A lacewing with the wanderlust: the European song species 'Maltese', *Chrysoperla agilis*, sp.n., of the *carnea* group of *Chrysoperla* (Neuroptera: Chrysopidae)

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Abstract. A fifth European member of the Holarctic *carnea* sibling species group, *Chrysoperla agilis*, sp.n. is described. This species was initially recognized because of its unique song phenotype. Both sexes produce one type of song, characterized by a single very long volley averaging 4.5 s in duration and repeated every 9.5 s. The unit of exchange during heterosexual duets (the shortest repeated unit) is the single volley. The carrier frequency is upwardly, then downwardly, modulated during each volley. The maximum frequency is higher (around 110 Hz) than in other members of the *carnea* group. Each volley ends with an audible, percussive 'rattle'. Song features vary only slightly over a large geographical range that extends from northern Iran westward to the Azores and northward to southern Switzerland. Discriminant function analysis confirms the uniqueness of the *C. agilis* song in comparison with nine other song species. Morphologically, the adult of *C. agilis* is very similar to *C. carnea* and *C. pallida* and is generally intermediate between them with respect to the size of the pretarsal basal dilation, the shape of the genital lip and chin, the colour and type of setae on the abdomen, and colour markings on the head and mouthparts. No single feature will distinguish *C. agilis* from either *C. carnea* or *C. pallida*, but a suite of physical attributes can be used with reasonable success. Larval morphology fails to distinguish clearly *C. agilis* from other song species. Ecologically, *C. agilis* shares an affinity for low vegetation with *C. lucasina* and *C. carnea*, and a preference for milder, Mediterranean climates with *C. mediterranea*. Adults undergo a colour change to pale yellowish brown during winter diapause, and eggs are laid singly rather than in groups. Based on its ecological characteristics, *C. agilis* may prove to be an effective agent of biological control in the agricultural fields of warmer, drier parts of southern Europe and the Middle East, where other members of the *carnea* group are less common or absent.

Introduction

Hidden within the large complex of cryptic, sibling species of green lacewings that comprise the *carnea* group of *Chrysoperla* is a taxon of unexceptional morphology but unusual courtship song and exceptional vagility. First identified in 1992 from Malta, it has since been collected in large numbers across all the warmer parts of Europe as far north

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as southern Switzerland, and from northern Iran in the east to the Azores archipelago in the central Atlantic Ocean. In the system of temporary names first proposed for cryptic song species by Duelli (1995), 'Maltese *carnea*' has been designated *Cc3*, an acronym of '*Chrysoperla carnea* group, species number three' (Duelli *et al.*, 1996).

As are its siblings in the *carnea* group, *Cc3* is characterized by a species-specific courtship and mating signal, produced by vibrating the abdomen in a temporally and spectrally patterned manner. These low-frequency vibrations are transmitted efficiently through the lacewing's legs to the lightweight substrates upon which it typically stands, and will travel up to a metre from the source (Henry & Wells, 1990b). Such substrate-borne signals are oscillatory rather than percussive, and the mode of sound production is called tremulation (Morris, 1980). In the *carnea* group, males and females of a species produce the same courtship song, establishing prolonged, 'polite' heterosexual duets that are necessary for copulation.

Even among species noted for their misleading morphologies, *Cc3* has proven to be one of the most difficult to diagnose from preserved specimens. Over much of southern Europe, for example, *Cc3* is easily confused with both *Cc4* 'motorboat' and *Cc2* 'slow-motorboat', now formally recognized as *C. carnea* (Stephens) and *C. pallida* Henry *et al.*, respectively (Henry *et al.*, 2002). Another source of diagnostic confusion is ongoing conflation of *C. carnea* with *C. kolthoffi* (Navás) from far eastern Asia, and of *C. pallida* with 'true *C. carnea*' (Leraut, 1992; Thierry *et al.*, 1998). Because of the critical importance of the *carnea* group to the biological control industry, it is imperative that we understand its systematics. Addressing this very problem, one recent work boldly recommended that entomologists disregard the *carnea* group song species altogether and refer only to '*Chrysoperla carnea sensu lato*' (Tauber *et al.*, 2000). Arguing against this retrograde approach is our increasing awareness that each cryptic species of the *carnea* group exhibits distinctive ecological characteristics, meaning that different members of the complex cannot necessarily be substituted for one another in a particular agricultural application or at a specific locality (Henry *et al.*, 2001, 2002). Consequently, mistaking *Cc3* for *C. carnea*, *C. pallida* or some other closely related species in the complex has an important economic cost, in addition to being a scientific error. The broadly sympatric ranges of the song species and the typically high abundance of each at a given site make species misidentification simultaneously more likely, and more damaging.

We describe here the *Cc3* song species, including its song phenotype, adult and larval morphology, and what we know of its ecology and ecophysiology. Sites from all portions of its range are represented, and analyses of geographical variation are presented. The phenotypic traits of *Cc3* are then compared and contrasted with those of other song species of the *carnea* group, with the goal of establishing a suite of useful diagnostic characters for both adults and larvae. The species is then named and formally described, as *Chrysoperla agilis*.

Materials and methods

Collecting, rearing and identification

Adults of *Cc3* and other *Chrysoperla* spp. were collected by the authors and many collaborators at numerous sites and elevations across Europe and adjacent regions between 1984 and 2002 (Table 1). All insects were shipped or hand carried alive to Storrs, CT for maintenance, rearing and song analysis. The protocols are described fully in other papers (summarized in Henry *et al.*, 1996, 1999a).

Individuals of *Cc3* were identified from their courtship songs using computer playback of previously recorded European song types to each insect (see below). Once identified, each individual was examined for diagnostic morphological features that might distinguish *Cc3* from other song species. 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 winter diapause. Larval studies were limited to the progeny of individual adults confirmed to be *Cc3* by song analysis.

Several adult and larval specimens of verified song phenotype from each locality were placed at -70 to $-100\,^{\circ}$C for molecular systematic studies (Henry *et al.*, 1999b), whereas others were deposited as holotype, paratypes or 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, Birmensdorf, Switzerland (SFRI-WSL); and the W. F. Barr Museum, Moscow, Idaho (WFBM).

Analysis of songs

Between five and twenty-one complete courtship songs (shortest repeated units (SRUs), the phrase exchanged between partners during a heterosexual duet) of each specimen of *Cc3* were recorded on cassette tape (Dolby^{TM} off), digitized at ≥ 500 Hz, and analysed with hardware and software on a personal computer (see Henry *et al.*, 1996, 2002). Males and females in the laboratory were induced to sing by playing back to them prerecorded songs of conspecifics, using methods described previously (Wells & 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 internal modulation of its carrier frequency. Some taxa have relatively simple songs composed of single-volley SRUs repeated many times, whereas others produce complex songs consisting of much longer, multivolley SRUs repeated only in response to other such songs. The *Cc3* analysed here has a simple, repeating, single-volley song in which the volley and the SRU are one and the same. Volleys are very long and frequency modulated (see Fig. 1); the relatively pure tones at the start and middle of each volley

Table 1. Collection sites of *Cc3* used in song analyses and morphological studies, 1984–2002.

Local site (with nearest city or region)	Country	Altitude (m)	Latitude (°N)	Date
Madeira archipelago[a]	Portugal	0–10	32°41'	July 2001
Azores archipelago	Portugal	0–10	37°44'	August 2000
Agadir, Morocco[a]	Northwestern Africa	100	30°30'	1985
La Mora (mountain pass, Granada)	Southern Spain	1390	37°13'	19 July 1995
Mojacar (Alicante, on pine)	Southern Spain	0–10	38°25'	9 July 1989
Carcès	Southern France	180	43°20'	August 1994
Ticino: Monte Caslano, Biasca, Agarone, Piodina, Brissago	Southern Switzerland	275–820	46°30'	1981–94
Cavaglio & Traffiume[a]	Northern Italy	500	46°30'	April/June 1994
Scaria, Campania	Central Italy	0–10	41°	July 1993
Cecita, Calabria	Southern Italy	1150	38°25'	July 1993
Gioiosa Marea	Northeastern Sicily	100	37°48'	July 1993
Francavilla	Northeastern Sicily	480	37°48'	July 1993
Malta	Malta	0–10	35°52'	1991
Xilokastron (pine forest on coast)	Greece	0–10	38°	June 1994
Kalentzi	Greece	1000	37°50'	June 1994
Taygetos Pass (field edge near Sparta)	Greece	1100	36°40'	June 1994
Monemvassia (light)	Greece	100	36°35'	June 1994
Gorgân (cotton field)[a]	Northern Iran	290	36°44'	June 2002
Eilat	Israel	0–10	29°34'	15 October 1993–94

[a]Confirmed *Cc3* song, but songs not included in this study.

decay into a noisy rattle towards its end. Measurements were taken on seven 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); the duration of the initial 'pure tone' portion of each volley; and the number of volleys per SRU (in *Cc3*, always one) (Table 2, Fig. 1).

Analyses were performed on the songs of seventy-four *Cc3* individuals. To minimize temperature effects, all songs were recorded at 25 ± 1 °C. Although many populations throughout the species' range were sampled (Table 1), we grouped these into eight regional areas (Fig. 2): the Azores archipelago (sixteen individuals), southern Spain (four), southern France (five), the Alps (ten), southern Italy and Sicily (twenty-one), Malta (four), Greece (ten) and Israel (four). Most statistical analyses were performed on these larger geographical units. The mean of each song feature was calculated from five to twenty-one songs (volleys or SRUs) per individual, taken as the representative value of the feature for each individual in other analyses. Coefficients of variation were calculated for each song feature, first for each individual (within-individual variation) and then for the entire population (between-individual variation). An analysis of variance (ANOVA) was performed on individual averages using the geographical region as the independent variable. Scheffé's (1953) contrast test was used to compare population means for significant differences. All statistical analyses were performed using STATISTICA/WIN version 5.5A (StatSoft, 1999).

Another approach to analysing multidimensional variation utilizes discriminant function analysis. In this pro-

cedure, several components of variance are extracted from the measured variables. To examine geographical variation in the songs of *Cc3*, the six song features showing variation were used to extract six roots. Statistical differences in songs among the eight geographical populations were determined from the matrix of squared Mahalanobis distances generated by the discriminant function analysis, assuming a priori classification probabilities proportional to group sizes (Table 3).

Global analysis of song differences among the cryptic species of the *carnea* group was limited to ten (of fifteen) ingroup taxa for which complete acoustical data for twenty or more individuals existed. Again, a discriminant function analysis was applied to song features. In discriminant function analysis, 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, eighteen possible song variables yielded seven 'least correlated' features (specified in Table 4), which included six used in earlier studies plus a new one characterizing within-volley frequency modulation (Henry *et al.*, 1999a,b, 2002). These seven features were then used to extract seven multidimensional roots, and statistical differences in songs among the ten lacewing taxa were determined from the Mahalanobis matrix (Table 4). The original set of eighteen measurements included features found in species with more complex songs than *Cc3*, which therefore had to be added to the seven basic features of *Cc3* as redundant data.
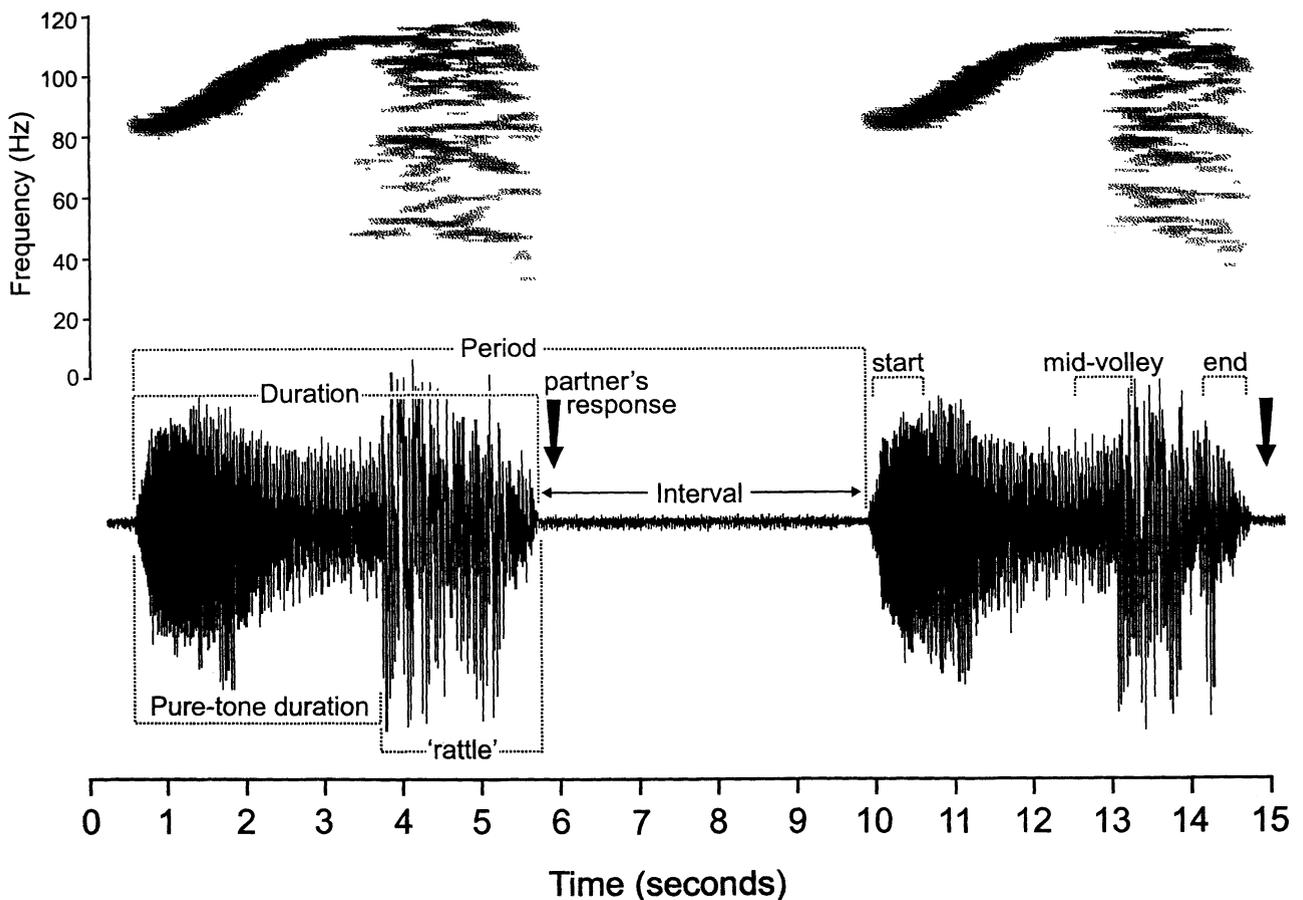
Fig. 1. Oscillograph of a typical song of *Cc3*, showing two complete shortest repeated units (SRUs). Song features discussed in the text are labelled. The specimen was collected near Carcès, France.

Adult morphology

Twenty-one males and ten females identified acoustically as *Cc3* were examined for external morphological features that might vary among populations across the geographical range. Localities included the Azores archipelago, August 2000 (two males, two females); Carcès, France, August 1994 (three males); Ticino, Switzerland, 1981–94 (four males, two females); Sicily, Italy, July 1993 (four males, one female); Greece, June 1994 (six males, four females); and Eilat, Israel, October 1993–94 (two males, one female). These sites were a geographically representative subset of the localities listed in Table 1.

The adults were examined for the states of nineteen characters. These included the ground colour of the body; the presence, extent and colour of markings on stipes, palps, gena, clypeus, frons, and the postoccipital region; the relative abundance and distribution of black and blond setae on the pronotum; the relative size of basal dilation of the tarsal claw expressed as a ratio (see Henry *et al.*, 2002); the extent to which the fore wing is rounded or tapered at the apex; the relative width of the fore wing expressed as the ratio of length to breadth at the widest point; the presence or absence of black markings on wing veins; the length and colour of costal setae; the length of abdominal setae; the relative abundance and distribution of black and blond setae on the three distal abdominal sternites; the shape and relative proportions of the genital 'lip' and 'chin' at the apex of sternite $8 + 9$ in males (Fig. 3); the length and colour of setae clothing the genital lip; the shape of the tignum of male genitalia; and the presence or absence of a dark brown stripe on the pleural membrane of the 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; Fig. 4 in Henry *et al.*, 2002), representing the extent of dilation of the claw base (see also Brooks, 1994 and Thierry *et al.*, 1998).

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 and drawn (using a *camera*

Table 2. Overall mean values at 25 ± 1 °C of the song characteristics of all *Cc3* collected from the eight geographical areas specified in Fig. 2. Each value is the mean of the means of *n* individuals in the population subsample ± one standard deviation. Pairwise comparisons of males to females were assessed for statistical significance using *t*-tests for independent samples. SRU = shortest repeated unit exchanged between individuals while dueting, equivalent to the volley in *Cc3*.

	Frequency measures of volleys (Hz)			Time measures of volleys (ms)			Volleys/SRU
	Start	Middle	End	Duration	Period	Pure tone duration	
All songs (*n* = 74)	80.00 ±6.64	108.55 ±6.67	98.58 ±7.23	4489.00 ±1082.69	9459.61 ±1226.74	2817.34 ±573.01	1
Males (*n* = 36)	77.93** ±6.01	108.27 ±5.68	100.21 ±6.44	4206.49* ±1217.05	9009.89*** ±1236.50	2645.97* ±646.44	1
Females (*n* = 38)	81.96** ±6.70	108.81 ±7.55	97.04 ±7.67	4756.64* ±872.00	9862.00*** ±1119.52	2979.69* ±443.70	1

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

lucida) through a binocular microscope at 100× magnification. Measurements of 'lip' and 'chin' dimensions were taken from the drawings (Fig. 3, line segments defined by points A–G). The ratio AC/AB (or AB/BC) reflected the relative prominence of the chin, whereas DE/FG was used to characterize 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 & Bickley, 1963; Brooks, 1994).

Larval morphology

Some 398 first-instar, 481 second-instar and 348 third-instar larvae from five acoustically identified populations of *Cc3* from France, Switzerland, Italy and Greece were examined. The larvae were offspring from adults collected at these localities and confirmed to be *Cc3* by song analysis. Specific sites and samples sizes (*n* = first, second and third instars) included Carcès, France (*n* = 0, 6, 6); Biasca in the Ticino region of southern Switzerland (*n* = 130, 146, 95); two sites in Sicily, i.e. Francavilla (*n* = 69, 106, 113) and Gioiosa Marea (*n* = 89, 115, 77); and Monemvassia, Greece (*n* = 110, 108, 57). The larvae were boiled in 100 ml of distilled water with a drop of liquid detergent, allowed to cool, then transferred to 70% ethanol + 5% glycerol + 25% distilled water for storage. The specimens were examined at 50× magnification (Fig. 4).

Results

Song phenotype

For song measurements taken from individuals of *Cc3*, coefficients of variation were very low, averaging 10.17% for the three temporal song features and 2.48% for the three frequency features. Therefore, we felt that it was valid to reduce the data to individual averages, as in previous studies of song variation in lacewing species (Henry & Wells, 1990a). Among-individual coefficients of variation for the entire sample of seventy-four individuals averaged 18.79 and 7.26% for temporal and tonal features, respectively.

Adult males and females of *Cc3* produced a single type of song (=SRU), which was used in both solitary calling and dueting. The SRU was monosyllabic but repeating, consisting of a single volley about 4.5 s long repeated every 9.5 s (Fig. 1, Table 2). During the first half or two-thirds of the volley, the carrier frequency rose from about 80 Hz to a peak average of 108.5 Hz, falling during the last half or third of the volley to approximately 100 Hz (25 °C). Each volley was also characterized by a progressive increase and decrease in intensity, such that the maximum amplitude was achieved near its frequency peak (Figs 1, 5). After achieving the maximum frequency and amplitude, the volley became
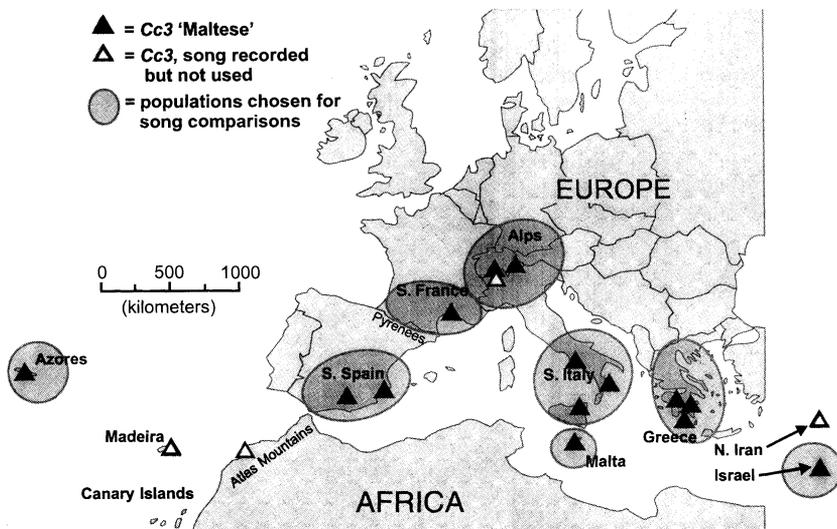
Fig. 2. Collecting sites of *Cc3* in Europe and adjacent regions, with ellipses drawn around the eight discrete geographical areas used in song comparisons.

distorted with noise and began to 'rattle', losing its previously pure tonality. This rattling noise was caused by numerous direct blows to the substrate by the abdomen, produced as the insect sharply curved the tip of its abdomen ventrally towards the substrate while continuing to sing (Fig. 1, spikes). About 2.8 s of each volley consisted of pure tone tremulation, prior to the noisy percussive section.

Heterosexual dueting in *Cc3* 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 sequence of run-on volleys, with the responses of the partners alternating with one another (Fig. 6). 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 his genitalia prior to copulation.

Sex differences in songs

Although oscillographs and sonographs of male and female songs look very much alike, the two sexes were not acoustically identical (Table 2, asterisks). Specifically, females were characterized by significantly longer volleys, longer volley periods and slightly higher carrier frequencies than males. However, sex differences were judged small enough to warrant the pooling of all individuals in other comparisons.

Other variation in songs

Using ANOVA and *post hoc* Scheffé's tests, populations of *Cc3* from eight geographical areas were compared with respect to measurements of their six variable song features, shown in Fig. 7. Differences among populations were not large, and reached significant levels for only two of the six features, initial and mid-volley frequency (different letters above the bars in Fig. 7). For initial volley frequency, Greece and Israel were the most different from the other populations, and were quite similar to one another. However, significant differences in the population means of mid-volley frequency did not follow the same geographical pattern.

Table 3. Results of a discriminant function analysis of six song features of eight geographical populations of *Cc3*, showing squared Mahalanobis distances (above the diagonal) and *F*-values (below the diagonal). Features included volley duration, volley period, duration of initial pure tone portion of volley, carrier frequency at volley start, carrier frequency at mid-volley, and carrier frequency at volley end. Wilks' lambda $= 0.1333$, approximate $F_{(42, 289)} = 3.6996$.

	Azores	Southern Spain	Southern France	Alps	Southern Italy	Malta	Greece	Israel
Azores	–	3.82	1.85	4.04	1.02	3.51	13.41	22.13
Southern Spain	1.47	–	4.75	4.97	5.05	9.69	11.95	23.69
Southern France	0.90	1.25	–	7.77	1.63	4.06	13.29	23.51
Alps	3.50**	1.72	3.31**	–	4.88	10.37	10.49	18.33
Southern Italy	1.35	2.03	0.84	4.67***	–	3.23	10.30	17.92
Malta	1.35	2.24	1.07	3.59**	1.30	–	11.41	14.52
Greece	11.62***	4.14**	5.67***	7.27***	9.85***	3.95**	–	4.21
Israel	8.52***	5.47***	6.21***	6.35***	7.20***	3.35**	1.46	–

$*P < 0.05; **P < 0.01; ***P < 0.001.$

Table 4. Results of a discriminant function analysis of seven 'least correlated' song features in ten song species of the *carnea* group, showing squared Mahalanobis distances (above the diagonal) and *F*-values (below the diagonal). Features included volley duration at mid-shortest repeated unit (SRU), volley period at mid-SRU, SRU duration, mid-volley frequency at SRU start, end-volley frequency at SRU start, initial volley frequency at mid-SRU, and mean maximum frequency change within a volley. All pairwise comparisons showed highly significant differences. The smallest distances, marked in bold, are between *Chrysoperla adamsi* (North America) and *C.* '*adamsi*-K' (Asia) and between *C. mediterranea* and *C. downesi* (*mohave*). Wilks' lambda = 0.00001, approximate $F_{(63, 3813)} = 388.37$.

	plorabunda	*adamsi*	'*adamsi*-K'	*johnsoni*	*mediterranea*	*lucasina*	*downesi* (*mohave*)	*pallida*	*carnea*	*Cc3*
plorabunda	–	21.64	19.38	26.44	82.66	236.16	85.20	216.37	160.87	435.26
adamsi	100.73	–	**6.42**	21.70	92.94	205.07	88.73	204.14	143.23	400.45
'*adamsi*-K'	67.60	21.43	–	18.86	98.80	230.88	100.51	241.41	174.76	383.31
johnsoni	154.79	118.05	73.76	–	86.28	193.86	85.25	216.58	161.11	310.99
mediterranea	371.28	394.37	321.18	450.14	–	53.08	**9.75**	122.21	69.60	263.18
lucasina	1599.42	1276.34	992.52	1661.31	314.97	–	56.39	133.87	81.04	231.18
downesi (*mohave*)	165.02	167.62	167.16	175.64	18.15	122.02	–	159.92	100.85	282.99
pallida	804.26	723.78	681.97	909.75	421.55	622.90	274.04	–	23.67	349.54
carnea	797.25	666.85	609.48	943.23	312.58	548.81	195.32	87.99	–	365.94
Cc3	2202.39	1901.07	1356.42	1865.98	1204.49	1610.86	552.54	1319.57	1851.65	–

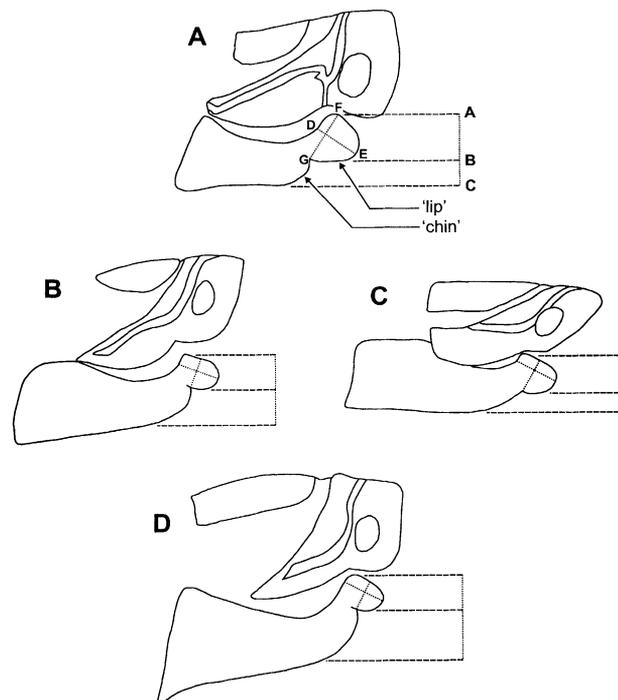Applying a discriminant function analysis to geographical variation revealed additional pairwise differences among populations of *Cc3*. As shown in Table 3, sixteen of twenty-eight possible pairwise comparisons exhibited statistically significant differences. Greece, Israel and the Alps were relatively distinctive populations, each differing significantly in six of seven possible comparisons; however, Greece and Israel did not differ from each other. Southern Spain was the least distinctive population, differing significantly from just two other regions. Roots 1 and 2 of the discriminant function analysis are plotted against each other in Fig. 8. Eighty-three per cent of total variation was contained within the first two roots of the analysis, 63% in the first root and 20% in the second (analysis not shown). Figure 5 illustrates songs of typical individuals from six of the eight geographical regions.

When the songs of *Cc3* were included with other cryptic song species of the *carnea* group in a discriminant function analysis, all ten song species were significantly different from one another in all pairwise comparisons, based on the matrix of squared Mahalanobis distances (Table 4, Fig. 9). The two most similar species pairs were *C.* '*adamsi*-K' (Asia) vs *C. adamsi* Henry, Wells & Pupedis and *C. mediterranea* vs *C. downesi* (*mohave*), both of which were comparisons between completely allopatric taxa living on different continents (Henry *et al.*, 1999b).

Although formal behaviour experiments were not conducted, it was observed throughout this study that individuals of *Cc3* responded only to conspecific songs in playback trials. Playbacks of songs from any of the eight geographical regions elicited normal dueting responses from individuals obtained anywhere within the range of the species.

Fig. 3. Diagnostic lip and chin at the apex of sternite 8 + 9 in two males of *Cc3* (B, Carcès, France; C, Biasca, Switzerland), with *Chrysoperla carnea* (A, Edinburgh, Scotland) and *C. pallida* (D, London, England) shown for comparison. Overdrawn are line segments ABC, DE and FG for calculating shape ratios. The lip was judged to be narrow and not protruding if DE > FG and the chin broad (strong) if AB < BC.

Adult morphology

Ground colour of the body. In all specimens examined, the body was uniform pale green, with a pale yellow dorsal stripe running the length of the body.
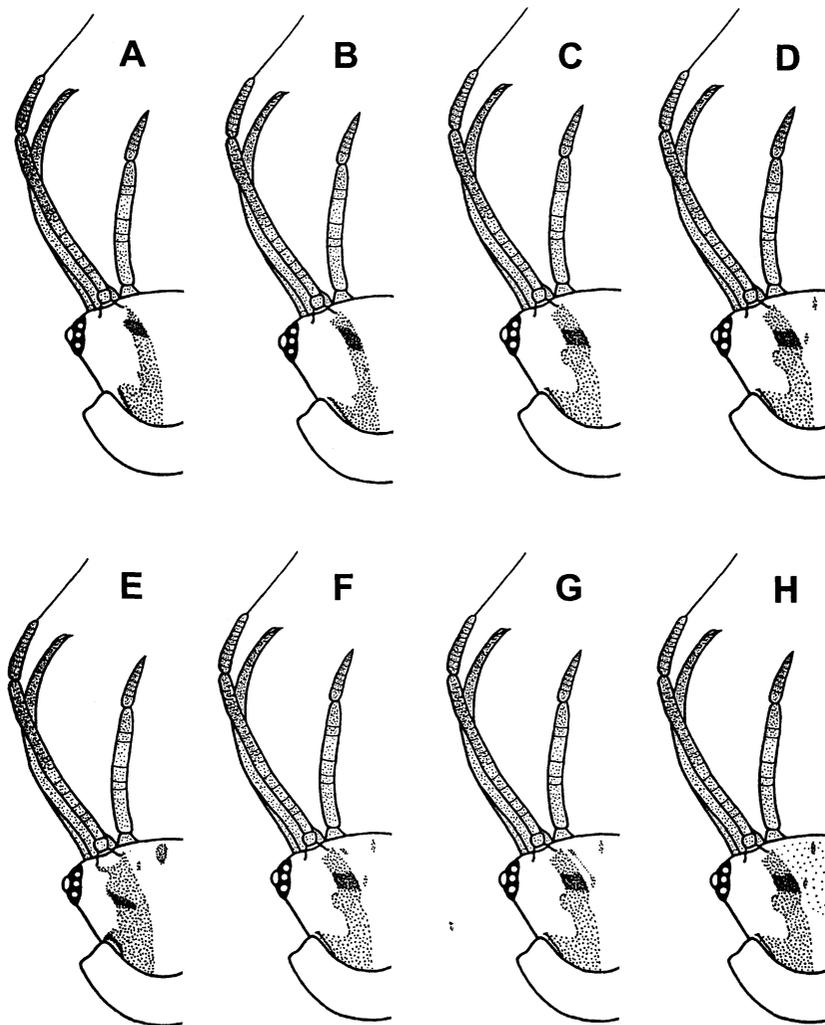
Fig. 4. The *Cc3* third-instar larval head capsules from selected localities across Europe, characterized from specimens A–H by progressively more 'ornate' colour patterns. A, Gioiosa Marea, Sicily; B, Francavilla, Sicily; C, F–H, Monemvassia, Greece; D, Carcès, France; E, Biasca, Switzerland. The most typical condition for the species is three spots, best shown in E (Biasca).

Extent of markings on the stipes. The stipes was entirely brown in twenty-two of thirty-one specimens. The remaining specimens possessed an apical brown spot on the stipes. The intensity of brown varied from light to moderately dark.

Colour of the palps. Most specimens possessed a brown dorsal stripe on the basal segment of the palps. However, in two specimens, the stripe was very pale, and three specimens were unmarked.

Extent and colour of genal markings. The gena was marked with a broad brown band in nearly all specimens. The two exceptions displayed a red rather than brown band.

Clypeal markings. In most specimens the clypeus was marked laterally with a brown stripe, highlighted in four individuals by a red outer edge. The two specimens possessing red genae also displayed red rather than brown stripes on the clypeus.

Frontal markings. The frons was unmarked.

Markings on the postoccipital region. The postocciput was unmarked.

Relative abundance and distribution of black and blond setae on the pronotum. The proportion of black (vs blond) setae on the pronotum ranged from 0 to 80%, averaging 25%. Five individuals possessed only blond setae. There was no discernible relationship between setal colour and the geographical origin of specimens, except that black setae were not present in the three specimens examined from Israel.
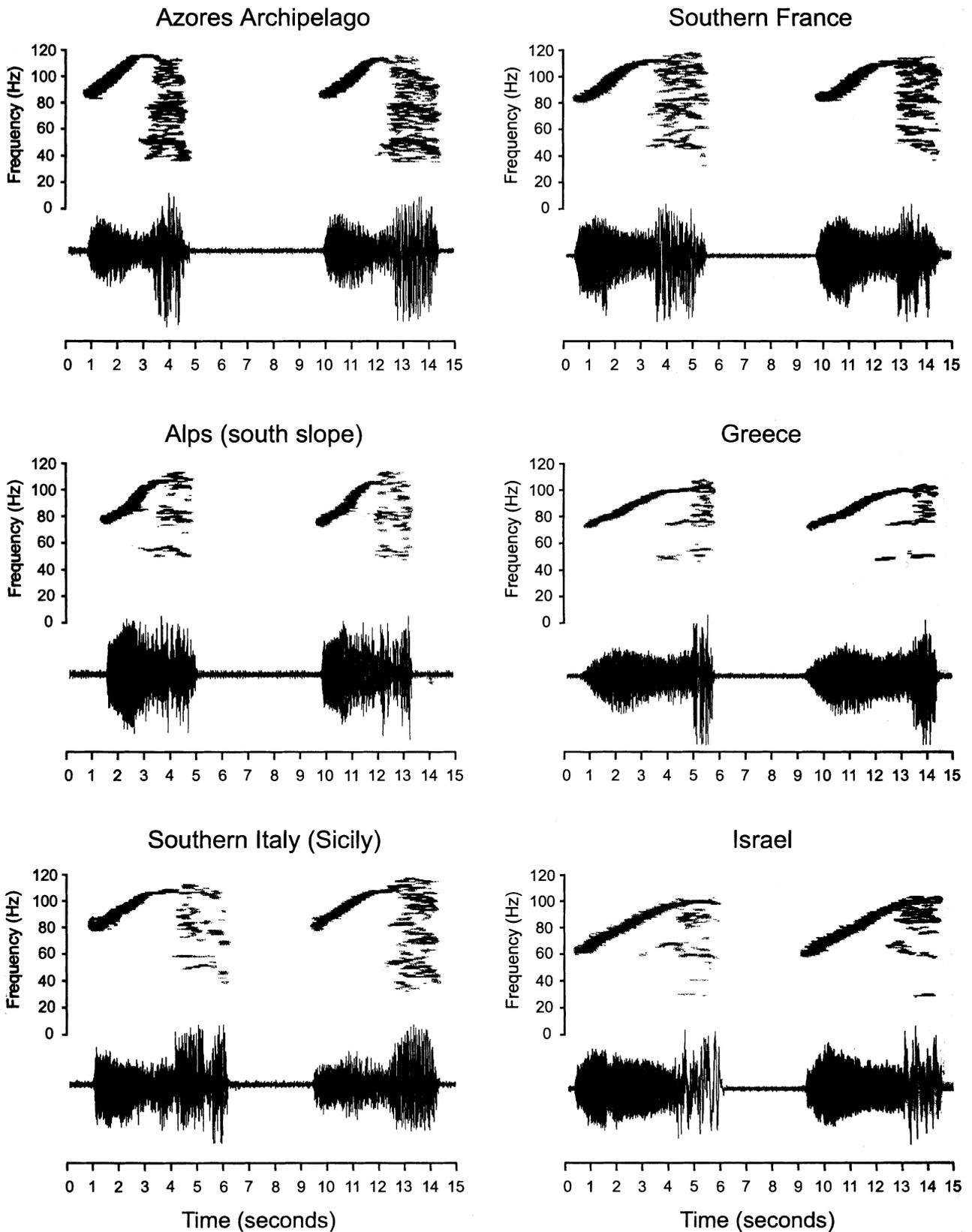
Fig. 5. Oscillographs and sonographs (above each oscillograph) of typical songs of *Cc3* from six different parts of its range.
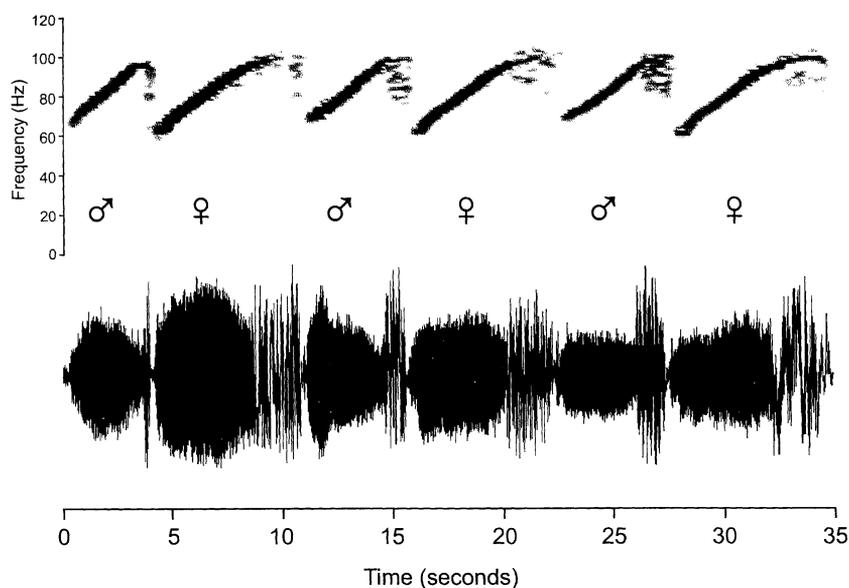
Fig. 6. Oscillograph showing a portion of an ongoing heterosexual duet between two individuals of *Cc3* collected near Eilat, Israel.

Relative size of basal dilation of the tarsal claw expressed as a ratio of the length of the claw tooth to the length of the basal dilation (the 'claw ratio'). The claw ratio ranged from 1.94 to 2.53 in the twenty-six specimens measured (mean ± standard deviation = 2.23 ± 0.15). Variation in this character was not correlated with geography.

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

Relative width of the fore wing expressed as a ratio of length to breadth at the widest point. The aspect ratio of the fore wing ranged from 2.78 to 3.14 in the twenty-six specimens measured (mean = 2.94).

Presence or absence of black markings on wing veins. All specimens displayed crossveins marked with black in the basal quarter of the fore wing.

Length of costal setae. The costal setae were relatively long (fringe length 0.38–0.75 mm).

Relative abundance and distribution of black and blond setae on abdominal sternites. The proportion of black (vs blond) setae on the three apical abdominal sternites ranged from 0 to 100%, averaging about 7%. Three individuals showed mostly (or all) black setae on one sternite, but mostly (or all) blond setae on the sternite just in front or behind it. There was no discernible relationship between setal colour and the geographical origin of the specimens, nor was the colour of the abdominal setae correlated with the colour of the pronotal setae (see above).

Length of abdominal setae. Setae clothing the abdomen were relatively long and fine.

Shape of the genital lip and chin at the apex of sternite 8 + 9 in males. In general, the genital lip was small (narrow) to moderate and not protruding, whereas the chin beneath it was moderate to small (DE > FG, AB ≥ BC; Fig. 3). However, the shape of both structures varied significantly among the specimens examined. Variation was not correlated with geography.

Length and colour of setae clothing the genital lip. The genital lip was clothed with very short, fine, pale setae, but with a thin scattering of longer setae.

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

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

Larval morphology

Larval head capsule markings (Fig. 4) of *Cc3* consist of a pair of longitudinal, dorsolateral brown stripes from near the mid-dorsal cervical margin to the medial margin of the antennal bases, each with a basolateral expansion extending towards the eye. This pattern is typical for larvae of *Chrysoperla* spp. (Henry *et al.*, 1996, 1999a, 2002). First-instar larvae had the palest and broadest (relative to head width) dorsolateral stripes, with broad basolateral expansions that extended nearly to the eyes. The basolateral expansions were poorly defined because of the width of the dorsolateral stripe. Second-instar larvae were intermediate.
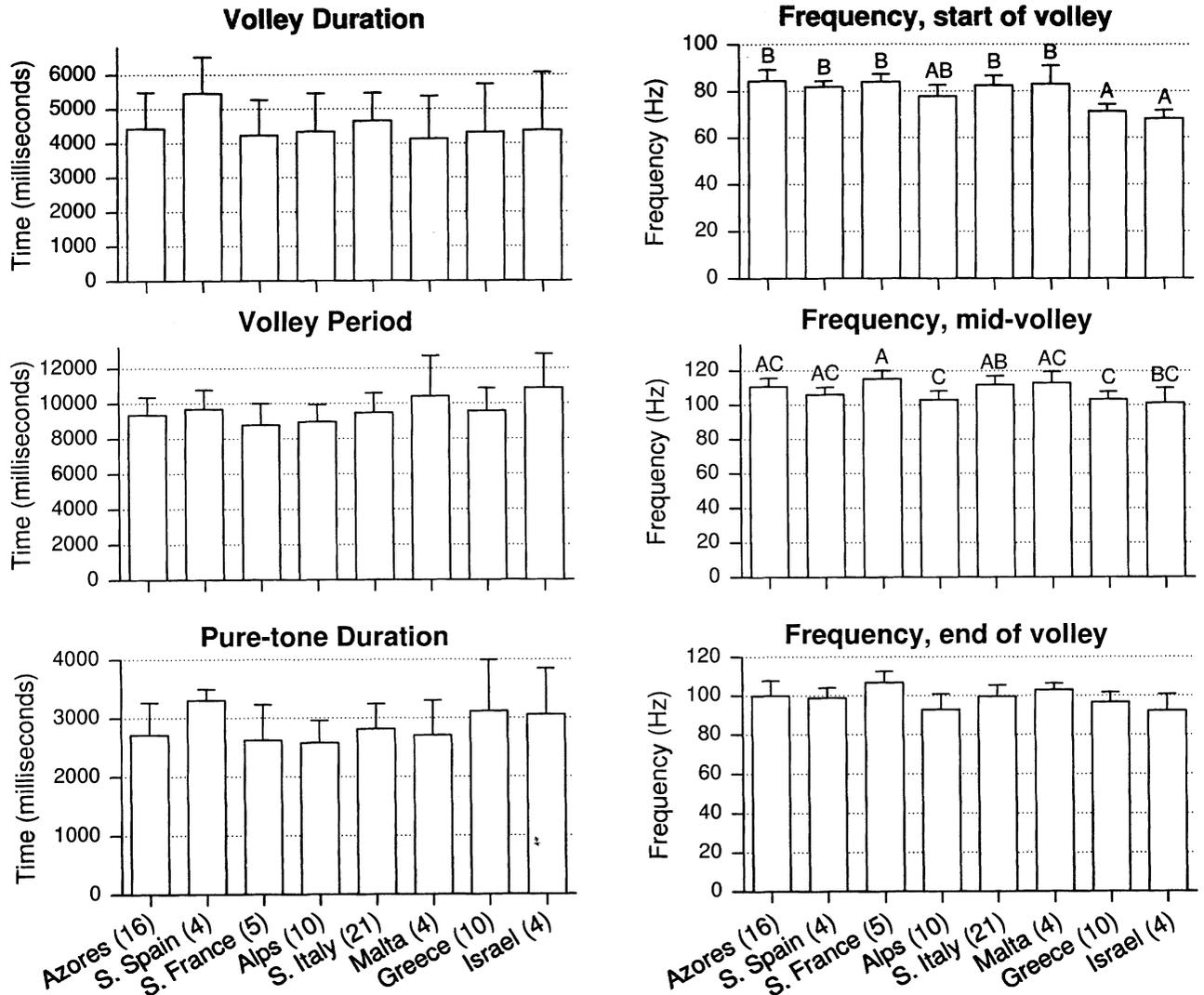
Fig. 7. Bar graphs comparing eight distinct geographical populations of *Cc3* with respect to the means (bars) and standard deviations (error bars) of six song features. Both sexes were included in the calculations. Only the carrier frequency at the start and middle of volleys showed significant geographical variation. For these two features, populations with significantly different means share no letters (determined by ANOVA and *post hoc* Scheffé's tests, $P \leq 0.05$).

Third-instar larvae had the darkest and relatively narrowest dorsolateral stripes with the narrowest but best-defined basolateral expansions. Third-instar larvae usually had a darker spot within the dorsolateral stripe mesad of the eye. They could also exhibit frontal spots between the two stripes, numbering one (mid-frontal, between the antennal bases; not illustrated), two (mesad of the eyes; not illustrated), three (a combination of the preceding, and the most common condition; Fig. 4D,E) or five (three spots as just described, plus two spots mesad of the antennal bases that occasionally fused with the dorsolateral stripes; Fig. 4F,G). In a few individuals with five frontal spots, the entire frons could be lightly pigmented (Fig. 4H). All instars varied within and among populations. The remainder of the results focus on third-instar larvae.

The breadth, colour intensity and regularity of the margins of the dorsolateral stripe varied within and among populations (Fig. 4), as in larvae of other *Chrysoperla* spp. (Henry *et al.*, 1996, 1999a, 2002). Individuals from Carcès (France), Biasca (Switzerland) and Monemvassia (Greece) tended to have a broader and darker dorsolateral stripe (Fig. 4C–H). The presence of zero, one, two, three or five frontal spots, or pigmentation of the entire frons, yielded six distinct patterns of head markings among *Cc3* larvae. The four specimens from Carcès included three head marking patterns, with two, three (Fig. 4D) or five spots. The sample from each of the other four populations included five or six colour patterns. However, the proportion of each pattern varied among these populations. Individuals from Biasca and Monemvassia
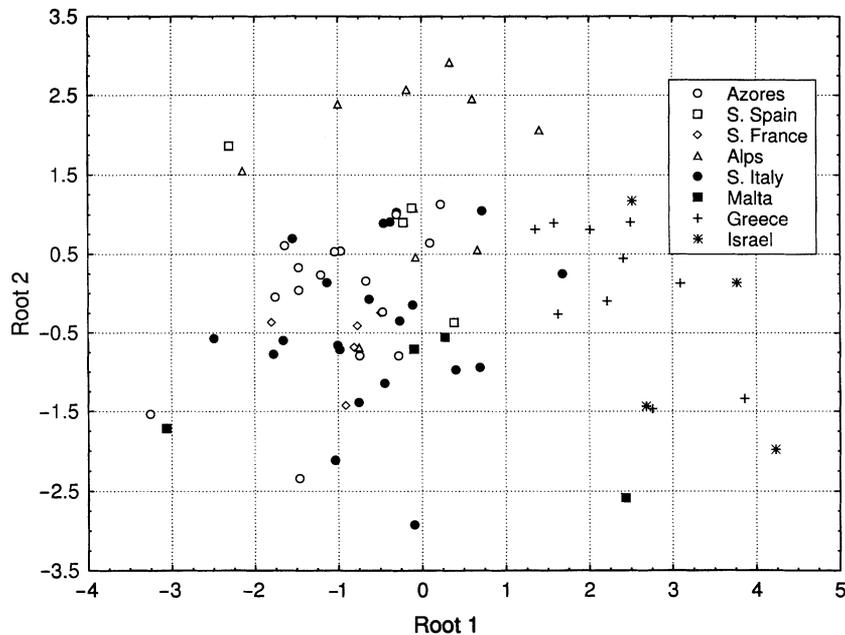
Fig. 8. Scatterplot of the first two roots of a discriminant function analysis of six song features of *Cc3* (see text for details). Each data point represents a single individual, coded by geographical region (shown in Fig. 2).

tended to have more and darker frontal spots (Biasca: three spots 63%, five spots 19%; Monemvassia: three spots 39%, five spots 35%). At the other extreme, 71% of individuals from Gioiosa Marea (Sicily) had no frontal spots (Fig. 4A). The population from Francavilla (Sicily) was bimodal, with 48% of individuals having no frontal spots (Fig. 4B) and 44% of individuals having three frontal spots. The frequency of coloration over the entire frons varied from 0% in Francavilla to 18% in Monemvassia (Fig. 4H).
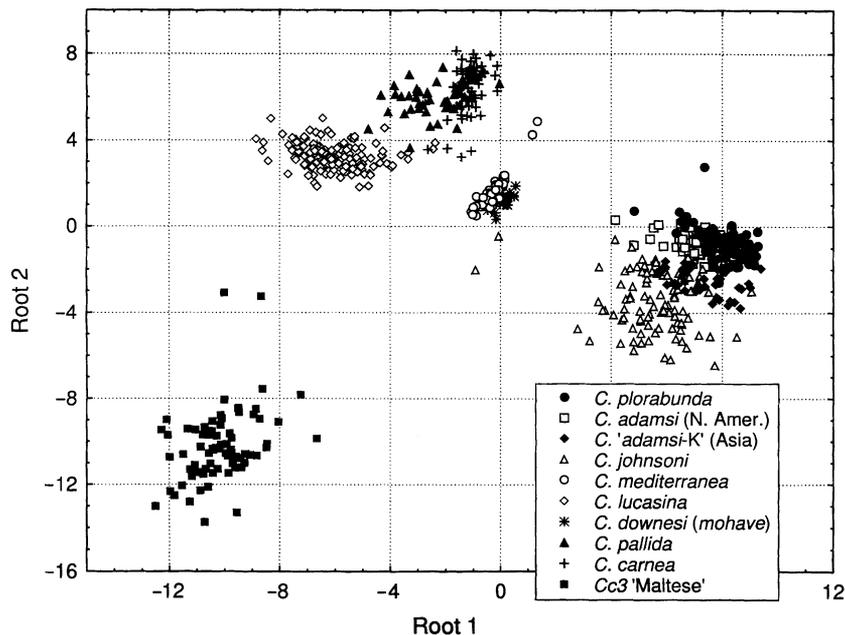

Fig. 9. Scatterplot of the first two roots of a discriminant function analysis of seven song features (see text) in ten distinct song species of the *carnea* group. Each data point represents a single individual, coded by species.

Ecology

'Maltese *carnea*' was restricted to areas of the western Palaearctic characterized by mild winters, and seemed not to be found north of the Ticino region (Biasca) in southern Switzerland. It was particularly common below 500 m in coastal habitats with Mediterranean climates, where it was often the most abundant lacewing species on herbaceous plants and shrubs. Neighbouring pines harboured *C. mediterranea* (Hölzel) at the same sites. At higher elevations and in agricultural crop lands, *C. lucasina* (Lacroix) became the dominant lacewing species in habitats otherwise favourable for *Cc3*. However, at drier sites in southern Spain, *Cc3* alone was found in cultivated alfalfa, and in northern Iran it was abundant in cotton fields (P. Duelli and H. Heydari, unpublished data).

We know little about the life cycle of *Cc3*. Eggs were laid singly on vegetation. In southern Switzerland, the species developed very locally on riverine shrubs and on herbaceous plants in meadows. In Mediterranean regions, larvae were found on alfalfa and streamside Asteraceae. Adults of *Cc3* experienced a colour change during winter diapause from green to pale yellowish brown, induced by short photoperiods.

In a mixed container of adult *Cc3*, *C. carnea* and *C. pallida*, the males of *Cc3* were conspicuously more active and agile than the males of the other two sympatric species.

Discussion

Intraspecific variation in song phenotype

Measurements of within-individual and between-individual variation are low in *Cc3*, indicating that song features are highly constrained, presumably by stabilizing selection acting on the specific mate recognition system (Paterson, 1986; Butlin & Ritchie, 1994). Males differ from females only slightly, and then principally in the shorter average duration and period of their SRUs (Table 2). This minor sex difference characterizes several other song species in Europe with multivolley SRUs, including *C. lucasina* (male 'short songs', Henry *et al.*, 1996), *C. mediterranea* (Henry *et al.*, 1999a), and *C. carnea* and *C. pallida* (Henry *et al.*, 2002). It results from the tendency for males of these species to sing more readily than females when alone, producing a truncated version of the courtship song that appears to be useful for initiating duets with potential partners in the vicinity. A similar sex effect is found in the multivolley North American species *C. johnsoni* (Henry, 1993), but not in *C. downesi*/'mohave' where it might also be expected (Henry, 1980). The effect has not been observed previously in lacewing species that reciprocally exchange single volleys when dueting.

Among populations of *Cc3* selected from different parts of the species' range, only small differences are found in any song feature (Figs 5, 7), and discriminant function analysis shows weak clustering of individuals by geographical loca-

tion (Table 3, Fig. 8). The differences which exist are most apparent in peripherally located populations such as Greece and Israel, as one might expect in a widely distributed species. However, the isolated population from the Azores is not different from most mainland populations (Table 3, Figs 5, 7, 8), suggesting that isolation by distance has little consistent effect on song phenotype in this species. Figure 5 also visually highlights the fundamental geographical homogeneity of *Cc3* courtship songs. More importantly, the insects themselves fail to discriminate between local songs and those recorded from individuals obtained from distant geographical locations.

Comparison of songs among species

The courtship and mating song of *Cc3* is highly distinctive. Its volleys are significantly longer (mean = 4.5 s) and attain higher carrier frequencies (mean = 108.5 Hz) than those found in any other known member of the *carnea* group. Although each species in the complex is significantly different from every other based on discriminant function analysis (Table 4), some species are more isolated in 'factor space' than others. For example, among sympatric taxa, North American *C. plorabunda* (Fitch) and *C. adamsi* are quite similar to each other, as are *C. carnea* and *C. pallida* in Europe (Fig. 9). Other sympatric pairs, such as *C. lucasina* and *C. mediterranea*, share fewer song attributes. The song of *Cc3* maps on to a remote region of song factor space, far from any of the other nine species included in the analysis (Fig. 9). However, *Cc3* does share upward modulation of the volley carrier frequency with its European siblings *C. lucasina*, *C. carnea* and *C. pallida* (Henry *et al.*, 1996, 2002). By contrast, the songs of most North American members of the *carnea* group, e.g. *C. plorabunda*, *C. adamsi* and *C. johnsoni*, exhibit downward frequency modulation of each volley (Henry *et al.*, 1993). It is not yet clear whether this trait represents a fundamental acoustical difference between the European and North American clades of the *carnea* group.

Morphology of adults

Within its geographical range, it is possible to confuse *Cc3* with any of the five cryptic song species of the *carnea* group sympatric with it (Wells & Henry, 1998: Fig. 16.1). One of these, *Cc5* 'generator' from the extreme eastern Mediterranean region, remains to be described. Of the other four, two are distinguishable from *Cc3* when examined carefully: *C. lucasina* because of the dark line on the second abdominal pleurite (Henry *et al.*, 1996) and *C. mediterranea* because of its darker green body colour and the red band across the front of the head (Henry *et al.*, 1999a). However, adults of *Cc3* are very similar to, and generally intermediate between, *C. carnea* (*sensu* Henry *et al.*, 2002) and *C. pallida*. The stipites, palpi, genae and lateral margins of the clypeus of *Cc3* are usually marked

with a black-brown stripe, as in *C. carnea*. However, these markings are variable, and in some specimens of *Cc3*, the black markings are reduced, absent or replaced by red markings, causing these individuals to more closely resemble *C. pallida*. Similarly, the setae of the abdominal sternites of *Cc3* are predominantly blond, with a scattering of black setae that are generally fewer in number than those found in *C. carnea*, but greater in number than those in *C. pallida*. The hairs clothing the genital lip of males of *Cc3* also show characteristics of both *C. carnea* and *C. pallida*. *Chrysoperla pallida* is characterized by very short and fine setae, whereas *C. carnea* has many additional coarse, long black setae. *Cc3* is intermediate: the majority of setae on the genital lip are short and fine, but there is a thin scattering of longer setae in most specimens. Finally, the relative size of the basal dilation of the tarsal claw in *Cc3* (1.94–2.53) overlaps nearly completely with *C. carnea* (2.15–2.5), but also with the upper part of the range observed in *C. pallida* (1.67–2.14).

The most promising morphological character to diagnose species reliably in the *carnea* group is the shape of the genital lip at the apex of sternite 8 + 9 in males (Henry *et al.*, 1999a). Specimens of *C. carnea* have a relatively broad, protruding lip when compared with specimens of *C. pallida* (Henry *et al.*, 2002). The lip in *Cc3* is usually intermediate between these two species (Fig. 3): it tends more towards *C. carnea* in one descriptive ratio (AB ≥ BC), but more towards *C. pallida* in the other (DE > FG). Unfortunately, there is some overlap with both taxa. It is therefore extremely difficult to recognize singleton specimens of *Cc3*, although in a mixed collection of other *Chrysoperla* species, individuals of *Cc3* are easier to discriminate because simultaneous comparisons of the lip character can be performed among specimens.

The fact remains that there is no reliable morphological character with which to distinguish adults of *Cc3* from all other members of the *carnea* group with which it might co-occur. Consequently, if morphology is the only means of identification available, some specimens of *Cc3* will be mistaken for *C. carnea* or *C. pallida*.

Morphology of larvae

The *Cc3* larvae are highly variable, making species diagnosis difficult. Unfortunately, several populations of preserved *Cc3* larvae were lost in the mail, so we have very few samples that are syntopic with specimens of other species that have been studied (Henry *et al.*, 1996, 1999a, 2002). Therefore, we cannot discuss the utility of *Cc3* larvae for recognizing *Chrysoperla* species within a locality.

On a continental basis, *Cc3* larvae are reasonably distinct from those of *C. mediterranea* (Henry *et al.*, 1999a), but are more easily confused with larvae of *C. pallida*, *C. carnea* and especially *C. lucasina*. Compared with *C. mediterranea*, *Cc3* exhibits darker pigmentation of the dorsolateral stripe and displays a dark spot within the stripe that is usually not present in *C. mediterranea*. Greater similarity is found between *C. pallida* and *Cc3*, and these two species can

resemble each other quite closely if their larvae exhibit their less ornate morphological states (a dorsolateral stripe accented by a dark spot and no frontal spots, e.g. Fig. 4A–C). However, more extensively pigmented specimens of *Cc3* and *C. pallida* can sometimes be distinguished by the broader dorsolateral stripe characterizing many *C. pallida*. Also, when frontal spots are present, the most common condition in *Cc3* is three spots (e.g. Fig. 4E), whereas two spots are more usual in *C. pallida*. The resemblance between *Cc3* and *C. carnea* is even stronger, with both species exhibiting the dark spot on the dorsolateral stripe, plus (usually) three frontal spots. However, like *C. pallida*, *C. carnea* typically has a broader, darker dorsolateral stripe than *Cc3* (Henry *et al.*, 2002). The greatest possibility for confusion exists between *Cc3* and *C. lucasina*. These two species are broadly sympatric and frequently share most characteristics of their larval head markings, including possession of a dorsolateral stripe marked by a darker spot and zero, one or three frontal spots. However, *C. lucasina* is more likely than *Cc3* to have a single frontal spot and a broader basolateral expansion of the dorsolateral stripe (Henry *et al.*, 1996). In summary, it is clear that differences between the larvae of *Cc3* and those of the other song species of the *carnea* group are subtle and nonexclusive, making positive identification of any European species from larval specimens nearly impossible.

Ecology

Of the five described song species of the *carnea* group found in western Europe and around the Mediterranean Sea, *Cc3* is most similar to *C. mediterranea* in its preference for mild, Mediterranean climates. However, it also shares several important ecological requirements with another widespread song species, *C. lucasina*. It seems likely that *Cc3* avoids competition with *C. mediterranea* by occupying deciduous rather than coniferous habitats (Henry *et al.*, 1999a). Likewise, *Cc3* may avoid competition with *C. lucasina* by displacing the latter to higher elevations in habitats otherwise suited to both species. Because *C. mediterranea*, and especially *C. lucasina*, are more tolerant of cold winters than *Cc3*, each of these species ranges far to the east and north of *Cc3*'s known geographical distribution (Fig. 2; Henry *et al.*, 1996, 1999a). Nevertheless, within its tolerance limits, *Cc3* is an exceptional colonizer, evident by its abundance on the Azores islands in the central Atlantic Ocean.

Three song species in western Europe, *Cc3*, *C. carnea* and *C. pallida*, change colour in the winter. Two others, *C. mediterranea* and *C. lucasina*, do not. It has been shown that brown winter coloration in *Chrysoperla* spp. is correlated with overwintering in the leaf litter beneath deciduous plants (Lacroix, 1926; Honek & Hodek, 1973; Sheldon & MacLeod, 1974). Therefore, we assume that adults of *Cc3*, like those of *C. carnea* and *C. pallida*, choose deciduous leaf litter in which to hibernate. However, the pigmentation of diapausing *Cc3* remains noticeably paler than the light brown hues typical of overwintering *C. pallida*, and never matches the rich reds and purples

often found in diapausing *C. carnea*. These consistent differences suggest that *Cc3*, *C. carnea* and *C. pallida* may choose different types of litter in which to diapause, possibly reducing competition among them. The potential for more intense competition exists between *Cc3* and its closer ecological analogues, *C. mediterranea* and *C. lucasina*. However, in contrast to *Cc3*, the latter two species retain their green body colour throughout the winter and have been shown to hibernate under the bark of pine trees (Henry *et al.*, 1999a) or in evergreen foliage (Thierry *et al.*, 1995). This is probably an important niche difference separating *Cc3* from the two species in the *carnea* group with which it is most likely to compete.

Egg laying in *Cc3* of single, dispersed eggs is similar to that found in *C. lucasina* and *C. carnea*. In this respect, *Cc3* differs from *C. mediterranea* and most populations of *C. pallida*, which deposit their eggs in groups (Henry *et al.*, 1999a, 2002). An explanation for such differences could be that both *C. mediterranea* and *C. pallida* are strictly arboreal, whereas *C. carnea*, *C. lucasina* and *Cc3* usually develop on low vegetation or shrubs. For lacewings developing on trees, where prey are likely to be scarce, clustering the daily portion of an individual's egg supply on single leaves or branches may guarantee survival of at least one larva per egg cluster, because sibling larvae will turn to cannibalism when deprived of food (Duelli & Johnson, 1992).

Ecological differences translate into differing effectiveness of the various sympatric song species as agents of biological control. For example, it has recently been shown that the niche characteristics of *C. carnea* make that species much more common in cultivated fields than *C. pallida*, even though the two species share nearly identical morphologies (Henry *et al.*, 2002). Like *C. carnea*, *Cc3* appears to have an affinity for agricultural fields in some parts of its range, e.g. southern Spain and northern Iran. If this association is confirmed by future studies, *Cc3* could prove to be an important new biological control agent in the warmer regions of southern Europe and the Middle East, particularly where *C. carnea* and *C. lucasina* are not found.

Conclusions

Confirming the results of earlier studies on other lacewing song species, we have shown that *Cc3* 'Maltese *carnea*' is nearly indistinguishable from its congeners based on single morphological criteria, but is nonetheless a distinct biological species based on its unique mating song. Additionally, *Cc3* can often be diagnosed successfully by a suite of morphological traits. We therefore formally describe *Cc3* below as *Chrysoperla agilis*.

Morphological analyses of adults and larvae together point to a particularly close resemblance between *C. agilis*, *C. carnea* and *C. pallida*. Furthermore, larval morphology, as well as adult and larval ecology, suggest additional similarities between *C. agilis* and *C. lucasina*. By most criteria, *C. mediterranea* appears to be the least similar to *C. agilis*, despite being most similar in their geographical ranges and

ecological preferences. From these patterns, it is tempting to infer something about the phylogenetic relationships among the song species of the *carnea* group. For example, one could argue in support of an especially close relationship between *C. agilis*, *C. carnea* and *C. pallida*, with *C. mediterranea* as the outgroup. However, little support for such phylogenetic conclusions can be gleaned from song analysis. Although *C. carnea* and *C. pallida* each produce a multivolley SRU (song) that bears a passing resemblance to that of the other, *C. agilis* has a single-volley song of truly unusual characteristics. One song feature shared by all three species, upward frequency modulation of volleys, is actually found in all European and Mediterranean members of the *carnea* group, and is therefore uninformative. (*Cc5* 'generator', an exception showing downward frequency modulation, is an Asian/African rather than European faunal element; see Henry *et al.*, 1996.) The most compelling song feature to connect *C. agilis* with either *C. carnea* or *C. pallida* is direct striking of the substrate by the abdomen, a trait that *C. agilis* shares uniquely with *C. pallida*. Nonetheless, it is premature to draw phylogenetic inferences from so few data.

If the cryptic members of the *carnea* group are to be used effectively and efficiently in programmes of biological control, it is mandatory that practitioners be able to distinguish *C. agilis* from *C. carnea*, *C. pallida* or any other sympatric song species. We are discovering that each song-diagnosed lacewing species is also characterized by a unique suite of ecological features that makes it best suited for a specific type of agricultural application, and completely ineffective in others. Misidentifying species can become a very expensive mistake when mass introductions of lacewings fail to control crop pests and harvests are reduced. This study identifies a new species with good potential for effective agricultural use over portions of its natural range. We also provide the information necessary to distinguish this species from its remarkably similar relatives in the *carnea* group.

Chrysoperla agilis, sp.n. (Figs 1, 3–6)

Holotype. ♂, FRANCE: Carcès, 180 m, July 1994 (P. Duelli) (BMNH).

Paratypes. Same data as holotype, 1 ♂, 2 ♀, 6 second-instar and 6 third-instar larvae, reared from parents collected July 1994 (P. Duelli) (1 ♂, 1 ♀, CSMNH; 1 ♀, BMNH; 2 second-instar, 2 third-instar larvae, BMNH; 2 second-instar, 2 third-instar larvae, CSMNH; 2 second-instar, 2 third-instar larvae, WFBM).

Etymology. Named for its hyperactivity in life, and its associated capacity to disperse great distances.

Adult. Ground colour uniform pale green. Head marked with broad black-brown stripe on gena and lateral clypeus. Maxillary palp sometimes unmarked or more usually marked with dorsal black-brown stripe of varying intensity

on basal segments. Stipes either entirely marked black-brown or marking restricted to small apical spot. Frons and postoccipital region unmarked. Antenna shorter than fore wing. Pronotum marked with median pale yellow stripe; lateral setae long, pale; dorsal setae sometimes entirely blond, or up to 80% mixed with shorter, dark setae. Tarsal claw basal dilation ratio 1.94–2.53. Fore wing length 9.4–12.5 mm, length : breadth ratio 2.78–3.14; crossveins in basal half of wing black, or green with black spot at each end; gradates green; costal setae relatively long. Abdomen sometimes entirely clothed with blond setae on apical sternites, or with about 10% black setae, or rarely with 100% black setae; lip of sternite 8 + 9 in male short, narrow, with short blond setae and a few scattered longer, dark setae.

Courtship song (25 °C). Song consisting of a single-volley SRU 2.5–6.5 s long, usually repeated several times with a period of 7–13 s; carrier frequency rising from a range of 70–95 Hz to 95–120 Hz during first two-thirds of volley, then falling to 85–110 Hz at volley conclusion. Amplitude smoothly modulated upward and then irregularly downward, with maximum at point of peak carrier frequency; terminal section of each volley punctuated by numerous blows of abdomen to substrate, producing an audible 'rattle'. Volleys overlap slightly or not at all during heterosexual duets.

Larva, third-instar. Head pale tan with a pair of relatively narrow, longitudinal dorsolateral brown stripes with basolateral expansions extending towards eyes; darker spot in dorsolateral stripe mesad of eyes. Frontal spots numbering 0 (not present), 1 (anteromedial, between antennal bases), 2 (between dorsolateral stripes mesad of eyes), 3 (combination of previous, or anteromedial spot plus dorsolateral pair between antennal bases), or 5 (combination of all previous). In 5-spotted individuals, entire frontal area of head between stripes sometimes lightly pigmented. Thorax cream-coloured, marked with a pair of longitudinal, dorsolateral stripes, reddish-brown to dark brown. Abdomen cream-coloured, marked with a pair of longitudinal, dorsolateral stripes, reticulate reddish-brown to solid dark brown.

Second instar. Similar to third-instar larva except as follows. Head with dorsolateral stripes paler, broader relative to width of head; basolateral expansions relatively larger, sometimes to lateral margin of head behind eyes; stripes more acute on medial margin of antennae. Frontal spots rarely developed. Thorax and abdomen paler, dorsolateral stripes less prominent, sometimes interrupted.

First instar. Similar to second-instar larva except as follows. Head with dorsolateral stripes paler, very broad relative to width of head; basolateral expansions sometimes reaching eyes. Thorax and abdomen with dorsolateral stripes reduced to a pair of spots anteriad on each segment.

Discussion. Chrysoperla agilis is most similar to *C. carnea* (*sensu* Henry *et al.*, 2002) and *C. pallida* among the European members of the *carnea* group, and can be separated reliably from these species by courtship song analysis. Although there are no morphological characters that will always distinguish *C. agilis* from its two closest congeners, the shape and setation of the genital lip on sternite 8 + 9 in males is often useful, despite being generally intermediate between *C. pallida* and *C. carnea* (see main Discussion).

The song of *C. agilis* is markedly different from that of any other known song species in the *carnea* group. The only other lacewing possessing single-volley SRUs of equivalent length is *Cc5* 'generator', but the carrier frequency in *Cc5* decreases rather than increases during the course of each volley.

The larva of *C. agilis* has no features that distinguish it absolutely from that of *C. carnea*, *C. pallida*, *C. mediterranea* or *C. lucasina*. However, as discussed earlier, particular attributes of the dorsolateral stripe and dorsal spots of the head capsule are more likely to be present in *C. agilis* than in the other European song species.

Distribution. Malta, northern Africa, Portugal (including Azores and Madeira archipelagos), southern Spain, southern France, southern Switzerland, Italy, Greece, Israel, northern Iran.

Acknowledgements

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