	32°01'S	ii.2001; x.2004
Oudebaas Kraal Farm (Tankwa Karoo)	Republic of South Africa	<i>C. zastrowi</i>	400	32°24'S	ii.2001
* Tokar Delta	Sudan	" <i>Cc5</i> "	31	18°26'N	–
* Fogo Island	Republic of Cape Verde	" <i>Cc5</i> "	–	14°53'N	–
* Ambouli Oasis (Djibouti)	Djibouti	" <i>Cc5</i> "	0–10	11°36'N	–
* Zanzibar	Tanzania	" <i>Cc5</i> "	0–10	6°10'S	–
* Ascension Island	UK	" <i>C. zastrowi</i> "	–	7°57'S	–
* St. Helena	UK	" <i>C. zastrowi</i> "	–	15°57'S	–
* Namib-Naukluft (Karibib)	Namibia	" <i>C. zastrowi</i> "	1200	22°10'S	–
* Transkei Region; Calvinia; Johannesburg	Republic of South Africa	" <i>C. zastrowi</i> "	–	26°10'–32°05'S	–

Asterisks indicate additional localities from BMNH collections (16 males, 13 females) where song phenotypes of specimens are not known. They are provisionally assigned to one of the two taxa based on adult morphology.

a single song phenotype. Individuals of *Cc5* were separated from collections of unidentified living lacewings by noting the presence of a dueting response to playback of a specific, previously recorded song type from the Middle East (see below).

Once identified, we examined each individual for diagnostic morphological features that distinguished *Cc5* and *C. zastrowi* from one another and from other Eurasian song species in the *carnea* group. For all individuals, the ground colour of the body was recorded at the time of collection to determine the presence or absence in living insects of colour changes associated with ontogeny or seasonal diapause. Larval studies were limited to the progeny of individual adults confirmed to be *Cc5* or *C. zastrowi* by song analysis.

Several living adult and larval specimens of verified song phenotype from each locality were placed in 95% ethanol or frozen at minus 70–100°C, whereas others were deposited as vouchers in the collection of C. S. Henry, Storrs; the Connecticut State Museum of Natural History, Storrs (CSMNH); The Natural History Museum, London (BMNH); the collection of Peter Duelli, Zürich, Switzerland (PD); and the W. F. Barr Museum, Moscow, Idaho (WFBM).

Analysis of songs

Three to 36 complete courtship songs (=shortest repeated units or SRUs, the phrase exchanged between partners during a heterosexual duet) of each specimen of *Cc5* and *C. zastrowi* were recorded directly to computer disk at a sampling rate of 500 Hz and analyzed with hardware and software on a personal computer (see Henry et al. 1996; Henry and Wells 2004). Males and females in the laboratory were induced to sing by playing back to them pre-recorded songs of conspecifics, using methods described in earlier papers (Wells and Henry 1992, 1994).

The songs of *Chrysoperla* Steinmann green lacewings consist of volleys of low-frequency abdominal vibration repeated with a regular period. Each volley can also exhibit changes in its carrier (fundamental) frequency. Some taxa have relatively simple songs composed of single-volley SRUs repeated many times, whereas others produce complex songs consisting of much longer, multi-volley SRUs repeated only in response to other such songs. *Cc5* and *C. zastrowi* analyzed here have simple, repeating, single-volley songs in which the volley and the SRU are one and the same. Volleys are relatively long and change in frequency over their duration (see Figure 2A–C). Measurements were taken on six song features: carrier frequency at the start, middle and end of each volley (=SRU); the duration of each volley; the volley period (from the start of one volley to the start of the next); and the number of volleys per SRU (in *Cc5* and *C. zastrowi*, always one) (Table II; Figures 2 and 3).

Analyses were performed on the songs of 51 individuals of *Cc5* and 50 of *C. zastrowi*. All songs were recorded at  $25 \pm 1^\circ\text{C}$ . For *Cc5*, we made statistical comparisons between

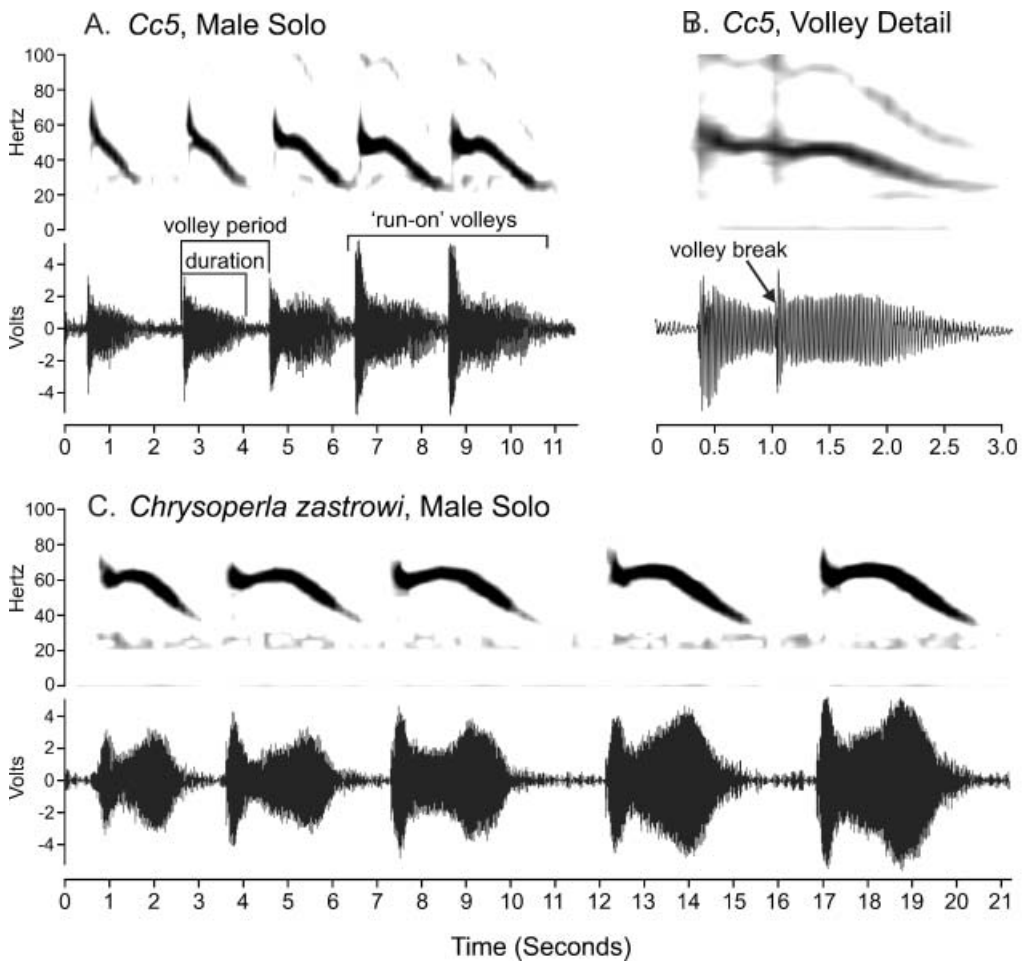


Figure 2. Oscillograms (volts on y-axis) and sonograms (Hertz on y-axis) of typical solo (non-dueting) vibrational songs. (A) *Cc5*, five volleys or shortest repeated units (SRUs); (B) *Cc5*, detail of a single volley/SRU; (C) *C. zastrowi*, five volleys or shortest repeated units (SRUs), drawn to same time scale as A. Song features discussed in the text are labeled.

Table II. Overall mean values at 25 ± 1°C of the song features of all *Cc5* and *C. zastrowi* collected from the three geographic areas of the Middle East.

	Frequency measures of volleys (Hz)			Time measures of volleys (ms)		Volleys/SRU
	Start	Middle	End	Duration	Period	
<i>Cc5</i> Israel ( <i>n</i> =33)	55.480 ± 2.863	42.897 ± 2.286	25.416 ± 1.769	2374.12*** ± 278.61	4325.96 ± 590.41	1
<i>Cc5</i> Oman/Dubai ( <i>n</i> =17)	55.396 ± 2.530	43.553 ± 2.409	23.956 ± 2.784	2023.04*** ± 163.80	4139.08 ± 558.02	1
<i>Cc5</i> N. Iran ( <i>n</i> =1)	56.104	45.173	27.338	2252.53	5066.52	1
<i>Cc5</i> males ( <i>n</i> =32)	55.258 ± 2.752	43.154 ± 2.200	24.143*** ± 2.093	2132.49*** ± 224.82	4190.04 ± 627.55	1
<i>Cc5</i> females ( <i>n</i> =19)	55.812 ± 2.654	43.171 ± 2.571	26.356*** ± 1.821	2460.56*** ± 283.43	4426.64 ± 488.02	1
<i>Cc5</i> all*** ( <i>n</i> =51)	55.464 ± 2.703	43.160 ± 2.320	24.967 ± 2.253	2254.71 ± 293.13	4278.18 ± 585.88	1
<i>C. zastrowi</i> males ( <i>n</i> =27)	66.287 ± 3.157	52.410 ± 2.834	32.118 ± 3.344	3855.49 ± 523.37	6960.69 ± 1035.51	1
<i>C. zastrowi</i> females ( <i>n</i> =23)	67.360 ± 2.191	51.705 ± 2.108	32.301 ± 2.389	4128.89 ± 670.67	7291.71 ± 1120.49	1
<i>C. zastrowi</i> all*** ( <i>n</i> =50)	66.681 ± 2.781	52.086 ± 2.526	32.202 ± 2.916	3981.25 ± 605.18	7116.07 ± 1077.85	1

Each value is the mean of the means of *n* individuals in the population subsample, ± 1 SD (standard deviation). Pairwise comparisons of Israel to Oman/Dubai *Cc5* individuals, males to females in each species, and *Cc5* to *C. zastrowi* were assessed for significant differences using *t*-tests for independent samples. Levels of significance are shown using asterisks: \**P* ≤ 0.05; \*\**P* ≤ 0.01; \*\*\**P* ≤ 0.001. SRU=shortest repeated unit exchanged between individuals while dueting, equivalent to the single volley in these two taxa.



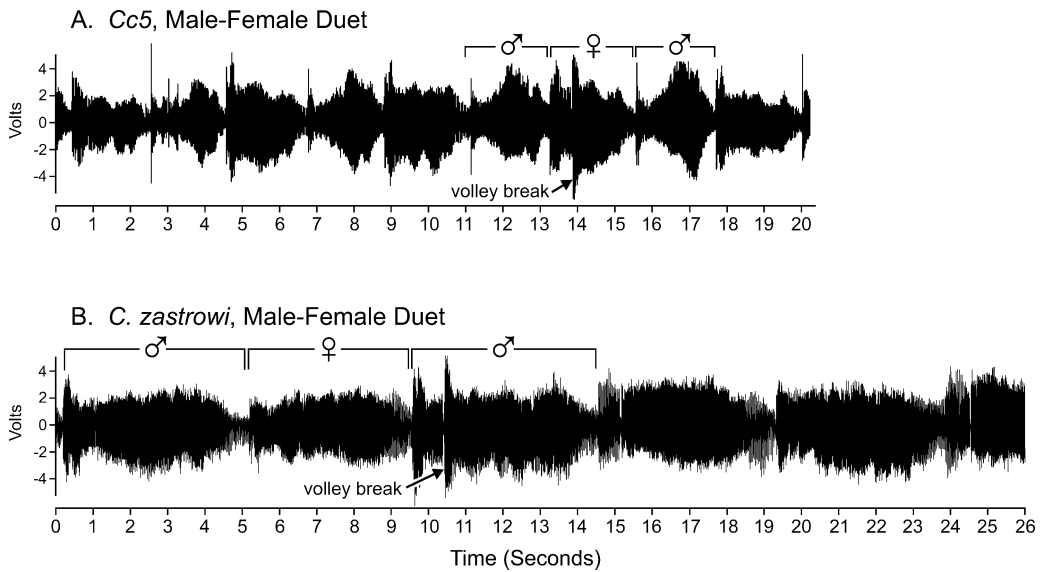


Figure 3. Oscillograms comparing typical heterosexual duets, drawn to the same time scale. (A) *Cc5*; (B) *C. zastrowi*. Note the presence of occasional transient volley breaks (arrows) in the songs of both taxa.

populations from the western and eastern edges of the Arabian peninsula, i.e. Israel versus Dubai/Oman, respectively (Figure 1). A northern population of *Cc5* was also identified near Tehran, Iran, but it was represented by just one singing male and, therefore, could not be used as an additional comparison. All *C. zastrowi* were collected within 100 km of each other in the Republic of South Africa (Figure 1), so they effectively constituted a single population in our analyses.

The mean of each song feature was calculated from all songs (volleys or SRUs) recorded per individual, and this mean served as the representative value of the feature for each individual in other analyses. Coefficients of variation (CVs) were calculated for each song feature, first for each individual (within-individual variation) and then for the entire population (between-individual variation). Analyses of variance (ANOVAs) were performed on individual averages using a variety of independent variables, including geographic region, sex and song morph (*Cc5* versus *C. zastrowi*). All statistical analyses were calculated using Statistica version 6.1 (StatSoft 2003).

A principal components analysis (PCA) was used to summarize and visualize the song differences between *Cc5*, *C. zastrowi*, and any other species of the *carnea* group with which they might co-occur and possibly hybridize in nature. Species potentially sympatric with *Cc5* and *C. zastrowi* in the Middle East and Africa and, therefore, included in the PCA, were *C. lucasina*, *C. mediterranea* and *C. agilis*. Nineteen measured song features contributed to the PCA, six of which, pertaining specifically to *Cc5* and *C. zastrowi*, are shown in Table II. Inclusion of all features was necessary to accommodate variables found in species with more complex songs (Henry et al. 1996, 1999, 2003). For the analysis to proceed, those extra features had to be added to the six basic features of *Cc5* and *C. zastrowi* as new variables filled with data copied from existing variables (redundant data) or calculated/estimated from existing variables.

To quantify overall song disparity among the five species or song morphs above, we used discriminant function analysis (DFA), which is another approach to analyzing

Table III. Results of a discriminant function analysis of nine least correlated song features in five potentially sympatric song taxa of the *carnea* group, showing squared Mahalanobis distances above the diagonal and *F*-values below the diagonal.

	<i>C. lucasina</i>	<i>C. mediterranea</i>	<i>C. agilis</i>	<i>Cc5</i>	<i>C. zastrowi</i>
<i>C. lucasina</i>	–	125.61	398.56	263.65	299.80
<i>C. mediterranea</i> (N. America)	568.21	–	385.11	223.01	233.77
<i>C. agilis</i>	2164.57	1353.10	–	727.51	660.52
<i>Cc5</i>	1457.70	792.62	2976.49	–	25.20
<i>C. zastrowi</i>	1887.58	901.50	2970.28	115.00	–

Features included volley duration at SRU start, volley period at SRU start, SRU duration, number of volleys per SRU, initial volley frequency at SRU start, mid-volley frequency at SRU start, end-volley frequency at SRU start, mean maximum frequency change within a volley and mean maximum frequency change within an SRU. All pairwise comparisons showed highly significant differences. Wilks' Lambda=0.00001, approximate  $F_{36,1646}=868.81$ . The smallest distance, marked by the box, is between *Cc5* and *C. zastrowi*.

multi-dimensional variation. In DFA, strong correlations between variables will bias or preclude an analysis, so one of each pair of variables exhibiting high correlation coefficients ( $R\geq 0.80$ ) was eliminated. The feature retained was chosen for its lower correlations, on average, with the other variables. In the present analysis, 19 possible song variables yielded nine least correlated features, which included the six shown in Table II plus SRU duration, frequency change within a volley and frequency change over the course of the SRU. The three additional features contributed critical information about the more complicated songs of *C. lucasina* and *C. mediterranea*, where the SRU includes more than one volley. Statistical differences in songs among the five taxa were determined from the matrix of squared Mahalanobis distances generated by the DFA, assuming *a priori* classification probabilities proportional to group sizes (Table III).

Adult morphology

A total of 121 specimens, identified acoustically as *Cc5*, were examined for external morphological features that might vary among populations across the geographic range. Localities included Al Buraymi, Oman, x.1994 (85 specimens, 44 males, 41 females); Dubai, United Arab Emirates, x.1994 (eight specimens, one male, seven females); Eilat, Israel, x.1993 (27 specimens, 11 males, 16 females); and Dāmghān, Iran, vi.2002 (one male). These sites are characterized further in Table I and located on the map in Figure 1 (black circles).

An additional 20 specimens from Cedarberge (six males, seven females) and Tankwa Karoo (four males, three females), Republic of South Africa (Table I; Figure 1, black stars), were identified geographically, morphologically and acoustically as *C. zastrowi*. These were studied in the same way as *Cc5*, to permit comparison with that taxon.

A further 29 preserved specimens were examined from the collections of The Natural History Museum, London. These were selected because they shared morphological characters with *Cc5* and *C. zastrowi* and occurred near or within the distributional range of those taxa. Collecting sites included Djibouti (three males, two females), Sudan (two males), Zanzibar (one male), Cape Verde Islands (one male), Ascension Island (one male, one female), St. Helena (two males), Namibia (one female) and South Africa (six males, nine females) (Table I, sites marked with asterisks; Figure 1, grey circles and stars).

Adults were examined for the states of 20 characters. These included ground colour of body; presence, extent and colour of markings on stipes, palps, gena, clypeus, frons and postoccipital region; relative abundance and distribution of black and blond setae on pronotum; relative size of basal dilation of tarsal claw expressed as a ratio (see Henry et al. (2002), and explanation below); extent to which fore wing is rounded or tapered at apex; relative width of fore wing expressed as the ratio of length to breadth at widest point; presence or absence of black markings on wing veins; orientation of the Rs crossvein with respect to the Rs vein (perpendicular or oblique, see Figure 4A); length and colour of costal

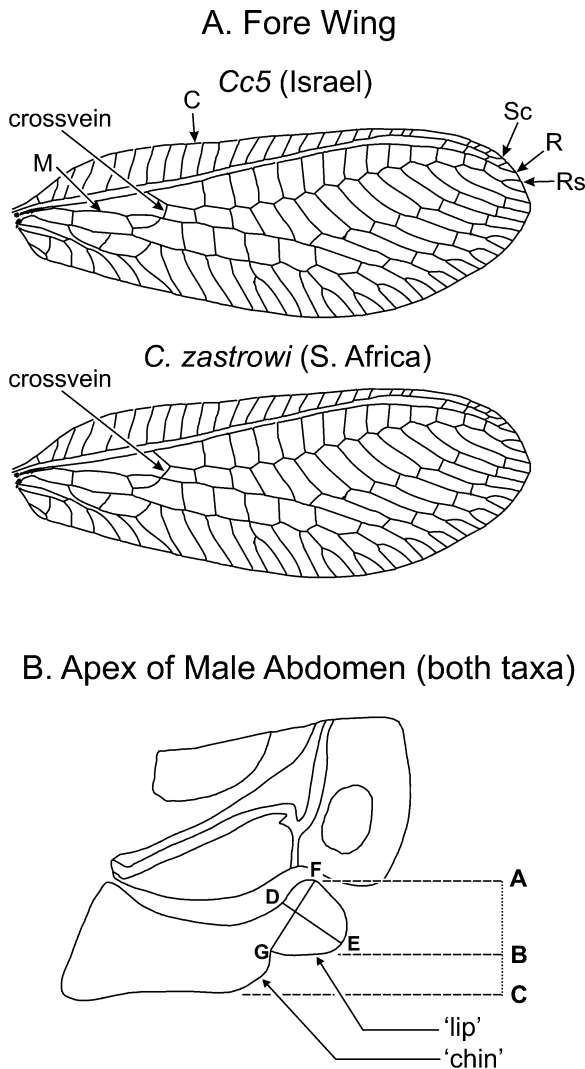


Figure 4. Two key morphological features of lacewing taxa. (A) Fore wing of *Cc5* (above) and *C. zastrowi* (beneath). Note the contrasting perpendicular versus oblique orientation of the Rs-M crossvein in the two taxa. (B) Lateral view of the lip/chin of sternite 8+9 of the male abdominal apex. Letters A–G represent landmarks used to determine relative shapes and sizes of the lip and chin. All specimens of both *Cc5* and *C. zastrowi* showed line segment  $AB > BC$ , indicating a relatively broad, protruding lip.

setae; length of abdominal setae; relative abundance and distribution of black and blond setae on the three distal abdominal sternites; shape and relative proportions of male genital “lip” and “chin” at apex of sternite 8+9 (see Figure 4B and explanation below); length and colour of setae clothing male genital lip; shape of tignum of male genitalia; and presence or absence of dark brown stripe on pleural membrane of second abdominal segment.

The shape of the pretarsal claw was assessed by removing one metathoracic leg, mounting it in Euparal on a microscope slide, splaying the claws by flattening the pretarsus beneath the cover slip, and viewing and drawing one or both claws using a camera lucida. A ratio was then calculated (AB/BD, Figure 4 in Henry et al. (2002)), representing the extent of dilation of the claw base (see also Brooks 1994; Thierry et al. 1998). Larger numerical ratios correspond to narrower basal dilations.

To determine the shape of the external genital area of the male abdomen, the tip of the abdomen was removed and placed in glycerol, then viewed laterally and drawn (using camera lucida) through a binocular microscope at  $100\times$  magnification. Measurements of lip and chin dimensions were taken from the drawings (Figure 4B, line segments defined by points A–G). The ratio AB/BC reflected the relative prominence of the chin, whereas DE/FG characterized the shape of the lip. Setal colour was judged to be black or blond by examination with reflected light under a dissecting microscope. Internal genitalia of selected males were dissected, stained, mounted and measured using established techniques (Bram and Bickley 1963; Brooks 1994).

### *Larval morphology*

We examined 104 first-instar larvae, 89 second-instar larvae and 72 third-instar larvae of *Cc5* from Eilat, Israel, and seven first-instar, four second-instar, and 13 third-instar larvae of *C. zastrowi* from Cedarberge, South Africa. Larvae were boiled in distilled water with a drop of liquid detergent and transferred to 70% ethanol with 5% glycerine. Specimens were viewed at  $50\times$ . Head markings of selected, representative individuals were illustrated.

## Results

### *Song phenotype*

Within-individual coefficients of variation (CVs) for song measurements were relatively low in both taxa, averaging 11.90% in *Cc5* and 12.87% in *C. zastrowi* for temporal song features and 3.03 and 2.25%, respectively, for frequency features. Therefore, we felt that it was valid to reduce the data to individual averages, as has been done in previous studies of song variation in lacewing species (Henry and Wells 1990; Henry et al. 2003). Between-individual CVs for temporal features were 13.35% among the 51 individuals of *Cc5* and 15.17% among the 50 individuals of *C. zastrowi*. For frequency features these numbers were 6.42 and 6.02%, respectively.

Adult males and females of *Cc5* produced a single type of song (=SRU), which was used both in solitary calling and dueting. The SRU was monosyllabic but repeating, consisting of a single volley about 2.25 s long repeated on average every 4.28 s (Figure 2A, Table II). The carrier frequency of each volley was unusually pure; that is, at any point in time only one frequency was present rather than a mixture of two or more frequencies. During the course of the volley, the carrier frequency decreased from an average maximum of 55.5 Hz to a minimum of about 25 Hz (25°C). Most volleys began with a burst of vibration that was

both more intense and fractionally higher in frequency than subsequent vibrations. Carrier frequency decreased by only a few Hertz during the first third of the volley, then more rapidly during the remaining two-thirds. When singing alone, individuals would sometimes initiate a new volley before the last volley was finished, producing a run-on sequence of volleys (Figure 2A). Another feature occasionally observed in both solo and dueting songs of *Cc5* was a very brief break in the middle of the volley, usually accompanied by a transient upward shift in carrier frequency (Figure 2B).

Heterosexual dueting in *Cc5* consisted of each individual repeatedly answering single volleys of its partner with the same kind of volley. The result of that interaction was a long series of iterated volleys, with the responses of the partners alternating with one another (Figure 3A). Overlap between adjacent male and female volleys was absent or slight. As in other lacewings of the *carnea* group (Henry 1979), the duet ended with the male repeatedly tapping the genital area of the female with the tip of his abdomen just prior to copulation.

Songs of *C. zastrowi* closely resembled those of *Cc5* in volley amplitude structure, volley frequency change and use of volleys during duets (Figures 2C and 3B). Even several details of the *Cc5* song were present, e.g. the higher-frequency burst at the onset of most volleys, the purity of the carrier frequency, the run-on nature of many solo volley sequences and the brief mid-volley break punctuating the occasional volley (Figure 3A, B). However, analyses of variance revealed highly significant differences ( $P \ll 0.0001$ ) between the taxa in every measured feature exhibiting variation. Individual volleys of *C. zastrowi* were nearly twice as long and were placed almost twice as far apart as those of *Cc5*, averaging about 4 s in duration and about 7 s in period. Carrier frequency was consistently higher throughout each volley in *C. zastrowi* compared with *Cc5* at the same temperature (Table II). These multiple differences are captured in the plot of the first two components of the PCA (Figure 5) and in the plot of roots one and two of the DFA (Figure 6), and are quantified as significantly different Mahalanobis distances in Table III.

#### *Sex differences in songs*

Songs of males and females were nearly identical within each taxon. In *C. zastrowi*, all sex differences were statistically insignificant, but males of *Cc5* exhibited shorter volleys with slightly lower ending frequencies than did females (Table II, asterisks). Sex differences were judged small enough to warrant pooling all individuals in other comparisons.

#### *Other variation in songs*

Using an analysis of variance, populations of *Cc5* from two geographic localities (Israel and Oman/Dubai) were compared with respect to measurements of their five variable song features. Differences between populations were not large and reached significant levels only for volley duration (Table II). Measures of song features from the single male from Iran were consistent with that individual belonging to either of the other two populations.

Multi-dimensional comparisons of song phenotypes in *Cc5*, *C. zastrowi* and three other sympatric song species are shown graphically in Figures 5 and 6. Whether generated using PCA or DFA, results demonstrated distinct taxon-based clustering with little or no overlap of individual means between taxa. In addition, the five taxa were significantly different from one another in all pairwise comparisons, based on the matrix of squared Mahalanobis distances generated by DFA (Table III). The most similar pair of species in the analysis was *Cc5/C. zastrowi*.

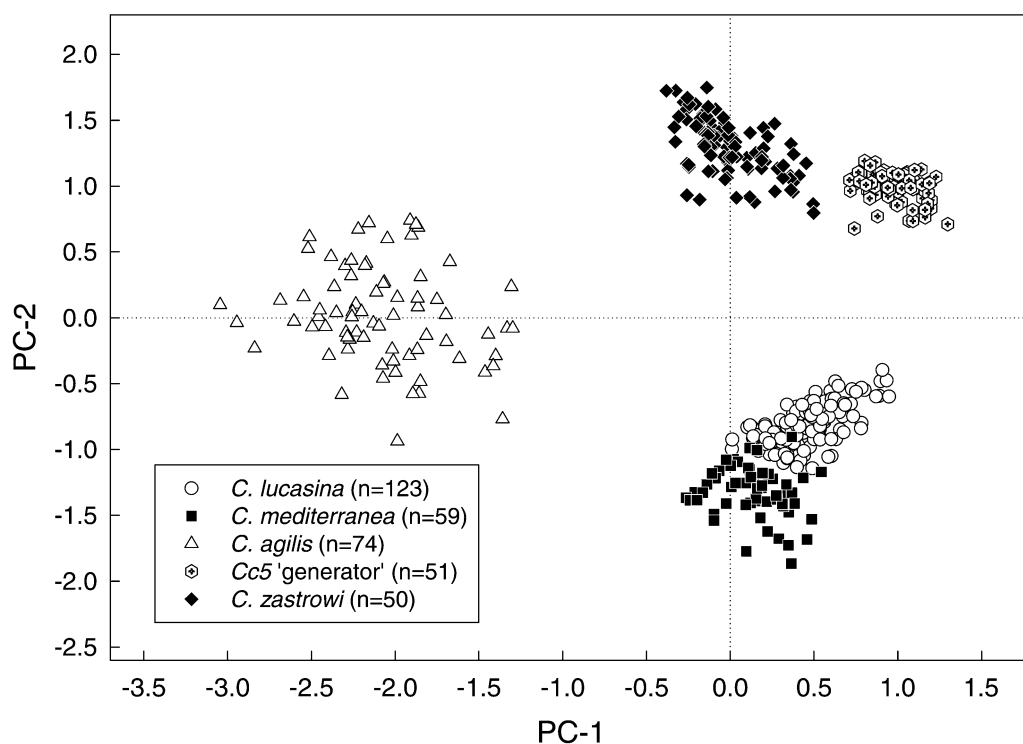


Figure 5. Scatterplot of the first two factors of a principal components analysis of 19 song features (see text) of *Cc5*, *C. zastrowi*, *C. lucasina*, *C. mediterranea* and *C. agilis*. Each data point represents a single individual, coded by taxon.

Although formal behaviour experiments were not conducted, it was observed that individuals of *C. zastrowi* responded readily to playbacks of songs of *Cc5* in spite of consistent acoustic differences. Neither species responded to the songs of any other Eurasian member of the *carnea* group. We were unable to test responsiveness of *Cc5* individuals to recorded songs of *C. zastrowi*.

#### Adult morphology

*Ground colour of body.* In all specimens of both taxa, the body was uniform pale green (where not discolored to straw yellow), with a pale yellow dorsal stripe running the length of the thorax and abdomen.

*Extent of markings on stipes.* In most specimens of both taxa, the stipes was marked with a mid-dorsal brown line along its entire length. In a few specimens of *Cc5*, the marking was restricted to the apical third of the stipes.

*Colour of palps.* In most specimens of both taxa, each segment of the palps was marked dark brown dorsally. In a few specimens of *Cc5*, the segments of the palps were unmarked.

*Extent and colour of genal markings.* The gena was marked with a broad dark brown band in the majority of specimens of *Cc5* and half the specimens of *C. zastrowi*. In some specimens

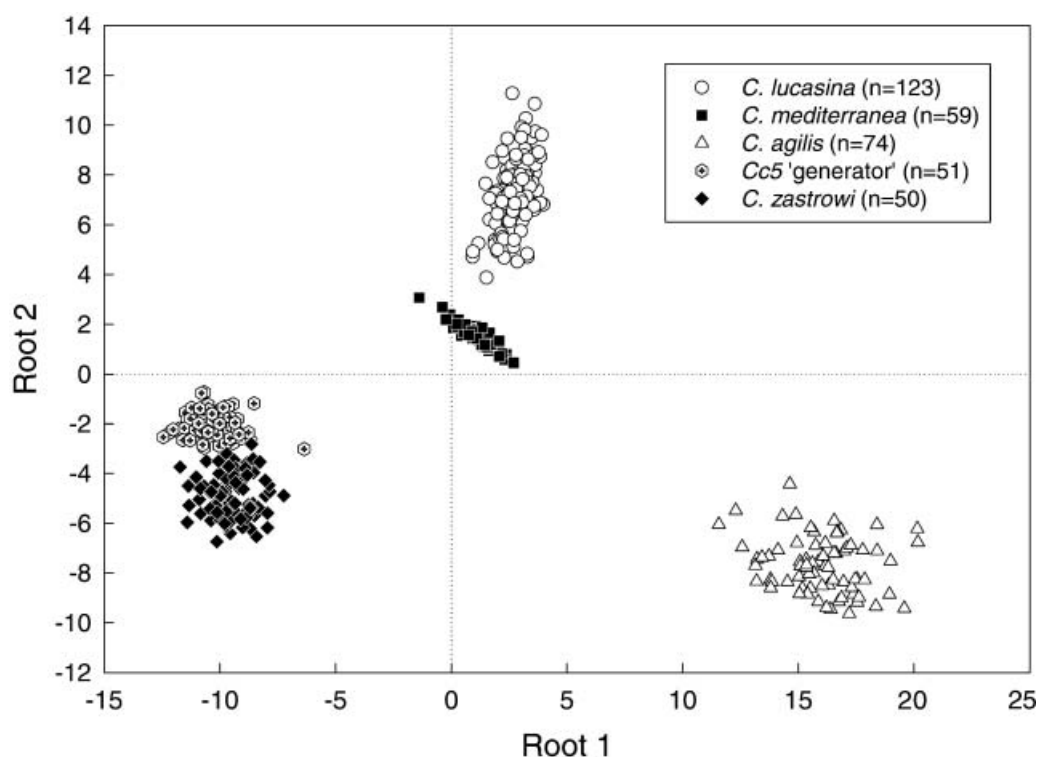


Figure 6. Scatterplot of the first two roots of a discriminant function analysis of nine song features (see text) of *Cc5*, *C. zastrowi*, *C. lucasina*, *C. mediterranea* and *C. agilis*. Each data point represents a single individual, coded by taxon.

of *Cc5*, the gena had a red outer edge. In half the specimens of *C. zastrowi* and a few of *Cc5*, the gena was marked only with red.

**Clypeal markings.** In half the specimens of *Cc5*, the lateral edge of the clypeus was marked with a narrow brown stripe, while in most of the remaining specimens of the taxon this stripe was red. In most specimens of *C. zastrowi*, the clypeus was marked red and sometimes these marks were broad, although in a few specimens the clypeus was brown laterally. In specimens of both taxa in which the gena was marked red, the clypeal stripe was also red. The clypeus was unmarked in a few individuals of both taxa.

**Frontal markings.** In most specimens of *Cc5* the frons was marked with a brown lateral stripe, although this stripe was often red when the clypeal markings were also red. Half the specimens of *C. zastrowi* exhibited the frons marked red, whereas the remaining specimens of that species showed a brown stripe. The red markings in *Cc5* and *C. zastrowi* were never more than a lateral stripe on the frons, although in some specimens this was broader than in others.

**Markings on postoccipital region.** The postocciput was unmarked.

**Relative abundance and distribution of black and blond setae on pronotum.** Setae were concentrated towards the lateral margins of the pronotum. In most specimens of *Cc5*, these

comprised 90–100% short, black setae, although in some specimens from the United Arab Emirates only about 60% of setae were black. Pronotal setae in all specimens of *C. zastrowi* were black.

*Relative size of basal dilation of tarsal claw expressed as a ratio of the length of the claw tooth to the length of the basal dilation (the “claw ratio”, AB/BD).* The claw ratio ranged from 3.5–5.1 (mean  $\pm$  SD =  $4.2 \pm 0.50$ ) in *Cc5* and from 3.6–4.9 (mean  $\pm$  SD =  $4.4 \pm 0.58$ ) in *C. zastrowi*. Variation in this character within each taxon was not correlated with geography.

*Extent to which fore wing is rounded or tapered at apex.* The fore wing was rounded apically.

*Relative width of fore wing expressed as a ratio of length to breadth at widest point.* The aspect ratio of the fore wing ranged from 2.6–3.4 (mean  $\pm$  SD =  $3.0 \pm 0.19$ ) in *Cc5* and 2.7–3.0 (mean  $\pm$  SD =  $2.9 \pm 0.14$ ) in *C. zastrowi*.

*Presence or absence of black markings on wing veins.* Apart from a black spot on the tympanal organ, the wing veins were unmarked.

*Angle of Rs crossvein.* In most specimens of *Cc5*, the Rs crossvein was at right angles to Rs. However, in one specimen from the United Arab Emirates and five from Oman, the crossvein formed an oblique angle with Rs. All specimens of *C. zastrowi* showed the Rs crossvein forming an oblique angle with Rs (Figure 4A).

*Length of costal setae.* The costal setae were relatively short and inclined.

*Relative abundance and distribution of black and blond setae on abdominal sternites.* In most specimens of *Cc5*, the three apical abdominal sternites were clothed by 90–100% black setae, ranging to 50% black setae in a few individuals. Setae on more basal sternites were mostly blond. *C. zastrowi* was characterized by 100% black setae on the apical abdominal sternites.

*Length and abundance of abdominal setae.* Setae clothing the abdomen were relatively short and sparse.

*Shape of male genital lip and chin at apex of sternite 8+9.* The genital lip of *Cc5* was moderately narrow and not protruding (DE slightly greater or equal to FG), whereas the chin beneath it was small (AB > BC). *C. zastrowi* was similar, although the chin tended to be relatively larger than in Middle Eastern specimens (Figure 4B).

*Length and colour of setae clothing male genital lip.* The genital lip was clothed with a scattering of long black setae.

*Shape of tignum in male genitalia.* The tignum was shaped as in all other members of the *carnea* group (see Henry et al. 1993: Figs 3, 4; Henry et al. 1999: Fig. 9).

*Presence or absence of dark brown stripe on pleural membrane of second abdominal segment.* There was no stripe on the pleural membrane of the second abdominal segment.



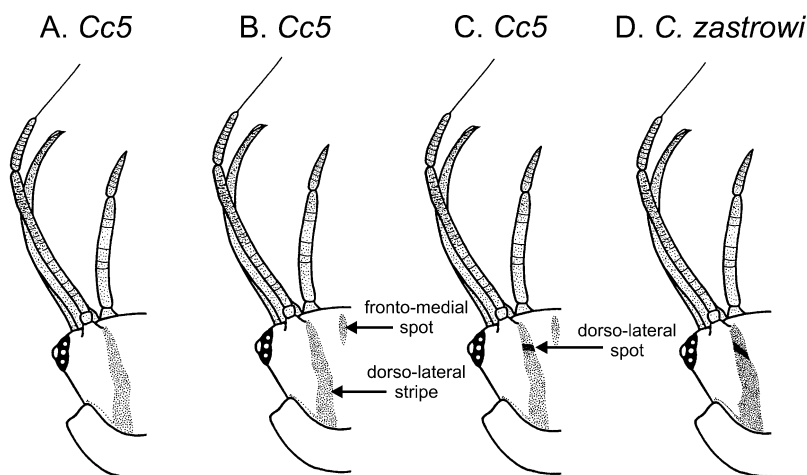


Figure 7. Dorsal view of left half of third-instar larval head capsules. (A)–(C) *Cc5* from Eilat, Israel; (D) *C. zastrowi* from Cedarberg, South Africa. Head markings discussed in the text are labeled. In *Cc5*, the most common condition for head markings is shown in B.

Most of the 29 preserved specimens examined from the BMNH (Table I, asterisks; Figure 1, grey circles and stars) showed morphological characteristics that fell within the range of characters described above. One exception included specimens from St. Helena, in which the apex of the fore wing appeared more pointed due to the flattening of the posterior margin, distal to the broadest part of the wing. Also, in specimens from Sudan, Djibouti, Zanzibar and Cape Verde, the first radial crossvein was at right angles to the radial vein, whereas in specimens from South Africa, Namibia, Ascension Island and St. Helena, the first radial crossvein was oblique (Figure 4A).

*Summary of morphological difference between Cc5 and C. zastrowi.* In nearly all cases, the angle of the Rs crossvein distinguished specimens of *Cc5* (right angles) from those of *C. zastrowi* (oblique). This character was first recognized as being diagnostic for *C. zastrowi* by Tjeder (1966). In addition, many *C. zastrowi* specimens had broad red markings on the lateral clypeus and frons, which were less prominent or absent in *Cc5*.

#### *Larval morphology*

*Cc5* (Figure 7A–C) and *C. zastrowi* (Figure 7D) larval head capsule markings were dominated by a pair of longitudinal, dorso-lateral brown stripes with baso-lateral expansions extending toward the eyes. This pattern is typical for larvae of *Chrysoperla* spp. (Henry et al. 2003). First-instar larvae had the broadest (relative to head width) dorso-lateral stripes and the least developed baso-lateral expansions. Second-instar larvae were intermediate and third-instar larvae had the relatively narrowest dorso-lateral stripes and most extensive baso-lateral expansions. All instars varied within populations. Because only a single population of each was represented in the material available, variation among populations could not be assessed. The remainder of the results focuses on third-instar larvae.

The *Cc5* population ( $n=72$ ) had a narrow, moderately pale dorso-lateral stripe (Figure 7A–C). The baso-lateral expansion was very small and usually present only as a

sinuous curve and the baso-lateral arm that is visible anteriorly of the pronotum was pale and very narrow. A darker spot was visible in the dorso-lateral stripe mesad of the eyes in seven (9.7%) of the larvae (Figure 7C). The spot was transverse. An elongate fronto-medial spot was evident in sixty (84%) of third-instar specimens (Figure 7B, C). The fronto-medial spot was usually present without the darker spot in the dorso-lateral stripe, thus Figure 7B represents the most common pattern observed.

*Chrysoperla zastrowi* ( $n=13$ ) showed limited variation within the population examined (Figure 7D). All larvae showed a dark, narrow dorso-lateral stripe with a weakly developed, but sometimes angulate, baso-lateral expansion. The baso-lateral arm was narrow but quite dark. All 13 individuals had a prominent darker spot mesad of the eyes in the dorso-lateral stripe. The spot was oblique. None had a fronto-medial spot.

### Ecology

All specimens of *Cc5* were collected from the desert regions of the Middle East. The taxon was locally abundant in irrigated agricultural fields, such as those for melon (Eilat, Israel), alfalfa (Dubai and Oman), and pistachio (Dāmghān Iran). Most of these green “islands” in the sandy desert were occupied by *Cc5*, indicating that at least a portion of the population was performing long dispersal flights across harsh habitats.

*Chrysoperla zastrowi* has been found principally in southwestern Africa. In the Great Karoo desert and in Western Cape Province, *C. zastrowi* was often very abundant in irrigated alfalfa fields. It also occurred locally on composite weeds (Asteraceae) at the edges of crop fields and roads, where irrigation water drained off. Light traps at night yielded numerous *C. zastrowi* several kilometers away from agricultural areas, suggesting the likelihood of long distance dispersal in the species.

In laboratory experiments (Duelli, unpublished data), single specimens of both *Cc5* and *C. zastrowi* displayed signs of adult diapause colouration change after the larvae had been kept in the cold (4°C) and under short-day conditions (10L:14D). Diapause colour was very pale green, with parts of the thorax, abdomen and head shaded purplish.

## Discussion

### *Intraspecific variation and sexual dimorphism in song phenotype*

Measurements of within-individual and between-individual variation are low in both *Cc5* and *C. zastrowi*, indicating that song features are highly constrained, presumably by stabilizing selection acting on the specific mate recognition system (Paterson 1986; Butlin and Ritchie 1994). Male songs differ from females only slightly and then principally in the shorter average duration and period of their SRUs (Table II). The other five Eurasian species of the *carnea* group (specified in the Introduction) show a similar pattern of shorter songs (SRUs) in males than in females, as does at least one North American song species, *C. johnsoni* (Henry 1993a). In general, the longer the characteristic SRU of the species, the more likely it is that the male will produce a shorter song than the female. Thus, species with short single-volleyed SRUs such as North American *C. plorabunda* and *C. adamsi* exhibit no sexual song dimorphism; Eurasian *C. agilis*, with single-volleyed SRUs of moderate length, shows modest but significant dimorphism (Henry et al. 2003); and multi-volleyed species with long SRUs such as North American *C. johnsoni* and Eurasian *C. lucasina*, *C. mediterranea*, *C. pallida* and *C. carnea* exhibit the largest relative sexual

dimorphism in song length (Henry et al. 1996, 1999, 2002). This trend may be explained by the fact that males of species with long songs often produce a shorter version of the lengthy courtship song to start up duets quickly with potential partners in their vicinity (Henry et al. 2002).

#### *Comparison of songs among species*

Although the songs of *Cc5* and *C. zastrowi* differ from each other in significant ways, they have in common two important song attributes not found in most of the other 15 song species of the *carnea* group. One is tonal purity and the other is the occasional occurrence of a transient volley break during otherwise normal episodes of singing (Figures 2B and 3A,B).

Tonal purity is the song quality that suggested the original nickname “generator” for *Cc5*, because each volley resembles the output of an electronic sweeping function generator producing a simple sine wave of decreasing frequency. The mixed frequencies in the songs of other *carnea*-group lacewings appear as several to many parallel frequency bands on plots of frequency versus time (e.g. *C. agilis*, Figure 5 in Henry et al. 2003). Only *C. lucasina* produces song tones as pure as those of *Cc5* and *C. zastrowi* (Henry et al. 1996). However, unlike the latter, each *C. lucasina* volley gradually increases rather than decreases in frequency from start to finish.

Volley breaks are very brief disruptions punctuating a volley in mid course. They have not been found in any other species of the *carnea* group. When volley breaks occur, the carrier frequency of the volley is re-set to a higher frequency, such that the volley appears to have been re-started (Figure 2B). The detailed structure of a volley break is nearly the same in *Cc5* and *C. zastrowi*, implying homology of that feature in both taxa. Thus, regardless of the other measurable differences that distinguish the songs of the two taxa, the volley breaks provide convincing evidence of common ancestry or single species status.

Although the songs of *Cc5* and *C. zastrowi* are unique among those of all species in the *carnea* group, it is more useful to compare them to the songs of species with which they are sympatric and with which they might, therefore, interact sexually. Across Africa and the Middle East, those species include *C. lucasina*, *C. mediterranea*, and *C. agilis*. The dueting songs of *C. lucasina* and *C. mediterranea* have long, multi-volley SRUs, making them impossible to confuse with the single-volley SRUs of *Cc5* and *C. zastrowi*. Also, the long, upwardly modulated and tonally complex volley of *C. agilis* is very different from the downwardly modulated pure-tone volleys of *Cc5* and *C. zastrowi*. These song disparities are clearly reflected in the two plots derived from principal components and discriminant function analyses, where all five sympatric taxa occupy nearly non-overlapping positions in factor space (Figures 5, 6). Based on what we know of other lacewings in the *carnea* group, *Cc5* and *C. zastrowi* are not likely to interact acoustically or sexually with *C. lucasina*, *C. mediterranea* or *C. agilis*.

The multi-dimensional analyses also confirm that the songs of *Cc5* and *C. zastrowi* are more similar to each another than they are to those of any of the other three sympatric species. Although PCA and DFA plots show *Cc5* and *C. zastrowi* as non-overlapping clouds of points, it is easy to see how their separation in factor space could be due to failure to sample songs from the geographic region between the Middle East and South Africa (Figure 1).

On balance, the evidence from song analysis supports the existence of a single species that includes both *Cc5* and *C. zastrowi*, with the distinctive song phenotypes of each taxon representing extremes on a continuum of clinal variation extending from the Middle East to

southern Africa. The existence of such a latitudinal song cline in a *carnea*-group lacewing species is not without precedent. In western North America, for example, the widely distributed song species *C. johnsoni* varies by a factor of two for volley duration and 1.7 for volley period between northern populations at 48°N latitude and southern populations at 32°N latitude (Henry 1993a). These ratios are even larger than those measured between *Cc5* and *C. zastrowi*, which differ by a factor of 1.76 for volley duration and 1.66 for period (Table II). However, until we have measured the songs of lacewings collected from the north African gap between the ranges of the two taxa, it is probably best to consider *Cc5* as a distinct subspecies of *C. zastrowi*.

### *Morphology of adults*

Specimens sharing the *Cc5* and *C. zastrowi* song type have a fairly uniform morphology, which is common to most of the other species in the *carnea* group. The most distinctive morphological feature shared by adult *Cc5* and *C. zastrowi* is the relatively small basal dilation of the claw (claw ratio AB/BD > 3.5). The only other green lacewings in the western European *carnea* group that have a claw ratio greater than 3.5 belong to populations of *C. mediterranea* in the western portion of its range (claw ratio > 4.0; for details, see Brooks 1994; Henry et al. 1999). Some Swiss specimens of *C. mediterranea* also have claw ratios similar to those found in *Cc5*. Additional morphological features present in *Cc5* and *C. zastrowi* that are otherwise shared only with *C. mediterranea* are the predominance of black setae on the pronotum and the uniformly green wing veins. Other *carnea*-group species possess mostly blond pronotal setae, and the basal veins of the fore wing are marked black at each end. Lastly, the proportions of the male apical sternites (the lip and chin) in *Cc5* and *C. zastrowi* are also similar to those measured in *C. mediterranea* (Figure 4B). *Cc5* and *C. zastrowi* can, therefore, be reliably distinguished morphologically from all the other western European species of the *carnea* group, except some specimens in western populations of *C. mediterranea*, on the basis of the small basal claw dilation, the predominance of black setae on the pronotum, and the absence of markings on the basal fore wing veins. The absence of a red or orange-red band extending across the front of the head in *Cc5* and *C. zastrowi* will distinguish these taxa morphologically from *C. mediterranea* (Henry et al. 1999).

The small differences in the courtship songs of *Cc5* and *C. zastrowi* are reflected in morphological differences between southern African specimens and specimens from the Horn of Africa and the Middle East. In all specimens from southern Africa, as well as those from Ascension Island and St. Helena, the Rs-M crossvein is at an oblique angle to the radial sector (Figure 4A). In addition, these specimens often have red frontal markings. In contrast, most specimens from the Horn of Africa and the Middle East show this crossvein at right angles to Rs, although a small proportion of them have the vein oriented obliquely. The occurrence of both forms of this venational character in these northern populations suggests that the southern African population of *C. zastrowi* is derived from *Cc5* or a *Cc5*-like ancestor that originated in the Middle East or Horn of Africa. This is consistent with the biogeographical distribution of the *C. carnea* group in which all species, apart from *C. zastrowi*, occur in the Northern Hemisphere.

Specimens from St. Helena have a more pointed fore wing than those from mainland Africa. It would be of interest to determine whether this distinctive island population also differs in song phenotype from continental populations.

*Chrysoperla sillemi* (Esben-Petersen), described from Kashmir (Esben-Petersen 1935) and known also from Gujarat (Ghosh 1976a, 1977) and Maharashtra (Ghosh 1976b) in

India, is morphologically indistinguishable from *Cc5*. However, we have been unable to obtain living specimens of *C. sillemi*. Consequently, its courtship song is unknown and, in the absence of such data, we cannot confirm its affinities. Additional specimens, also morphologically identical to *Cc5*, have been found throughout the Sahel region of central Africa (Hölzel, unpublished), but without their courtship songs positive identification is not possible.

### *Morphology of larvae*

Larvae of *Cc5* and *C. zastrowi* are typical of species in this genus (Tauber 1974; Henry et al. 1996, 1999, 2002, 2003). Although first and second instar larvae of *Cc5* and *C. zastrowi* are hard to tell apart, third instars can usually be distinguished from one another. The bodies of *C. zastrowi* larvae are darker than *Cc5* larvae. *C. zastrowi* third-instar larvae also have a darker and slightly broader dorso-lateral cephalic stripe that uniformly includes a darker spot mesad of the eyes, and they lack a fronto-medial spot. *Cc5* larvae have a distinctly paler and usually slightly narrower dorso-lateral stripe. Most *Cc5* (90.3%) also lack the darker spot in the dorso-lateral stripe and usually (84%) have a fronto-medial spot.

The degree of variation seen between larval *Cc5* and *C. zastrowi* falls well within the limits observed within all wide-ranging Palaearctic species of the *Chrysoperla carnea* complex (Henry et al. 1996, 1999, 2002, 2003). The colour differences between the two populations examined in this study also reflect the pattern seen within other species, where larvae from cooler areas farther from the equator possess darker and more extensive head markings. Similar larval head markings also occur in other species. In this case, the markings of *Cc5* particularly resemble those of *C. mediterranea* from Carcès, France (Henry et al. 1999), while those of *C. zastrowi* resemble markings of some *C. carnea* from Belgorod, Russia (Henry et al. 2002). Thus, larval morphology alone will not resolve whether *Cc5* and *C. zastrowi* share a most recent common ancestor or are possibly even conspecific.

### *Ecology*

Both *Cc5* and *C. zastrowi* live in desert regions, where places suitable for their survival did not exist prior to cropland irrigation. Thus, it seems probable that they originally occupied the herbaceous belts along desert streams and scattered alluvial fans in gallery forests. Today, most of these likely historical habitats have been converted to intensively managed agricultural lands. Consequently, *Cc5* and *C. zastrowi* presently occupy areas that probably do not resemble their original environments very much at all.

Both *Cc5* and *C. zastrowi* show high dispersal capabilities, suggesting that they belong to the highly successful guild of crop dwellers within the *carnea* group characterized by migration behaviour. In North America, the guild is represented by *C. plorabunda*, which performs long preovipositional “adaptive dispersal flights” over and between crop fields (Duelli 1984). In Europe, *C. carnea* behaves similarly and is the best known member of the guild (Duelli et al. 2002); in fact, a recent study documents even longer migration flights in *C. carnea* than in *C. plorabunda* (Chapman et al. 2006). Additional guild members include *C. agilis* (Henry et al. 2003) in southern Europe and *C. nipponensis* (Okamoto) in eastern Asia (Tsukaguchi 1995). All of these nomadic species within the *carnea* group are associated principally with herbs or grasses, while other less migratory species are found on trees and shrubs (Henry et al. 2002).

In laboratory experiments (Duelli, unpublished data), single specimens of both *Cc5* and *C. zastrowi* displayed signs of diapause colouration after the larvae had been kept in the cold (4°C) and under short day conditions (10L:14D). Neither diapause nor diapause colouration had previously been observed in the two taxa, nor were these responses expected considering that both taxa live today in regions characterized by mild winters. The diapause experiment suggests, however, that the two taxa share common ancestry in the northern hemisphere, where diapause colouration is a particular attribute of the crop-dwelling guild of migratory species in the *carnea* group.

## Conclusion

Evidence from songs, adult and larval morphology, and ecology supports the notion that *Cc5* and *C. zastrowi* are very closely related taxa that are most likely populations of a single, trans-equatorial species belonging to the nomadic guild of the *carnea* group. Also supported is the origin of southern African *C. zastrowi* from progenitors in the Northern Hemisphere, where all other cryptic species of the *carnea* group currently reside and presumably originated. If, indeed, these two taxa constitute one species, that species has the largest geographic distribution of any member of the *carnea* group yet described. In view of *C. zastrowi*'s extensive range, the differentiation of its courtship song into distinct phenotypes and the trans-equatorial gap in its known distribution, it is probably best to recognize the South African and Middle Eastern populations as different subspecies. Thus, the southern population becomes *Chrysoperla zastrowi* subspecies *zastrowi* (Esben-Petersen) and *Cc5* becomes *C. zastrowi* subspecies *arabica* (Henry et al. this paper).

## Taxonomy

### Order NEUROPTERA

### Family CHRYSOPIDAE

### Subfamily CHRYSOPINAE

### Genus *Chrysoperla* Steinmann, 1964

Type species: *Chrysoperla carnea* (Stephens, 1836)

### *Chrysoperla zastrowi arabica* n. subsp.

HOLOTYPE: male, Oman: Al Burymi, 285 m, October 1994, coll. P. Duelli. BMNH.

PARATYPES: same data as holotype, 13 males, 15 females, 15 first-instar, 15 second-instar and 15 third-instar larvae, reared from parents collected x.1994, coll. P. Duelli. 13 males, 15 females, BMNH; 5 first-instar, 5 second-instar, 5 third-instar larvae, BMNH; 5 first-instar, 5 second-instar, 5 third-instar larvae, CSMNH; 5 first-instar, 5 second-instar larvae, 5 third-instar larvae, WFBM.

*Etymology.* Named for its occurrence in the Arabian Peninsula of the Middle East.

*Adult.* Ground colour uniform pale green. Head marked with broad dark brown band, sometimes outlined in red on gena and clypeus. Maxillary palp marked dark brown dorsally on each segment, occasionally unmarked. Stipes marked with mid-dorsal brown line along its entire length; occasionally, marking restricted to the apical third of the stipes. Clypeus with lateral edge marked with narrow brown or red stripe. Frons marked with brown lateral stripe, or red stripe when the clypeal markings are red. Postoccipital region unmarked.

Antennae shorter than fore wing. Pronotum marked with median pale yellow stripe; lateral setae mostly short, black. Tarsal claw basal dilation ratio 3.5–5.1. Fore wing length 11.3–14.0 mm, length:breadth ratio 2.6–3.4; venation entirely green; costal setae relatively short; basal Rs-M crossvein leaves Rs at right angles or sometimes obliquely. Abdomen bearing black setae on three apical sternites, more basal sternites bearing blond setae; lip of sternite 8+9 in male relatively short and narrow with sparse long black setae.

*Courtship song* (25°C). Song consisting of a single-volley SRU 1.8–3.3 s long, usually repeated several to many times with a period of 2.2–5.1 s; carrier frequency is a pure (single-frequency) tone, falling from a range of 48–61 to 21–30 Hz during the course of the volley. Amplitude peaks sharply as the volley begins, then declines smoothly but rises again to a broad maximum toward the end of the volley. Volleys of the participants overlap slightly or not at all during heterosexual duets.

*Larva, third instar.* Head pale tan with a pair of relatively narrow, moderately pale, longitudinal dorso-lateral brown stripes with narrow baso-lateral expansions extending towards the eyes; uncommonly (9.7%) with darker spot in dorso-lateral stripe mesad of eyes; elongate fronto-medial spot usually (84%) present; pale lateral stripe present behind eye. Thorax cream coloured; pronotum with tan, longitudinal, dorso-lateral stripes; meso- and metanota with small brown spots near mid-length. Abdomen cream coloured, unmarked, except tubercles sometimes tan.

*Second instar.* Similar to third-instar except as follows. Head with dorso-lateral stripes broader relative to width of head, especially anteriorly; stripes narrowing more abruptly on medial margin of antennae; frontal spot rarely developed; lateral stripe behind eye darker. Thorax with pronotal dorso-lateral stripes usually more prominent, meso- and metanotal spots smaller. Abdomen with tubercles sometimes darker.

*First instar.* Similar to second-instar larva except as follows. Head with dorso-lateral stripes broader relative to width of head; baso-lateral expansions sometimes absent; frontal spot absent; lateral stripe behind eye sometimes darker. Thorax with pronotal dorso-lateral stripes variably prominent; meso- and metanotal spots very small, paler. Abdomen with tubercles frequently pigmented.

*Remarks.* *Chrysoperla zastrowi arabica* can be separated with certainty from the nominate subspecies only by courtship song analysis. However, in most cases adult *C. z. arabica* can be distinguished from *C. z. zastrowi* by the angle of the basal Rs-M crossvein, which in *C. z. zastrowi* always leaves Rs at an oblique angle; in most specimens of *C. z. arabica*, this vein is at right angles to Rs. Both subspecies of *C. zastrowi* can be distinguished from other members of the *C. carnea* group by the relatively small basal dilation of the tarsal claw (large claw ratio). The tarsal claw ratio is larger in *C. zastrowi* than in any other western European member of the species group except for western populations of *C. mediterranea*, but in the latter taxon the claw is hardly dilated at all. Other characters which help to distinguish *C. zastrowi* from other *carnea*-group species, but which are not diagnostic (i.e. black setae on pronotum, genital lip characteristics and green venation), are described further in the main Discussion.

The song of *Chrysoperla z. arabica* is best distinguished from that of *C. z. zastrowi* by its much longer volley duration and volley period, each of which is longer than that of the

nominate subspecies by a factor of 1.6 or more. The song of *C. z. arabica* is also markedly different from that of any other known song species in the *carnea* group. The only other lacewing sometimes showing single-volley SRUs of equivalent length is *C. agilis*, but the carrier frequency in *C. agilis* has a more complex harmonic structure and increases rather than decreases during the course of each volley.

Larvae of *C. z. arabica* and *C. z. zastrowi* are similar, but can usually be distinguished from each other by the frequent presence in *C. z. arabica* of a fronto-medial spot, which is absent in all *C. z. zastrowi*. Another distinguishing feature is the absence in most *C. z. arabica* of a darker spot in the dorso-lateral stripe mesad of the eyes, which is always present in the nominate subspecies. None of the *C. z. arabica* larvae examined simultaneously lacked the fronto-medial spot yet possessed the darker spot in the dorso-lateral stripe, which is the universal condition in *C. z. zastrowi*. The larva of *C. z. arabica* has no features that distinguish it absolutely from that of *C. carnea*, *C. pallida*, *C. mediterranea*, *C. agilis* or *C. lucasina*. Its head markings particularly resemble those of *C. mediterranea* from Carcès, France (Henry et al. 1999) while those of *C. z. zastrowi* most closely resemble markings of some *C. carnea* from Belgorod, Russia (Henry et al. 2002).

*Distribution.* Oman, United Arab Emirates, Israel, Iran.

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