Commercialization of Predators: Recent Lessons from Green Lacewings (Neuroptera: Chrysopidae: Chrosoperla)

Article · January 2000

DOI: 10.1093/ae/46.1.26

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Commercialization of Predators: Recent Lessons from Green Lacewings (Neuroptera: Chrysopidae: *Chrysoperla*)

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THE COMMERCIALIZATION OF NATURAL ENEMIES and their increased use in pest management present applied entomologists and ecologists with formidable challenges. A response to these challenges requires reducing the cost of mass-rearing and manipulating natural enemies; improving the success rate and predictability of biological control procedures; and demonstrating the effectiveness, ecological benefits, and safety of biological control under commercial conditions.

Given the above objectives, laboratories around the world are striving to improve the production and appropriate use of green lacewings in the genus *Chrysoperla*. Recent progress in crucial areas of research with this important group of predators illustrates significant lessons that can be applied to the integration of research and commercial development. These crucial areas include the following: (1) *systematics:* generic and species revisions that make correct identification, biological comparisons, and field evaluation a practical reality; (2) *mass-production:* development and improvement of procedures for economical mass-rearing; (3) *field applications:* use of information from ecological studies to augment, conserve, and manipulate natural populations; and (4) *evaluation:* rigorous quantification of release methodology and lacewing efficacy under commercial field conditions. In this article we illustrate how research in these areas promoted the commercialization of *Chrysoperla*; the results from these studies have significance for facilitating commercialization and delineating future research with other predaceous species.

Chrysoperla spp. have long been considered important naturally occurring predators in many horticultural and agricultural cropping systems, including vegetables, fruits, nuts, fiber and forage crops, ornamentals, greenhouse crops, and forests. Worldwide, they also rank as some of the most commonly used and commercially available natural enemies. For many years, two *Chrysoperla* species [*C. carnea* (Stephens) and *C. rufilabris* (Burmeister)] have been mass-reared and marketed commercially in North America and Europe (Wang and Nordlund 1994, Daane et al. 1998) (see Figs. 1 and 2, adult and larva of *C. carnea*; Figs. 3 and 4, larvae of *C. rufilabris*). Two additional species, *C. externa* (Banks) and *C. nipponensis* (Okamoto) [=*C. sinica* (Tjeder)], are used in Latin America and Asia (Nuñez 1989, Wang and Nordlund 1994). In response to a questionnaire in 1992, members of the Association of Applied Insect Ecologists ranked *Chrysoperla* spp. as unrivaled on the list of commonly applied, commercially available predators (Fig. 5).

Chrysoperla spp. are used in integrated pest management (IPM) systems in two principal ways: (1) periodic release of mass-reared individuals and

Fig. 1. *Chrysoperla carnea* adult (photo by Jack Kelly Clark).

Fig. 3. *Chrysoperla rufilabris* larva feeding on a lepidopteran larva (photo by Jack Kelly Clark).

Fig. 2. *Chrysoperla carnea* larva feeding on grape mealybug, *Pseudococcus maritimus* (Ehrhorn) (photo by Jack Kelly Clark).

Fig. 4. *Chrysoperla rufilabris* larva feeding on an aphid (photo by Jack Kelly Clark).

(2) manipulation of the habitat (e.g., to attract or conserve naturally occurring field populations). Recent work has focused on improving both approaches. As discussed below, significant new developments in artificial larval diets, mechanized production methods, long-term storage, and quality control can reduce the cost and increase the availability and reliability of mass-reared *Chrysoperla* spp. Similarly, a re-examination of existing information on the chemical ecology and movement of lacewings reveals ways for improving the ability to attract and retain their populations in agricultural situations. Furthermore, the efficacy of procedures for both releasing and attracting *Chrysoperla* is being evaluated rigorously with quantitative methods under field conditions.

Systematics

Virtually every aspect of IPM depends on a sound systematics base. Systematics provides stable names that enable communication and access to the scientific literature; also, it offers a comparative, phylogenetic perspective that is essential for understanding the biological traits of pest and natural enemy taxa. Consequently, systematics forms the framework for virtually all biological control procedures—from the initial planning of projects and surveys of natural enemies to monitoring for contamination and the quality of insectary-reared or mass-collected natural enemies; and from choosing and collecting specific, well-adapted taxa for rearing and release to evaluating the efficacy of biological control.

With the publication of the first worldwide systematic treatment of the family Chrysopidae (Brooks and Barnard 1990), it now is possible for specialists to differentiate adults of *Chrysoperla* from other genera of green lacewings. Also, accurate identification of both larvae and adults of some New World species of *Chrysoperla* [e.g., *C. rufilabris*, *C. comanche* Banks, *C. externa* (Hagen), *C. harrisii* (Fitch)] can be achieved with current keys and descriptions of larvae (Tauber 1974; see Fig. 6 for a comparison of *C. carnea* and *C. rufilabris* larvae) and adults (Adams 1962, Brooks 1994). However, the remaining North American *Chrysoperla* require close examination because they constitute a morphologically uniform but biologically variable species-complex.

It generally is accepted that the *C. carnea* species-complex in the eastern and midwestern United States is represented by two distinct and reproductively isolated entities: *C. carnea* [called *C. plorabunda* (Fitch) by some] and *C. downesi* (Banks). *C. carnea* generally occurs in agricultural ecosystems. In comparison, populations of the *C. carnea* species-complex in the western United States have more diverse and variable seasonal cycles, greater

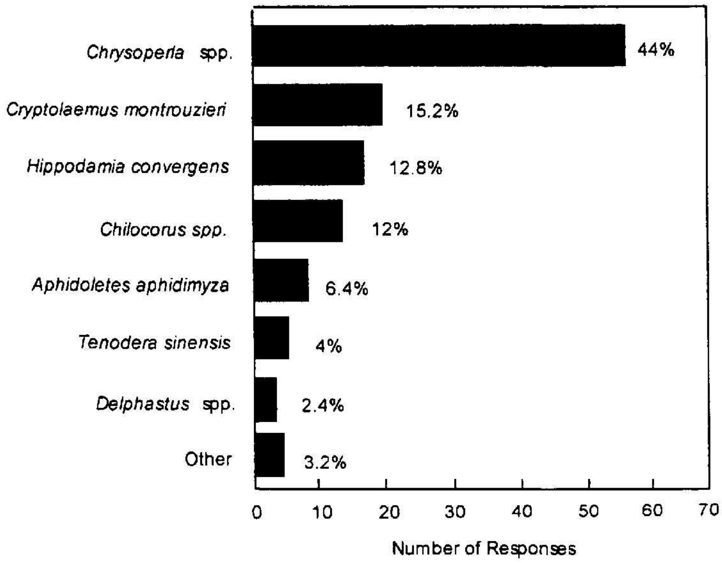

Fig. 5. *Chrysoperla* was the most common insect predator commercially purchased and released into agricultural systems, as determined by a 1992 survey of California members in the Association of Applied Insect Ecologists [*n* = 72; almond, grape, citrus, tomato, and cotton crops listed as the five most common target sites; *Trichogramma* spp., *Chrysoperla* spp. (*C. carnea* and *C. rufilabris* combined), and *Galendromus* (=*Metaseiulus*) *occidentalis* (Nesbitt) listed as the three most common natural enemies (predators and parasitoids) purchased].

geographic variation in patterns of habitat choice and seasonal movement, and a broader range of polymorphism for all the seasonal characteristics that have been studied (Tauber and Tauber 1986, 1987). Therefore, based on current knowledge, we conclude that the diverse populations constitute biotypes of unknown species-status (see Diehl and Bush 1984). Further, the recent descriptions of new species based solely on courtship songs (e.g., Henry et al. 1993) are of questionable value because, to date, there are little data on seasonal or geographic variation in the songs (e.g., Henry and Wells 1990) or on the relationship between the various song patterns and other biological traits.

Fig. 6. Larvae of *Chrysoperla carnea* (left) and *C. rufilaris*; note head and thoracic marks.

Given the indispensability of accurate and stable scientific nomenclature, we believe the current proliferation of names for the diverse *C. carnea* biotypes is inappropriate (Tauber and Tauber 1987). A comprehensive systematic analysis of the *C. carnea* species-complex constitutes an urgent need for IPM practitioners and systematists. Meanwhile, for uniformity in communication, nomenclatorial stability, and scientific verifiability in the future, we recommend the following. (1) For populations in the eastern and midwestern United States, use the names "*C. carnea*" and "*C. downesi*." (2) For populations in the western United States (Rocky Mountains, westward and southward), use the names "*C. carnea* species-complex", "*C. carnea* sensu lato", or "*C. carnea* biotype." (3) For *all populations* studied (including those from commercial insectaries [see O'Neil et al. 1998]), preserve large series of voucher specimens. If possible, preserve some specimens in 95% ethyl alcohol for future DNA analysis. Deposit voucher specimens in a university collection or well-established museum and indicate (in publication) where they can be found. Historically, biological control projects have contributed valuable biological data and specimens for systematics work (e.g., Knutson 1981, DeBach and Rosen 1991); here is another opportunity for such significant synergism.

Mass-Production

The commercialization of biological control depends on the ability of insectaries to produce and profitably market a highly reliable and relatively inexpensive supply of natural enemies. Achieving these objectives first requires efficient, standardized mass-rearing procedures: (1) the use of inexpensive, nutritious diets, (2) mechanized and space-efficient production systems, (3) reliable storage methods, and (4) periodic evaluation of natural enemy quality (e.g., Tauber and Helgesen 1978, Ruberson et al. 1999). In each of these areas, broadly based physiological, ecological, and behavioral research with *Chrysoperla* has contributed to practical and economical improvements in mass-rearing. However, the effective marketing of natural enemies and the training of targeted customers continue to be serious issues in need of attention.

Rearing. Currently, rearing of larvae constitutes the most costly aspect in *Chrysoperla* mass-production largely because all three instars are predaceous. Most insectaries depend on mass-produced insect prey as food (generally lepidopteran eggs: *Sitotroga, Anagasta,* or *Corcyra*), which is relatively expensive compared with artificial diets. All *Chrysoperla* spp. tested performed well when larvae were reared on these diets (Nordlund and Morrison 1992, Albuquerque et al. 1994, Wang and Nordlund 1994; M. J. Tauber and C. A. Tauber, unpublished data). Nevertheless, the cost of production remains high, as shown when the prices of "pre-fed" larvae ($0.0305 per individual) and adults ($0.3587 per individual) are compared with that of eggs ($0.0054 per individual)

(Cranshaw et al. 1996). Relatively recent work has focused on reducing the quantity of prey necessary for rearing larvae by establishing minimum levels of prey needed (Zheng et al. 1993a, b) and supplementing prey with artificial diet (McEwen 1996).

The development of an artificial diet should continue to receive a high priority. Lacewing larvae will feed and develop on either liquid or solid diets (see Nordlund and Morrison 1992, Cohen and Smith 1998). Although some automation is available for producing and encapsulating liquid diets, the cost has remained relatively high (Wang and Nordlund 1994). Recent research that focused on detailed observations of predator feeding behavior has resulted in a fully artificial, solid or semisolid diet that apparently offers significant advantages over other diets. The new diet is relatively inexpensive, does not require encapsulation, and does not spoil quickly (Anonymous 1997, Cohen 1998, Cohen and Smith 1998). When this diet becomes generally available, it is projected to reduce the cost of larval-adult rearing from $0.3587 to $0.00025 per adult lacewing (compare Cranshaw et al. 1996, Anonymous 1997).

Adult dietary requirements often present major practical problems for mass-rearing and marketing predators. For example, *Chrysopa* (as opposed to *Chrysoperla*) adults require prey to maintain egg production; this trait complicates the rearing process and adds greatly to the costs of rearing. In contrast, *Chrysoperla* has an advantage over many other predators because adults feed on honeydew or nectar and harbor mutualistic yeasts (*Torulopsis* spp.) that synthesize essential amino acids missing from their diet (Hagen 1950, Hagen et al. 1970, Hagen 1986). Early research on *C. carnea* nutrition yielded relatively inexpensive and effective artificial diets that sustain high rates of oviposition (Hagen and Tassan 1966). With these diets, females of all species of *Chrysoperla* tested thus far can produce 500 to 1,000 eggs in ~30 days (Hagen and Tassan 1970, Albuquerque et al. 1994, Chang et al. 1996). This successful diet provides a fine example of the practical benefits derived from fundamental research in insect nutrition.

Mass-rearing of insects (especially cannibalistic predators) requires considerable space and manual labor; currently, space-efficient, automated mass-rearing systems for *Chrysoperla* are under development (Nordlund and Greenberg 1994; Nordlund and Correa 1995a, b). These systems include compact holding units for adults, mechanical devices for feeding adults and harvesting eggs, mechanized methods for presenting the larval diet, and automated systems for packaging larval-rearing units. When fully developed, such mechanized systems would enhance production greatly and reduce costs drastically. Progress thus far illustrates the advantages (biological and economic) that can accrue when engineers and biologists combine their expertise in solving practical problems.

Medium and long-term storage of entomophagous species is a key, often-missing element in the cost-effective production and distribution of natural enemies (Tauber and Helgesen 1978, Ravensberg 1992, Ruberson et al. 1999). Storage capabilities offer insectaries the opportunity to stockpile supplies of natural enemies for use during periods of high demand. Moreover, an effective storage system may provide alternative methods for distribution and permit the long-term, low-cost maintenance of valuable stock for use in mass-rearing or research.

Results from recent eco-physiological studies with *C. externa*, *C. nipponensis* (as *C. sinica*), and several geographic populations of *C. carnea* indicate that long-term storage of adults can be accomplished simply, economically, and without loss of quality (Tauber et al. 1993; Wang and Nordlund 1994; Chang et al. 1995, 1996; Tauber et al. 1997). Equally important, poststorage adults can be brought into a reproductive state quickly, predictably, and synchronously. Producers now have two new options for distribution: they may (1) supply eggs or larvae from poststorage adults to retail customers or distributors, or (2) provide distributors with cold-stored adults that can be brought into production as needed (Fig. 7).

Short-term storage of eggs, which is essential for efficient, cost-effective distribution, is more problematic for *Chrysoperla*. Several studies demonstrated that *C. carnea* eggs remain viable for up to 3 weeks when they are held at 8°C (Kuznetzova 1970, Osman and Selman 1993). Unfortunately, the studies offer contradictory results regarding the best age to store the eggs. Recent tests show that newly-laid *C. externa* eggs can be stored at ~13°C for up to three weeks without significant reduction in quality (López-Arroyo et al. 2000). We conclude that it is reasonable to store young eggs because this practice would reduce hatching

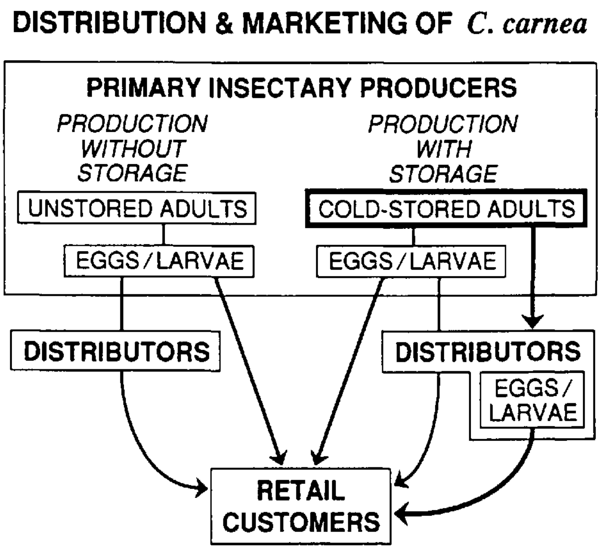

Fig. 7. Strategy for distributing mass-produced *Chrysoperla carnea* encompasses two complementary tactics: the traditional method of continuous rearing and shipment without storage, and the new method of production with cold-storage of diapausing adults. Storage (1) increases the shelf-life of the biological control agent, and (2) allows the option of shipping cold-stored adults, as well as eggs or larvae, to distributors. The life stages sold for release usually are the eggs or young larvae.

and cannibalism during distribution. Additional, carefully controlled studies are necessary.

Quality Control. The standardized production of high quality natural enemies is crucial for both the practice of biological control and users' perception of biological control as a dependable pest management tactic (e.g., Tauber and Helgesen 1978, Leppla and Fisher 1989, Bigler 1992). However, the quality of commercially marketed natural enemies can be variable because there are no strict quality control standards in the United States. For example, in a recent evaluation of shipments from insectaries, growers' orders for *C. carnea* were not filled consistently with the correct species, and cannibalism significantly reduced the survivorship of lacewings in transit (O'Neil et al. 1998). Such problems can be overcome through greater care in maintaining correctly identified, pure colonies and improved procedures during mass-production and packaging (see Leppla and Fisher 1989, Bigler 1992). We recommend the following.

In viewing the overall issue of quality control, it is essential for the insectary industry to develop standards that promote the reliability and standardization of commercially produced natural enemies.

Confirmation of Species Identification. The species of *Chrysoperla* stock should be verified at initiation of the culture. Species identity should be reexamined periodically during rearing to monitor for contamination (see *Systematics* section above).

Deterioration of Stock. Periodically during mass production, cultures should be evaluated for survival and performance (e.g., van Lenteren 1998). Although *Chrysoperla* stock can deteriorate during continuous rearing (Jones et al. 1978), recent studies indicate that (1) the timing of collecting the stock in the field and (2) the periodic intervention of diapause or cold storage may prevent this. For example, adults caught early in the season produced higher quality offspring than adults collected late in the season (Chang et al. 1996). Moreover, the induction of diapause restored the reproductive performance of offspring derived from late-season cohorts. With some carefully focused research, these eco-physiological results could be applied profitably to standardizing the quality of commercial stock.

Shipping and Handling. If eggs are the marketed stage, they should be shipped in insulated containers, with cold-packs, soon after oviposition to prevent hatching and cannibalism en route. When prefed larvae are ordered, packaging with appropriate packing material and food (e.g., *Sitotroga* or *Anagasta* eggs) can reduce cannibalism and mortality. Additional, well-focused research is needed here.

In viewing the overall issue of quality control, it is essential for the insectary industry to develop standards that promote the reliability of commercially produced natural enemies. In this regard, there appears to be greater coordinated efforts and more cooperation between the insectary industry and scientists in Europe than in the United States (van Lenteren 1998).

Field Applications

Augmentation with Mass-Reared *Chrysoperla*. Given the amenability of *Chrysoperla* spp. and biotypes for mass rearing, it is clear that species or biotypes can be chosen strictly on the basis of how well they are matched with the pest management situation. Below, we discuss aspects of the habitat, crop, and target pest that can influence the success of augmentative biological control with *Chrysoperla*. We also consider new information on release methods and rates, and we offer suggestions for research in the future.

Chrysoperla spp. and biotypes exhibit considerable variation in their responses to physical and biotic factors in the habitat, habitat preference, adult cryptic coloration, seasonal cycles, and, perhaps, prey preferences (see summaries in Tauber and Tauber 1983, 1993; Luck et al. 1995). Similarly, release sites for lacewings vary greatly (they range from cotton fields in Texas and apple orchards in Washington to greenhouses in a variety of locations). Unfortunately, the innate variation among *Chrysoperla* taxa and the differences in geographic areas, agroecosystems, or environmental conditions rarely have been considered in developing release tactics; consequently, the effectiveness of releases varies greatly (Daane et al. 1998). However, a few studies that incorporated these issues led to recommendations for matching species and biotypes with certain pest management situations, and some of these recommendations have resulted in improvements for the insectary industry (e.g., Tauber and Tauber 1993). Nevertheless, evaluation of the recommendations under field conditions is necessary. Two examples provide useful lessons.

First, comparative studies of the developmental and reproductive responses of *C. carnea* and *C. rufilabris* to relative humidity led to different recommendations for using each species (Tauber and Tauber 1983). *C. rufilabris* does not perform well in dry areas but generally is the best choice for use in greenhouses or sites with moist conditions. In contrast, *C. carnea* does well under low humidity and should be used in dry regions. Some U. S. insectaries successfully adopted these recommendations in their sales promotions, and the species are marketed appropriately. At present, follow-up studies (comparative quantitative field tests of the two species) are needed to evaluate the cost-effectiveness of the recommendations. Similarly, recent findings regarding mortality of *C. carnea* eggs under high temperatures (>37°C) (Daane and Yokota 1997) should be incorporated into the recommendations for release and evaluated under field conditions.

In the second example, studies on the variation in seasonal responses and habitat preferences among the various *C. carnea* biotypes (species or populations) led to tentative recommendations for matching biotypes with specific pest management situations (cropping systems). For example, the dark green *C. downesi* is recommended for use in evergreen trees, whereas the light green *C. carnea* from the eastern United States is recommended for annuals or deciduous perennials (e.g., field crops or vineyards). However, these recommendations were based on limited information and comprehensive recommendations require additional data (e.g., on the responses of the biotypes to plant characteristics and to prey). Most importantly, the recommendations should be evaluated under commercial conditions.

Even seemingly small differences in plant structure and chemistry may influence lacewing effectiveness. For example, the smooth and hirsute leaf surfaces of certain cotton cultivars affect *C. rufilabris* larval mobility and prey consumption differently (Treacy et al. 1987). The effectiveness of *C. carnea* also varies in response to the surface and structure of cabbage and wheat plants (Eigenbrode et al. 1995, 1996; Messina et al. 1995). These excellent examples illustrate the necessity of matching the predator's biological characteristics not only with the physical conditions of the environment, but to the crop as well. They also illustrate the necessity for comparative studies so that species-specific recommendations for using lacewings can be developed.

Similar types of comparative studies should examine *Chrysoperla* responses to prey. Currently, all *Chrysoperla* spp. are considered generalist predators of soft-bodied insects and mites, a trait that underlies their great commercial demand. However, their prey preferences appear to vary significantly (Shands et al. 1972a, Principi and Canard 1984, Obrycki et al. 1989, Nordlund and Morrison 1990). These preferences should be defined better and the differences among species and biotypes should be clarified in comparative quantitative studies. With data from such investigations, reliable recommendations could be made for the improved use of *Chrysoperla* species (and biotypes) against specific types of pests (Tauber and Tauber 1993).

An important consideration is that in open-field releases, introduced predators may themselves become prey. Indeed, the absence of resident predators in enclosed systems, and thus the avoidance of predator-predator interactions, may explain the high success rates of *Chrysoperla* spp. in greenhouse and cage studies. In some circumstances, ants, assassin bugs, earwigs, and other predaceous arthropods can attack lacewing eggs and sometimes larvae, thereby disrupting the effectiveness of releases (e.g., Nyffeler et al. 1987; Rosenheim et al. 1993, 1995). For example, the Argentine ant, *Linepithema humile* (Mayr), removed 98% of the *C. carnea* eggs that were dispensed on tulip trees to control the aphid *Illinoia liriodendri* (Monell) (Dreistadt et al. 1986). To reduce disruption, prefed larvae, rather than eggs, can be used; however, at present, the high cost of larvae makes this method prohibitive in most agroecosystems. But, the lesson is clear: intraguild predation is a factor that should receive more attention than it has in the past.

Less well-documented, but of equal importance, is the potential disruptive effect of parasitoids in augmentative release programs. Several species of parasitoids attack *Chrysoperla* eggs and larvae (Lyon 1979, Gerling and Bar 1985, Ruberson et al. 1989, Ruberson and Kring 1995, Legaspi et al. 1996). Rates of parasitism can be high, especially at the end of the season. In pecan orchards with season-long releases of *C. carnea* eggs, parasitization increased such that overall lacewing densities (introduced and resident populations) were lower in experimental than control (non-release) fields. Similarly, in one of two trials, the scelionid *Telenomus tridentatus* Johnson & Bin parasitized considerably more eggs in experimental plots (~30%) than in control plots (~2%) (Ehler et al. 1997). In some cases, release of mature (rather than newly laid or young) eggs can reduce parasitism greatly (Ruberson et al. 1995).

The impact of pathogens on augmentative releases of predators is poorly understood (e.g., Sajap and Lewis 1989). However, recent studies report that *C. carnea* larvae are susceptible to *Bacillus thuringiensis* (Berliner) toxins that are being incorporated into corn, potato, and other crop plants (Hilbeck et al. 1998). Thus, the large-scale use of transgenic plants should be tested for significant negative effects on this important predaceous insect.

Pesticides constitute another common disruptive component in many agroecosystems. Here, *C. carnea* may have an advantage over other introduced or resident natural enemies because it has a relatively broad tolerance to many insecticides, particularly during the larval and cocoon stages (Grafton-Cardwell and Hoy 1985, Singh and Varma 1986, Pree et al. 1989, Mizell and Schiffhauer 1990). However, sublethal effects are rarely studied (e.g., Lawrence et al. 1973, Hassan and Gröner 1977). Moreover, tolerance varies geographically; *C. carnea* individuals associated with heavy pesticide usage often are less vulnerable than those from areas with low insecticide usage (Grafton-Cardwell and Hoy 1985). In contrast, *C. rufilabris* displays generally higher vulnerability to insecticides than does *C. carnea* (Lawrence 1974), and knowledge of *C. externa*'s response to insecticides is limited (Ribeiro et al. 1988, Beije 1993, Albuquerque et al. 1999). Insectary managers should consider these issues when they choose or market lacewings. Also, generalized statements regarding lacewing susceptibility to insecticide residues may not be appropriate.

An important consideration is that in open-field releases, introduced predators may themselves become prey.

Release Methodology. Development of efficient methods for commercial releases is a crucial factor in the success of augmentative biological control. Nevertheless, until recently there was little field evaluation of lacewing release tactics since the 1970s when they were originally developed and tested (e.g., Shands et al. 1972b, Reeves 1975, Jones and Ridgway 1976, Ables et al. 1979). When considered together, recent studies provide a crucial lesson: there is a great need for quantitative evaluations under commercial conditions. Below are three examples.

Delivery Systems. Historically, chrysopid eggs were dispensed manually, typically mixed with a solid medium such as rice hulls or vermiculite; this practice fostered uniform field distribution. New delivery systems, some of which use liquid biological carriers, have been developed to improve lacewing delivery to the crop.

In the simplest system, lacewing eggs in small containers (e.g., paper cups) were distributed throughout the plants. This system produced unsatisfactory results in vineyards (Daane and Yokota 1997). When eggs were mixed with corn grit, cannibalism rates were high and <20% of the surviving larvae dispersed from the paper cups. In another simple delivery system, lacewing eggs were mixed with a medium and then dropped onto the plants either by hand or through an adjustable funnel (Ables et al. 1979). In field tests, this method gave better egg distribution than the paper cup method, but during mixing and distribution significant mortality occurred (35% of the eggs) (Daane and Yokota 1997).

Recently, agricultural engineers tested new, much improved mechanized systems. In one test, *C. rufilabris* eggs and larvae were mixed with vermiculite mechanically and distributed evenly over the plants without significant mortality (Giles et al. 1995, Morisawa and Giles 1995, Gardner and Giles 1996a).

One disadvantage of solid carriers is poor retention of eggs on the plants—eggs fall off the leaves, whereas liquid carriers help attach eggs to the targeted plants. Early tests with liquid carriers used sucrose or methyl cellulose solutions to attach eggs directly to the foliage (Doutt and Hagen 1950, Ridgway and Jones 1969, Shands et al. 1972b, Barry et al. 1974, Jones and Ridgway 1976). Unfortunately, the sucrose-based carriers often attracted predators of the lacewings, especially ants.

Although lacewings commonly are sold and dispensed as eggs, larval releases sometimes may be more effective

Recently, there have been notable advances in the development of liquid carriers and commercial sprayers. For example, distributing *C. carnea* eggs in an agar solution has the advantage of lowered attractiveness to ants and other predators (McEwen 1996). In "prototype" applicators, *C. rufilabris* eggs were immersed in a commercial liquid carrier (BioCarrier, Smuckers, Harrisburg, OR), pneumatically agitated to create uniform egg suspension, and discharged into the targeted crop without damage to the eggs and with good retention on the leaves (Gardener and Giles 1996b, Giles and Wunderlich 1998). A commercial sprayer for delivering insect eggs to the field efficiently is also under development (BioSprayer, Beneficial Insectary, Oak Run, CA).

Developmental Stage for Release. Although lacewings commonly are sold and dispensed as eggs, larval releases sometimes may be more effective (Daane et al. 1998). Releases of *C. carnea* larvae were superior to releases of eggs for control of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Nordlund et al. 1991). Although larval releases remain expensive, new advances in insectary production and dispensing systems (discussed above) may improve the economics of commercial releases of larvae. Meanwhile, it is crucial to evaluate the biological and economic advantages of releasing one or the other developmental stage and to begin devising efficient methods for introducing the larval stage. Here is an area where the insectary industry could cooperate profitably with researchers.

Release Rates. Few studies have assessed release rates in relation to pest reduction and costs of application. In most early studies, large numbers of lacewings were dispensed to insure a reduction in pest densities; the release rates generally were too high to be commercially practical at prevailing insectary costs (Daane et al. 1998). Recently, a few field studies addressed this problem by testing lacewing release rates that approximate commercially feasible rates (e.g., Breene et al. 1992, Ehler and Kinsey 1995). However, these tests yielded conflicting results. For example, *C. rufilabris* individuals were dispensed on grapevines at rates varying from 6,175 to 1,235,000 larvae per hectare; in one test, there was a positive correlation between release rate and pest density but in another no significant correlation occurred (Daane et al. 1996, Daane and Yokota 1997). Clearly, more field tests using commercially feasible release rates are necessary.

Habitat Manipulation: Food Sprays. *Chrysoperla* adults are not predaceous; rather they feed on honeydew and pollen. Consequently, the behavioral responses of *Chrysoperla* adults to flowering plants and to chemical and other stimuli associated with their habitats and food can be used to augment populations in targeted areas. For example, populations of *C. rufilabris* were greater in the pecan canopy in orchards with a leguminous ground cover than in those with a grass cover (Smith et al. 1996). Similarly, food sprays that imitate honeydew can attract or arrest adults and stimulate oviposition (Hagen 1987). However, the effectiveness of food sprays in manipulating field populations varies, and recent studies indicate that further basic and applied research in this area is needed.

Apparently, *Chrysoperla* adults find food by responding anemotactically to volatile chemicals (kairomones) that emanate from honeydew or plant nectar (Hagen et al. 1976, Duelli 1984). For example, the kairomone that attracts *C. carnea* to honeydew comes from L-tryptophan, particularly indole acetaldehyde (van Emden and Hagen 1976, Dean and Satasook 1983). It appears that *C. carnea* adults respond to the kairomone only when a synomone is received simultaneously (Hagen 1986). In this case, the synomone that attracts *C. carnea* to cotton is the terpene caryophyllene, a common volatile emitted from cotton leaves (Flint et al. 1979). Identifying and synthesizing the kairomone and synomone that attract *Chrysoperla* provide opportunities to manipulate field populations of lacewing adults. However, application of artificial honeydew is of no value if natural honeydew is present (Hagen et al. 1970).

The best commercially available food sprays contain both enzymatic protein hydrolysates and sugar or honey (Hagen and Tassan 1966). In most trials, protein-sprays without sugar fail to increase the number of lacewings, and sugar-sprays without protein attract lacewing adults but do not stimulate oviposition (e.g., Shands et al. 1972a, Hagley and Simpson 1981).

Early work showed that by using food sprays to attract and induce chrysopids to oviposit before natural honeydew becomes abundant, it is possible to suppress honeydew-producing or other pests before their numbers become large (Hagen et al. 1970, Hagen and Hale 1974, Ben Saad and Bishop 1976). However, in some cases, the application of food sprays increases the densities of lacewing adults but not the eggs or larvae (Duelli 1984, McEwen et al. 1994, Ehler et al. 1997). Given the above, we recommend two areas of research that could be of great value: (1) the seasonal variation in the reproductive responses of lacewings to food and (2) the impact of food sprays on nontarget organisms that could reduce lacewing effectiveness (see Evans and England 1996, Ehler et al. 1997).

A few studies have combined augmentative releases with the application of food sprays to induce both released and naturally occurring lacewings to remain within the crop. Augmentation of *C. externa* in soybeans and corn did not affect the resulting number of lacewing larvae or the three targeted noctuid pest species (Barclay 1990), but applying "Wheast" and sugar at the time of the release gave a two- to six-fold increase in the densities of adults and eggs of *C. externa* in corn fields. These results indicate that with some well-focused research, novel uses of food sprays have considerable potential for application in commercial agriculture.

If the goal is to attract and retain *Chrysoperla* adults in the field, then there is a particular need to focus new research on their seasonal patterns of movement. In *Chrysoperla,* the adult is both the dispersing and reproductive stage and the stage that undergoes hibernal and aestival dormancy. Effective and reliable manipulation of *Chrysoperla,* therefore, requires knowledge of the seasonal timing of (1) adult movement (dispersal, migration) and reproductive development, and (2) responsiveness to the chemical, visual, and other cues that attract adults, arrest their movement, and promote oviposition.

Although diurnal and age-related patterns of adult movement have been investigated (e.g., Duelli 1984), the seasonal components remain relatively poorly known. Seasonal movement has been noted for two geographical populations of *C. carnea* (Sheldon and MacLeod 1971, Duelli 1984), but the cues that initiate it remain largely unstudied. These cues are probably linked to reproductive diapause (because they are in many insects; see Tauber et al. [1986] and Dingle [1996]). Significantly, the timing of diapause and reproductive development can be highly variable in *C. carnea* (Tauber and Tauber 1986, 1993). Such variation could affect the seasonal pattern of dispersal, mating, and oviposition, and this variation needs prime consideration in the development of tactics for manipulating this species. For example, sampling for the presence (or density) of adults is not sufficient to predict the success of manipulative procedures. It is essential to know the reproductive status of the adults and to be able to predict the seasonal changes in the responsiveness of adults to cues that affect their movement and reproductive behavior. Here is another valuable opportunity for integrating applied and basic research.

Evaluation of Augmentative Releases

Although the use of mass-produced natural enemies generally has increased (Ridgway and Inscoe 1998), most releases have not been evaluated under commercial conditions either for efficacy or economic returns (Parrella et al. 1992, van Lenteren et al. 1997). Below, we discuss the need to understand crucial areas in lacewing biology, especially as they relate to cost-effectiveness under field situations, and we suggest methods to improve evaluation efforts.

Numerous field studies have shown that lacewings can reduce populations of targeted pests (e.g., see Daane et al. 1998). However, the reports differ greatly in the degree of detail (the reported levels of control range from 0 to 100% pest reduction), and <10% of the tests used commercial release methods (Daane et al. 1998). Some of the failures may have stemmed from mismatching lacewing species with targeted prey or prey habitat (see above). Other field evaluations implicated problems in commercial mass-rearing or release methods. For example, when lacewings had no effect on the bean aphid, *Aphis fabae* Scopoli, in sugarbeets, Ehler et al. (1997) suggested that the quality of the insectary-reared stock or use of the wrong lacewing species or biotype might underlie the low effectiveness. In cotton, intraguild predation hampered lacewing releases (Rosenheim and Wilhoit 1993). In each of these cases, the negative field evaluations delineated areas in need of improvement.

Substantial variation in lacewing effectiveness in field tests can result from differences in release methods and rates used.

Similarly, substantial variation in lacewing effectiveness in field tests can result from differences in release methods and rates used. (Daane and Yokota 1997). For example, *C. carnea* has been dispensed at rates from ~7,500 to ~2,000,000 eggs per hectare and methods have varied from gentle hand-release of larvae to mechanical distribution of eggs (Daane et al. 1998). This variation can be expected to influence the outcome of field trials, but rarely is it controlled or assessed in evaluation tests.

Finally, most trials were conducted under highly artificial situations (e.g., in enclosed systems with release rates and methods that tend to favor predator effectiveness) (Daane et al. 1998). Sometimes, these methods are justified because of high crop value [e.g., in greenhouse crops (Heinz and Parrella 1990, Breene et al. 1992)]. In other cases (e.g., in vineyards), they are not (Daane et al. 1996).

Improving the Accuracy of Evaluations. Given the above issues, we recommend three avenues for improving the accuracy of evaluation trials. First, researchers and insectaries should collaborate to investigate how *Chrysoperla* spp. or biotypes can be well-matched to the targeted prey and prey habitats. In doing so, studies in the laboratory or in field-cages, as well as careful behavioral observations, could be employed (e.g., see Clark and Messina 1998). For example, properly conducted cage studies can determine lacewing functional responses to estimate effective release rates for specific targeted pests and crops. Factors to consider include prey density, prey and lacewing developmental stages, temperature, and humidity.

Second, although cage studies have the advantage of controlling the experimental design and conditions (e.g., treatments, lacewing numbers, and stages), they do not duplicate field conditions and their results are not always directly applicable to the natural situation. Therefore, before release trials, the targeted prey habitat should be surveyed, and the densities and species composition of resident lacewings, as well as other predators that might interfere with the release, should be taken into account in developing recommendations. Here again, the importance of systematics and comparative biological data is evident. The survey can help determine the most effective lacewing species and the actual need to supplement generalist predators.

Third, after lacewings have shown their effectiveness against the targeted pest species in cage or laboratory studies, and after surveys of the targeted prey habitat indicate a need to augment lacewings, *in situ* field evaluations should begin. There are many obstacles to evaluating lacewing activity in field trials. In all cases, there is a need for improved sampling methods for *Chrysoperla* larvae because egg and adult counts may not reflect the number or effectiveness of the predaceous larvae. Also, there are difficulties in distinguishing released lacewings from the resident population. However, new methods for marking natural enemies may be employed (Hagler 1997) and, in some cases, the released *Chrysoperla* species may be new to the environment and thus distinguishable from resident lacewings.

Hand-dispensing of larvae during tests provides precision in the number, location, and condition of tested species; however, commercial release methods and release rates must be evaluated. Finally, the role of ecosystem enhancement (food sprays, or cover crops in perennial systems) to increase resident lacewing densities should be evaluated rigorously.

Summary

The commercial use and economic success of *Chrysoperla* and related genera depend on (1) gaining a better understanding of lacewing systematics, biology, and ecology, (2) reducing the costs of mass-rearing and marketing, and (3) commercial-scale evaluation of lacewing performance in agricultural and horticultural systems. Accomplishing these goals with *Chrysoperla*, other green lacewing genera (e.g., *Ceraeochrysa*; see López-Arroyo et al. [1999]), and predators in general, could dramatically increase the arsenal of effective natural enemies available for augmentative releases and greatly accelerate the commercialization of biological control agents.

Acknowledgments

We thank the two anonymous reviewers and the editor for constructive comments on the manuscript. We thank L. Tedders for personal communication. This work was supported, in part, by Western Regional Project No. 185 (all authors) and NRI/CREES Competitive Grants No. 93-37302-9001 and 98-02447, several National Science Foundation grants, and Cornell University's administration (M.J.T. and C.A.T.).

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