

REPRODUCTIVE AND CALLING BEHAVIOR IN TWO CLOSELY
RELATED, SYMPATRIC LACEWING SPECIES,
CHRYSOPA OCVLATA AND *C. CHI*
(NEUROPTERA: CHRYSOPIDAE)

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Abstract.—The sister species *Chrysopa oculata* Say and *C. chi* Fitch, like other green lacewings of eastern North America that have been studied, jerk their abdomens vigorously while courting and mating. The substrate-borne signals (calls) produced principally by male insects are simple and repetitive, consisting of more or less extended trains of discrete volleys or bursts of abdominal vibration. The calls of both species are similar but distinctive, differing significantly and consistently from one another in their volley spacing, volley duration, and frequency of abdominal vibration. Some inter- and intra-individual variation in call parameters exists within each species; for example, vibration frequency is particularly well correlated with ambient temperature, at least in *C. oculata*. Acoustical communication in these two *Chrysopa s. str.* species seems much less crucial to successful courtship than it is in *Chrysoperla* species, indicating that calling patterns probably do not serve a reproductive isolating function within species of the *oculata* group. Alternative functions for jerking behavior are therefore considered, and an attempt is made to relate acoustical performance with other aspects of lacewing reproductive biology and ecology.

A special form of acoustical communication, in which courting conspecific individuals exchange substrate-borne low-frequency signals, has been shown to be widespread in North American green lacewings of the family Chrysopidae (Henry, 1979, 1980a, b, c; Smith, 1922; Toschi, 1965; Tauber, 1969). Transverse "sound" waves are generated in lightweight substrates by vigorous jerking motions of a lacewing's abdomen and are thereby transmitted over short distances to other insects standing on those surfaces (Henry, 1980c). Calls consist of bursts or volleys ("pulse trains"—see Graf, 1970) of such abdominal jerking or vibration, usually modulated with respect to frequency and amplitude structure and released over a period of time at

species-characteristic intervals. Calling duets are usually established between two sexually receptive conspecifics of opposite sex, and often copulation will not occur without a period of such reciprocal signaling.

Chrysopa (broad sense) in North America includes at least three distinct species-groups, called subgenera by Tjeder (1966) but recognized as full genera by Séméria (1977). These, commonly known in the United States as the *oculata* group, *carnea* group, and *lineaticornis* group, are defined by features of the male terminalia (Bram and Bickley, 1963), but possess distinctive and consistent bionomic characteristics as well. For example, members of the *oculata* group (*Chrysopa s. str.* Séméria) produce strong-smelling "repugnatorial" secretions, are predatory as adults, and overwinter as prepupae within the cocoon, while those of the *carnea* group (*Chrysoperla* Steinmann) are neither odoriferous nor obligatorily carnivorous as adults and pass the winter as diapausing, reproductively immature imagos (Tauber and Tauber, 1974; Séméria, 1977). This strong dichotomy between *Chrysopa s. str.* and *Chrysoperla* is substantiated by calling behavior patterns: members of the latter taxon will not mate without first participating in prolonged, often elaborate calling duets, while those of the *oculata* group that I have studied call in a simpler, more perfunctory, and less predictable manner and will occasionally copulate without acoustical preliminaries. In this paper, I describe abdominal jerking behavior and courtship and mating patterns in two closely related species of *Chrysopa s. str.*, *C. oculata* Say and *C. chi* Fitch, confirming in this case that members of species-pairs not dependent for mating success on acoustical communication can be more similar in their calls than those for which such communication is a necessary adjunct to copulation. That prediction is derived from the hypothesis that calling in lacewings functions at least in part, or once functioned, to isolate closely related species reproductively from one another; in two close relatives which utilize acoustical signals extensively, selection against hybrids would likely cause rapid divergence in call characteristics, as seen in *Chrysoperla* species.

Chrysopa oculata and *C. chi* are common Nearctic green lacewings of medium size. *Chrysopa oculata* is found throughout most of North America north of Mexico and is the most abundant chrysopid species at most sites (Smith, 1922; Bickley and MacLeod, 1956; Bram and Bickley, 1963). It is a meadow species, confined to low vegetation, and passes through three generations each summer in New England (Propp et al., 1969). *Chrysopa chi* is thought, on morphological grounds, to be *C. oculata*'s closest relative (Bram and Bickley, 1963), and similarly occupies a large but rather more northerly range in the United States, Canada, and Alaska. It is described as an "early" species (Smith, 1922), inhabiting the taller shrubs, like meadowsweet (*Spiraea latifolia*), of overgrown fields; little is known of its life history and habits beyond the brief comments by Smith (1922) on hatching,

larval development, and eclosion. The reproductive behavior of neither species has been described in detail, although Smith (1922) observed abdominal jerking, courtship, and copulation in *C. oculata* on two separate occasions.

METHODS AND MATERIALS

Specimens of the two species were collected during the summers of 1977 through part of 1981 from Mansfield, Connecticut; Rensselaerville, New York; Echo Lake, Vermont; and North Conway, New Hampshire. Breeding colonies in 2-gallon cardboard cartons were provided with water, artificial WHEASTTM diet (Hagen et al., 1970), and black aphids from *Nasturtium*. Eggs were removed daily and larvae reared on ether-killed *Drosophila* spp., as described in an earlier paper (Henry, 1979). All adults and larvae were maintained under long day (16L:8D) light conditions at $28 \pm 1^\circ\text{C}$ and 40–80% relative humidity. Populations from the different collecting locales were maintained separately only until calling patterns were shown to be identical in lacewings from all four areas. First through third laboratory generations were tested for reproductive and acoustical behavior.

Since lacewing signals are of low frequency and are transmitted through the substrate, a simple piezoelectric transducer contacting the thin plastic cover of the experimental arena sufficed as a detector of insect-induced substrate vibrations, as in earlier experiments (Henry, 1979, 1980a, b, c). The electrical output of that transducer was then fed to a TektronixTM 511 storage oscilloscope through a matching 5A25 dual differential amplifier; tracings of lacewing calls could then be viewed and photographed for future analysis. Both *Chrysopa oculata* and *C. chi* displayed greater sexual activity under red rather than fluorescent illumination; a GETM 60-watt BCJ incandescent bulb was used for that purpose.

The results and conclusions that follow are based upon 193 hours of observations, approximately equally divided between *C. oculata* and *C. chi*. For *C. oculata*, 197 calls consisting of three or more volleys were analyzed; these represent the recorded activities of 11 different males and 4 females, including two heterosexual duets involving 4 different individuals. Six copulations (12 individuals) were also observed in that species. For *C. chi*, I recorded and analyzed 158 calls of three or more volleys, representing the activities of 8 males and one female. Additionally, one heterosexual duet produced 7 male and 11 female recordable responses (calls). Nine *C. chi* copulations (7 different males, 8 females) were tabulated. During observation sessions of *C. oculata* and *C. chi*, temperature averaged $26.46 \pm 1.62^\circ\text{C}$ ($n = 53$ sessions) and $25.94 \pm 3.01^\circ\text{C}$ ($n = 36$), respectively.

Any reference in the Results or Discussion sections to "significant differences" indicates that the means of two normally distributed samples were demonstrated to differ from one another by a 2-tailed t-test using confidence

limits of 95% or better. Similar confidence limits were used in chi-square evaluations. Values following a \pm sign are one standard deviation of the mean.

RESULTS

My collecting records confirm the ecological observations of earlier workers (Smith, 1922). In three successive years at the New York State site, adult *C. chi* appeared at least as early in the spring as *C. oculata*, and in one year (1980) were abundant on the 29th of May when no *C. oculata* could be found. At all locales, populations of both species were emphatically sympatric throughout the summer; moving one or two meters from a meadow dominated by *Solidago* spp. to an open aspen grove with a thick *Spiraea* understory resulted in complete replacement of *C. oculata* by *C. chi* in the collecting samples. Adults of both species disappeared from all my sites by 15 September, with *C. oculata* persisting consistently longer (by a week or two) than its relative in each of three consecutive years.

Reproductive behavior is basically similar in both *Chrysopa oculata* and *C. chi*, although it differs significantly from that described for members of the *Chrysoperla* group. Sexual receptivity in both sexes is first signaled by lowered head and elevated abdomen, accompanied by vigorous antennal movements. The abdomen is then waved slowly back and forth several (up to 12–15) times at 1.5 second intervals and is flexed ventrally at its tip as it approaches the left and right limits of its excursion. The wings on that side of the body toward which the abdomen is swinging are partially raised and lightly fluttered; simultaneously, one can detect the characteristic, unpleasant odor of species in this taxon. The male may then produce a series of volleys of abdominal vibration (Fig. 1A–D), either continuously for a minute or more (*C. oculata* and highly receptive *C. chi*) or more sporadically (less receptive *C. chi*). Females may also jerk their abdomens in a manner quite similar to that of the males; however, female activity of this kind is rare in either species. In the unlikely event of a heterosexual duet, the male and female will reciprocally exchange bouts of abdominal jerking, exchanging volley for volley in *C. chi* but alternating longer trains (series) of volleys in *C. oculata* (Fig. 1E, G). More commonly, however, courtship will be brief and copulation sudden, accompanied by little if any jerking activity: typically the female will approach and antennate the male, after which the two insects will immediately swing their bodies into parallel positions and effect copulation. Individuals of each species averaged 30.60 ± 8.02 (*C. oculata*; $n = 5$) and 14.00 ± 4.76 (*C. chi*; $n = 7$) minutes *in copulo* ($t = 2.62$). In *C. oculata*, three out of six copulations were preceded by at least one series of volleys from the female, while in *C. chi* three of nine included such participation.

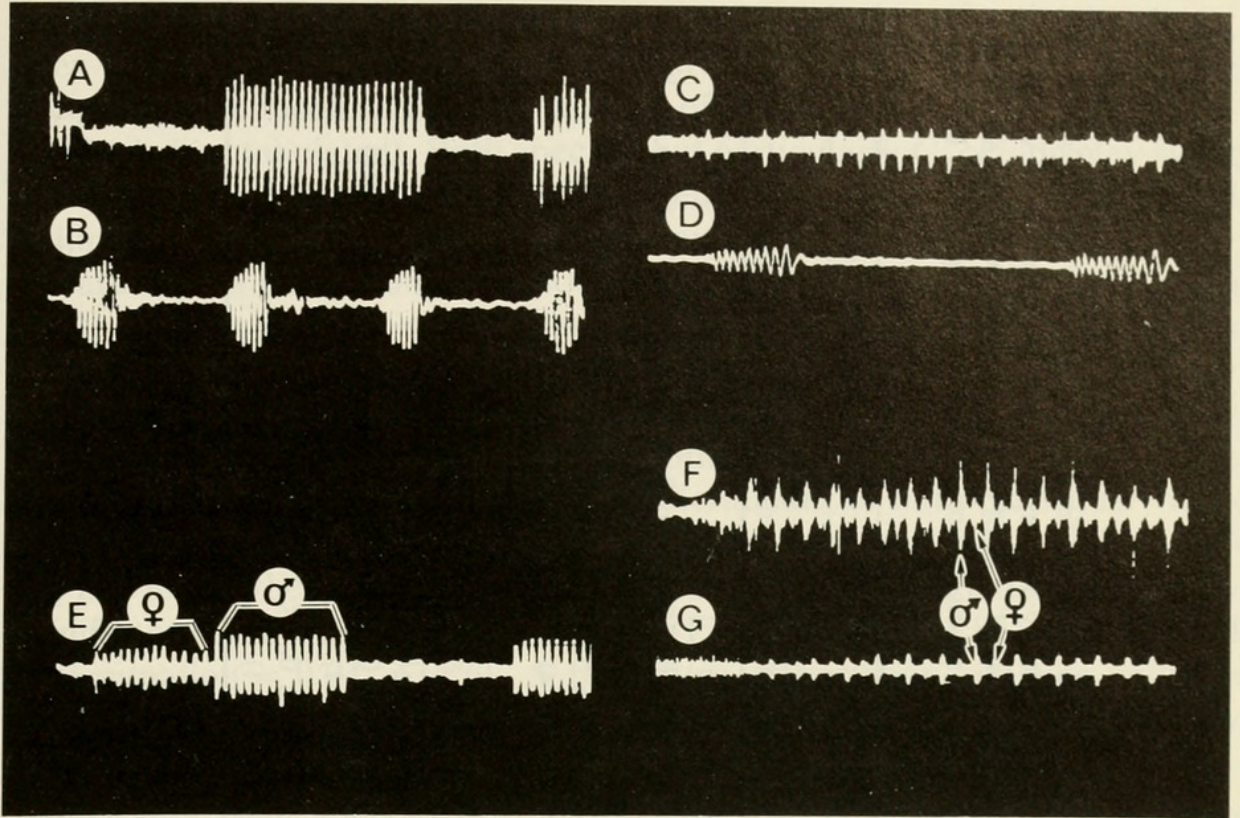


Fig. 1. Oscillographs of abdominal vibration patterns produced by sexually receptive individuals of *Chrysopa oculata* (A, B, E) and *C. chi* (C, D, G). Heterosexual duets are recorded in E and G at an oscilloscope writing speed of 2 seconds/major division; in *C. oculata*, whole trains of volleys of abdominal jerking are exchanged between partners, while in *C. chi* each insect exchanges single volleys with its partner. Note striking convergence between the duet sequence of *C. chi* (G) and that *C. (Chrysoperla) carnea* (F), recorded at the same writing speed. Traces B and D are 20 \times details of A and C (writing speed = 0.10 sec/div. vs. 2 sec/div.), showing volley structure characteristic of each species.

Calls of both *Chrysopa oculata* and *C. chi* are simpler in structure than those of any *Chrysoperla* species yet studied, consisting of long trains of identical volleys of abdominal vibration lacking pronounced frequency or amplitude modulation (Fig. 1). Differences between the calls of the two species include (a) average volley spacing, (b) frequency of abdominal vibration within volleys, (c) volley duration, and (d, calculated from b and c) number of abdominal jerks per volley (Table 1). In *C. oculata* (Fig. 1A, B), volleys are spaced closely together (interval = 0.266 sec) and are characterized by high rates of abdominal jerking (av. = 109.18 abdominal strokes/sec), short durations (av. = 0.082 sec), and relatively few total strokes (jerks) per volley (av. = 8.95). On the other hand, *C. chi* produces volleys (Fig. 1C, D) that are more distantly spaced (interval = 0.813 sec), lower in vibration frequency (76.11 strokes/sec), longer by a factor of two (0.168 sec), and composed of considerably more abdominal strokes (12.79) than

Table 1. Important measurable characteristics of the calls (volley trains or sequences) of males and females of *Chrysopa oculata* and *C. chi*. Mean values and their standard deviations are tabulated. Sample sizes are entered parenthetically; the larger figure of each pair represents either the number of calls ("volley spacing" part of table) or the number of volleys ("volley parameters" part of table) measured, while the smaller one is the number of individuals producing those calls or volleys. Volley spacing is measured from onset to onset of each jerking volley. Portions of calls consist of eight volleys selected from appropriate regions of continuous volley trains.

	Temp. (°C)	Volley Spacing Within Calls (in Seconds, ± SD)			Volley Parameters (± SD)			
		Early Portion	Middle Portion	Late Portion	Average	Frequency (Strokes/sec)	Duration (Seconds)	# Abd. Strokes
<i>C. oculata</i>								
Male calls (all)	26.34 ± 1.59 (48)	0.244 ± 0.046 (118, 11)	0.259 ± 0.048 (130, 11)	0.289 ± 0.063 (125, 11)	0.269 ± 0.059 (184, 11)	109.18 ± 15.43 (168, 4)	0.082 ± 0.015 (217, 4)	8.95 (168, 4)
Female calls (all)	27.62 ± 1.67 (5)	0.215 ± 0.038 (8, 3)	0.227 ± 0.048 (9, 2)	0.249 ± 0.045 (10, 3)	0.229 ± 0.040 (13, 4)	—	—	—
<i>C. chi</i>								
Male calls (all solos)	25.79 ± 3.04 (34)	0.680 ± 0.195 (25, 5)	0.819 ± 0.207 (28, 5)	0.956 ± 0.304 (27, 5)	0.813 ± 0.225 (155, 7)	73.47 ± 10.21 (45, 4)	0.176 ± 0.021 (49, 4)	12.79 (45, 4)
Female calls (all solos)	28.50 (2)	—	—	—	0.851 ± 0.277 (3, 1)	82.07 ± 4.58 (20, 1)	0.148 ± 0.016 (20, 1)	12.15 (20, 1)
All duets	28.50 (2)	1.260 (1)	1.489 (1)	1.725 (1)	1.38 ± 0.507 (7, 1)	—	—	—

those of *C. oculata*. These differences are all significant to a high degree, even when data are averaged for each individual insect and sample sizes are accordingly reduced from total number of calls to number of different individuals (not tabulated). Both species, but particularly *C. chi*, display slight but detectable frequency modulation of each volley: the rate of abdominal jerking decreases somewhat toward the end of each volley (Fig. 1B, D).

Variation in call parameters exists both among individuals and within a single individual of *C. oculata* and *C. chi*. Inter-individual variation was not usually very pronounced in either species; however, one *C. oculata* displayed consistently and significantly longer intervals between its volleys than any other conspecific individual (other features of its call were less deviant). Temperature was the major determinant of intra-individual variation: decreasing temperatures tended in both species to increase volley spacing but lower the frequency of abdominal vibration, the latter in a highly significant linear manner for *C. oculata* (Fig. 2; slope = 5.87, coefficient of determination = 0.94, $n = 6$). A third type of variation, existing within a call, was also identified. Here, it was noticed in both species that volley spacing nearly always increased significantly during the course of an extended call. Table 2 documents this observation, for each individual studied, and includes the highly significant results of a chi-square analysis; the trend is also reflected in the average volley spacing of "early" vs. "late" portions of calls listed in Table 1. It should be mentioned that, despite such multifaceted variation, no significant interspecific overlap existed in any call parameter between *C. oculata* and *C. chi* even when calls of the most extreme (and therefore most similar) individuals, under unrealistically different temperature conditions, were compared with each other.

As mentioned earlier, *C. oculata* and *C. chi* differ from one another in their manner of alternating acoustical signals during heterosexual duets (Fig. 1E, G). The longer spacing between volleys in *C. chi* seems consistent with the interdigitated volleys typical of dueting insects of that species, while *C. oculata* individuals produce volleys so rapidly that exchanging volley for volley is probably not feasible. In *C. oculata*, calls produced by an individual during a duet appear to be physically indistinguishable from those produced by that same individual alone. However, individuals of *C. chi* make their already-large solo volley spacing significantly greater when dueting, as if to make it even easier for their partners to synchronize with them: the best-studied male, CHM-41, increased its between-volley interval from 0.873 ± 0.251 sec ($n = 16$) to 1.376 ± 0.507 sec ($n = 7$; same temperature) when alternating volleys with the female CHF-41 ($t = 3.23$). It should be stressed again, though, that acoustical alternation during heterosexual interactions is rarely seen in either species.

Male-male interactions in *C. oculata* and *C. chi* are infrequent and involved the exchange of acoustical signals on only one occasion (in *C. chi*).

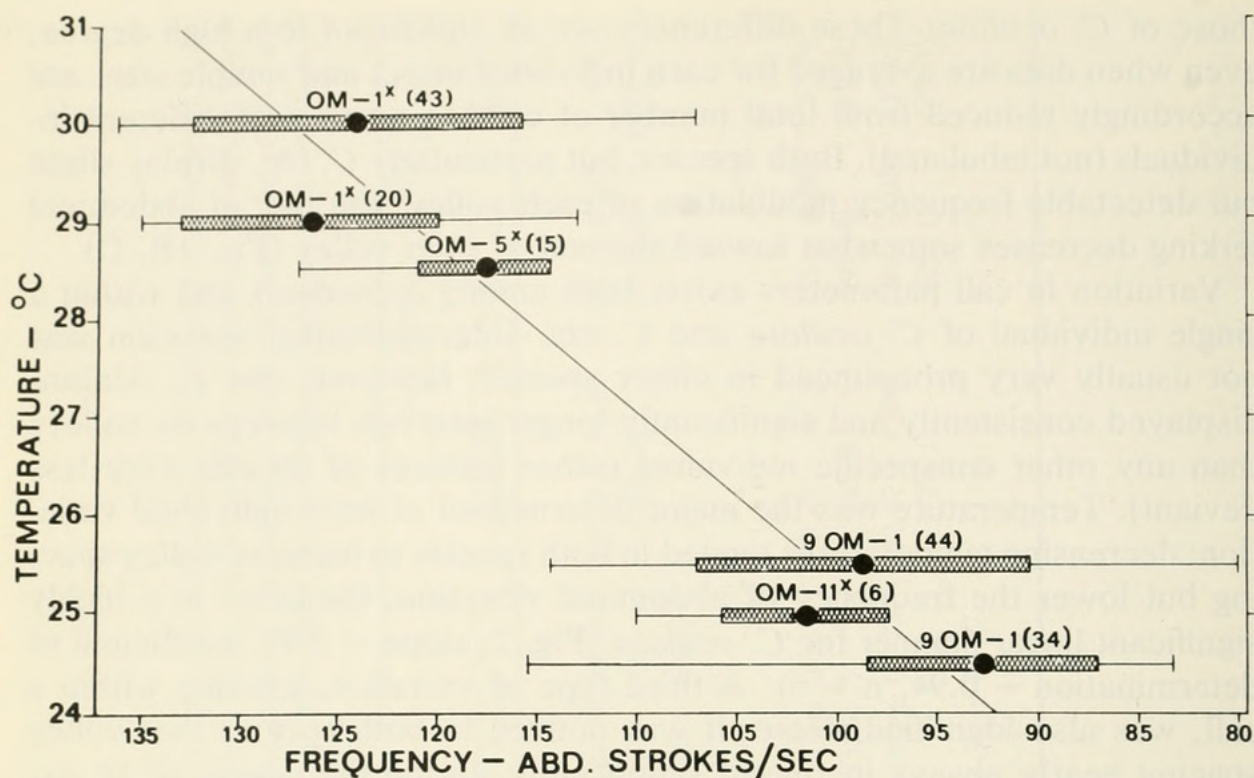


Fig. 2. Graph showing the effect of temperature on abdominal vibration frequency in *Chrysopa oculata*, for four different individuals. Solid dots are means, shaded areas are standard deviations, and lines extend to extremes. In each case, sample size, in parentheses, is the total number of volleys measured. The sloping line corresponds to the linear equation $y = 5.87x - 48.77$, with vibration frequency plotted on the y-axis (turn graph clockwise 90 degrees).

No special patterns could thus be discerned. My impression is that males do not interfere acoustically with the reproductive activities of other males, since on 30 out of 34 occasions peripheral males showed no interest in courting and copulating conspecifics in the cup-sized experimental arenas. However, when crowded together for long periods of time, males undoubtedly interact aggressively, since nearly every individual of both species exhibited antennal injury under those conditions.

DISCUSSION

Collecting data suggest that little interaction will occur between *Chrysopa oculata* and *C. chi* under natural conditions, since each species occupies a different microhabitat. For most of the summer, *C. oculata* seems to be the only lacewing species inhabiting the low vegetation at most meadow sites in the Northeast; only *C. (Chrysoperla) carnea* Stephens is likely to co-occur with it (Smith, 1922; Bickley and MacLeod, 1956), but in practice I have never collected those two species together. On the other hand, *C. chi*'s ecological preferences overlap with those of several other lacewings, including *C. nigricornis* Burmeister, *C. quadripunctata* Burmeister, *C. (Chrysoperla) rufilabris* Burmeister, *C. (?) lineaticornis*, and even the conifer-associated *C. (Chrysoperla) harrisii* Fitch and *Meleoma* Fitch (two

species) (Balduf, 1939; Bickley and MacLeod, 1956); in fact, all of those species have been found associated with *C. chi* at one time or another at the New York State site alone. Perhaps this abundance of competitors partially explains why populations of *C. chi* always remain smaller and more patchy than those of its closest relative. Of course, factors underlying species composition are completely unknown in this case.

As mentioned, calls are much simpler and less consistently delivered in *C. oculata* and *C. chi* than they are in *Chrysoperla* species. Of the call types so far described, their calls most closely resemble that of *C. (Chrysoperla) carnea*, which also produces trains of short, identical volleys during courtship and mating (Henry, 1979, 1980c). In fact, volley spacing is virtually the same in *C. (C.) carnea* and *C. chi*, and both species alternate single volleys rather than whole trains of volleys during heterosexual duets (Henry, 1979), so that dramatic convergence is readily apparent in oscillographs of their calls (Fig. 1F, G). However, closer inspection of volley structure reveals that *C. carnea*'s volleys are significantly longer and characterized by much more pronounced frequency modulation than those of either *C. chi* or *C. oculata* (see Fig. 1B in Henry, 1980c); additionally, neither of the latter two species depends for its mating success upon acoustical interactions between the sexes. At any rate, convergence in calls between two such distantly related species as *C. chi* and *C. carnea* has little biological meaning even if calls are important premating barriers, since differences in the habitats, food preferences, pheromone repertoires, and behavioral responses of the two species preclude such close-range interactions.

In the basic components of their reproductive and calling behavior, *C. oculata* and *C. chi* are not only similar to each other, but also resemble other members of their species-group, including *C. nigricornis* (Toschi, 1965, and personal observation) and *C. quadripunctata* (unpublished data). All species of *Chrysopa s. str.* that have been studied assume a characteristic "head down" position when sexually receptive, wave their abdomens in the manner described earlier, and produce superficially similar, simple volleys of abdominal vibration that differ primarily in repetition rate (temporal patterning). Additionally, copulation is usually swift and preceded by the release of a strong-smelling secretion, presumably from the prothoracic "repugnatorial glands" of one or both sexes (McDonnough, 1909; Sulc, 1914; Withycombe, 1924). As mentioned earlier, *Chrysoperla* species never produce noticeable odors, although the prothoracic glands seem to be as fully developed in them as in members of *Chrysopa s. str.* (E. G. MacLeod, pers. comm., 1967). It is thus tempting to correlate the production of odors during copulation with relatively low acoustical sophistication, speculating that more complex, intense pheromones have replaced acoustical modes of communication as species-isolating mechanisms in *Chrysopa s. str.* Selec-

tive pressures favoring radically different calling patterns in closely related sympatric species, as seen in *Chrysoperla*, are thus weakened in *Chrysopa s. str.*, leading incidentally to the relatively weak distinctions described here between the calls of *C. oculata* and *C. chi*. That complex jerking behavior is the primitive, rather than derived, condition in green lacewings is an assumption that needs more support: outgroup comparison can tell us that some Hemerobiidae, the sister-group to Chrysopidae, also jerk their abdomens (Smith, 1922), but those calls have never been studied. Similarly, it is not necessarily valid that lacewing odors can function as reproductive pheromones, since their repugnatorial function has always been taken for granted and has even been confirmed by Blum et al. (1973), who isolated the active ingredient skatole from the prothoracic exudate of *C. oculata* and showed that it repelled fire ants (*Solenopsis richteri* Forel) and some albino mice. Nevertheless, skatole might both repel enemies and attract conspecifics in *C. oculata*, and slightly different substances could function as sexual attractants in other members of *Chrysopa s. str.*; Blum et al. (1973) did not analyze the secretions of any other species. Even if skatole is present in other "stinkflies," it may be mixed with other, rarer active ingredients (Blum et al.'s 5% unidentified "volatiles") in unique, species-specific proportions for sexual attraction, as are other blends of pheromones in certain groups of Lepidoptera (Roelofs and Cardé, 1974; Silberglied, 1977). Certainly the release during lacewing courtship and mating of secretions presumed to be defensive is provocative and suggests the need for further research.

I feel that to reject the hypothesis that calls serve a species-isolating function in *Chrysopa s. str.* is premature, especially in view of the measurable and consistent differences detected between the calls of *C. oculata* and *C. chi*. However, alternative functions for acoustical behavior in these insects must also be considered, since calling differences do seem weak among species of this group. For example, jerking behavior may additionally serve to induce sexual activity in a partner, to facilitate dispersal of some other pheromone from an exocrine gland in the male genitalia (MacLeod, pers. comm. 1967; personal observation), or even to interfere with the mating success of other males in competition for females (see Cade, 1980, for a review of competition among singing crickets). Short-distance attraction of females to calling males may also be important in nature, occurring after aggregation of conspecific individuals to a site by pheromones, local prey abundance (Hagen et al., 1976), or plant odors (Flint et al., 1979). Several of the above alternatives predict intensified sexual selection in males of *Chrysopa s. str.*, especially in view of the polygamous or even polygynous (unpublished data) mating systems characteristic of species of that taxon (see Halliday, 1978, for a general discussion of sexual selection). In fact, as predicted, males of both *C. oculata* and *C. chi* do most of the calling and

display considerably more aggression toward other males than do males of any *Chrysoperla* species yet studied. However, as far as I can tell, male-male competition has not generated in males of either species studied here the kinds of aggressive calls and chorusing interactions found in some other polygynous singing insects and amphibians (Alexander, 1975; Wells, 1977).

The physiological basis of jerking behavior in green lacewings is not known. Earlier work (Henry, 1980b, c) demonstrated that conspecific individuals of different size (mass) do not differ significantly from one another in abdominal vibration frequency, suggesting that abdominal motion is controlled by a neural oscillator rather than by the resonant properties of the moving mass. That view is substantiated by the pronounced temperature effects described in this study (Fig. 2), since resonant properties should not change much, if at all, with temperature. In fact, the linear relationship observed in *C. oculata* is consistent with the more complex exponential and logistic curves describing various inorganic and organic chemical reactions and biological processes (Wigglesworth, 1965), since most of those curves approximate linear equations over a narrow range of temperatures. Here, the temperature coefficient Q_{10} for vibration frequency in *C. oculata* is 1.86, meaning that for temperatures from 24.5–30°C, frequency will increase by a factor of 1.86 for each 10°C increment. If frequency differences are at all important to lacewings in the recognition of conspecifics, for whatever fundamental purpose, neural control provides the best means of achieving consistency among individuals of different sex and sizes under a given set of environmental conditions.

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