

PREDACEOUS COCCINELLIDAE IN BIOLOGICAL CONTROL

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ABSTRACT

Coccinellids have been widely used in biological control for over a century, and the methods for using these predators have remained virtually unchanged. The causes for the relatively low rates of establishment of coccinellids in importation biological control have not been examined for most species. Augmentative releases of several coccinellid species are well documented and effective; however, ineffective species continue to be used because of ease of collection. For most agricultural systems, conservation techniques for coccinellids are lacking, even though they are abundant in these habitats. Evaluation techniques are available, but quantitative assessments of the efficacy of coccinellids have not been done for most species in most agricultural crops. Greater emphasis is needed on evaluation, predator specificity, understanding colonization of new environments, and assessment of community-level interactions to maximize the use of coccinellids in biological control.

PERSPECTIVES AND OVERVIEW

The predaceous coccinellids are linked to biological control more often than any other taxa of predatory organisms. The beneficial status of these organisms has a rich history that is recognized by the general public and biological control practitioners alike (82, 114, 117a, 138, 146, 163, 185). Coccinellidae are important natural enemies of pest species, especially whitefly (69), aphids (66, 90, 94, 114), mealybugs (90, 109, 114), scales (45, 48), and mites (28, 90, 114, 168). The widely cited importation biological control project using the

vedalia beetle (19, 46) has been followed by numerous, although frequently unsuccessful, programs (82, 90). Similarly, many attempts have been made to encourage increased predation through augmentation, which have had varying results (41, 44, 90, 235). The role of naturally occurring Coccinellidae in suppressing pest populations is significant (113, 114, 117a, 189) but poorly documented in many pest management programs that purport to conserve natural enemies.

The efficacy of predaceous coccinellids in natural or managed systems is difficult to determine given their mobility and typically polyphagous nature (66). Evaluation of coccinellid efficacy involves (a) careful sampling, (b) insecticidal disruption, (c) exclusion experiments, and (d) prey enrichment, marking, direct observation, and behavioral experimentation (161). Many evaluations rely on correlation of prey and predator densities, which vary in reliability, particularly with highly polyphagous species (e.g. 101, 127). Only experimental evaluation methods provide tangible evidence of the impact of predaceous coccinellids (113, 153, 154, 161). Luck et al (161) reviewed experimental methods for evaluating natural enemies and cited 11 examples involving coccinellids.

Sampling techniques that provide accurate estimates of coccinellid densities are critical for evaluation and include the following: (a) passive collection (traps), (b) dislodgement (e.g. sweep net) or removal technique, or (c) visual estimation. Accurate assessment of coccinellid densities is difficult, and errors in sampling may underestimate coccinellid densities by a factor of 10 (66). Methods to sample coccinellids have been evaluated in numerous systems, and the preferred technique varies with habitat and species (e.g. 56, 81, 157, 171, 233).

Research on predaceous coccinellids occurs worldwide and represents a significant portion of the international *Ecology of Aphidophagous Insects* symposia (24, 112, 115, 188). Comprehensive reviews of the biology of the Coccinellidae have been published (89, 111, 114, 117a, 146, 163), but no review has focused on the use of Coccinellidae in biological control since the early 1970s (90, 113, 114). In addressing this topic, we used the tactics of biological control (46)—conservation, importation, and augmentation—to organize this review.

CONSERVATION

Conservation of natural enemies involves environmental modification to benefit (or minimize harm to) natural enemies (46). Minimal disruption of natural enemies can be attained by (a) reduction of the impact of pesticides, (b) selective use of pest-resistant plant varieties, (c) changes in cultural practices including maintenance of refugia for natural enemies through the use of strip-plantings, field borders, or cover crops, or (d) alteration of regional landscapes. Because many coccinellids are highly mobile generalists, these tactics often affect coccinellid population dynamics, regardless of the targets of the conservation program.

Pesticides

The cultural practice that has the greatest effect on local populations of coccinellids is the application of insecticides. Accordingly, the greatest gains may be attained through reduction of toxic pesticides in coccinellid habitats. Insecticides and fungicides (both biologically and chemically derived) can reduce coccinellid populations. They may have direct (e.g. direct contact, residual toxicity) or indirect (e.g. consumption of treated prey resulting in consumption of a fatal dose) toxic effects (46). Surviving coccinellids may also be directly affected, e.g. reductions in fecundity or longevity, or indirectly affected by decimation of their food source(s). Adults may disperse from treated areas in response to severe prey reductions or because of insecticide repellency (186). Pesticides vary widely in their effect on coccinellids, and similarly, coccinellids vary greatly in their susceptibility to pesticides. Standardized techniques for testing the impact of pesticides on natural enemies have been developed by a western Palearctic working group of the International Organization of Biological Control (IOBC/OILB) (97), although they are not accepted worldwide. Government-imposed standards for evaluation of nontarget effects probably will be put into practice in the United States (38).

Several biologically based "pesticides" (e.g. bacterial toxins, entomogenous fungi, nematodes) have been evaluated for their impact on coccinellids (80). A reduction in *Coleomegilla maculata* predation of Colorado potato beetle eggs was noted when eggs were treated with 10 times the field dosage of *Bacillus thuringiensis* var. *san diego*, and the reduction was not from delta-endotoxin-induced paralysis (77). Use of the commercial product (M-One[®]) at the recommended dose did not reduce *C. maculata* larval populations (76). Maize pollen expressing a Cry1Ab protein derived from *B. thuringiensis* did not affect development, survival, or abundance of *C. maculata* (204). Entomogenous fungi (*Metarhizium anisopliae*, *Paecilomyces fumosoroseus*, and two strains of *Beauveria bassiana*) cause significant mortality in young *Hippodamia convergens* larvae, although this predator is not susceptible to *Nomuraea rileyi* (137). Similarly, *C. maculata* and *Eriopis connexa* are highly susceptible to *B. bassiana* (162). Conversely, no mycoses developed in *C. maculata* larvae or adults exposed to isolate ARSEF 3113 of *B. bassiana* in laboratory or field studies (205). Nematode applications may affect *Coccinella septempunctata* densities under conditions of high moisture, which are caused by direct nematode infection (179).

Studies have evaluated the impact of chemical insecticides on predaceous coccinellids, and toxicities vary widely among and within classes of insecticides and coccinellid species (140). However, laboratory tests may not provide realistic evaluation of field application effects (177, 260, 263). Furthermore, if the insecticide causes prey mortality, field evaluation is complicated by predator

emigration in addition to direct pesticide-induced mortality (186, 263). Evaluation of residual toxicities in glasshouses must often be carried out independently from field evaluations because toxic effects can be significantly prolonged owing to reduced environmental degradation from rain or UV light (17). Coccinellids rapidly recolonize agricultural fields after insecticide applications if sufficient prey are present (263). Although insecticide applications in potato significantly reduce coccinellid densities, coccinellids remained the same proportion of the overall predator guild and increased their populations shortly after treatment (110).

Although often less susceptible to insecticides than are their prey (38), predaceous coccinellids are highly susceptible to several insecticides applied to celery (139), citrus (17), cotton (2), fruit orchards (13), peach (178), pecan (176), and wheat (207, 260). *Stethorus punctum* tolerates several organophosphate insecticides applied at recommended rates (13). *H. convergens* was more tolerant of 14 different insecticides than were three other coccinellid species in wheat (10). In these evaluations, acephate showed the lowest toxicity to predaceous coccinellids. Some newer products, for example, imidacloprid (177) and abamectin (13), are toxic to coccinellid adults and larvae.

Insecticide selection (type and dosage) and application timing are used to minimize effects on coccinellids while retaining efficacy against pests in alfalfa (72), pecan (176), and winter wheat (207). Fenvalerate has been described as a useful product in conservation of coccinellids (207), although others found fenvalerate highly toxic to coccinellids (140). A moderately selective insecticide, abamectin, is highly toxic to *S. punctum* in the laboratory, but it may be less toxic in the field (13).

H. convergens experiences significant indirect mortality (through predator consumption of treated prey) from several classes of insecticides (130). Adult *H. convergens* are moderately susceptible to methomyl-treated aphids, whereas pyrethroid-treated aphids are most toxic (130). The fungicide benomyl causes little direct mortality of numerous natural enemies, including coccinellids in wheat (208) and pecan (176) or *C. maculata* in the laboratory (219). However, significant sublethal effects have been observed for coccinellids surviving applications of benomyl (219) and the insecticides permethrin and primicarb (202). Insect growth regulators are moderately toxic to *S. punctum* pupae in the field (13), but no other coccinellids have been evaluated.

Harvesting

Modifications of agronomic practices may conserve coccinellids. For example, harvesting (cutting or swathing) alfalfa in lieu of insecticide applications is recommended in southern Alberta when aphid densities are high and alfalfa is near 10% bloom stage. This recommendation is based on studies showing

that cutting alfalfa reduced all arthropod densities but that predator populations (including coccinellids) recover rapidly (96). In Iowa, densities of six species of coccinellids found in alfalfa were significantly reduced in harvested strips, but these predatory species recolonized these areas within 10 days of cutting (72).

Pest Resistant Varieties

Plants may directly or indirectly influence coccinellid effectiveness as a result of altered prey suitability or host-finding success of the predator. Prey reared on resistant host plants may have a significant impact on the fitness of coccinellids. However, because these effects are generally complex and interacting, generalities about the compatibility of plant resistance and biological control are lacking. For example, a diet of aphids reared on resistant grain sorghum cultivars had variable effects on *H. convergens* (215), which suggests that these interactions must be examined on a field scale to evaluate population effects. A secondary metabolite (DIMBOA, or 2,4-dihydroxy-7methoxy-1,4-benzoxazin-33-one) confers resistance to aphids in wheat but can reduce survival and increase developmental time of *E. connexa* (164). Although plants with highest DIMBOA levels produced aphids that had the most detrimental effect on *E. connexa*, the reductions in aphid survival on these plants may offset the toxic effects on *E. connexa*.

Searching behavior of coccinellids is influenced by the complexity of the substrate searched (190). Variations in pea plant architecture significantly influenced *C. septempunctata* and *Hippodamia variegata* foraging behavior (141). Predation of aphids by *Adalia bipunctata* is reduced on plants with dense hairs or trichomes, although the reduction varies with coccinellid species and developmental stage (21). Waxes on plant surfaces searched by coccinellids, particularly on cole crops, interfere with their locomotion and efficiency in capturing prey (52). A significant reduction in predation of *Bemisia argentifolii* by *Delphastus pusillus* was observed as poinsettia leaf trichome density increased (105). Thus, the probability of achieving biological control of whitefly through augmentation with *D. pusillus* is considered greater on poinsettia cultivars with fewer trichomes (105). However, field studies indicated that longer coccinellid residence times on pubescent tomato plants apparently ameliorate this effect (106). These findings are similar to discrepancies noted between a predicted negative effect of glandular trichomes of potato in greenhouse (195) versus field studies (196); the latter support the compatibility of pubescent potato plants and biological control (198).

Refugia

Establishment of refuges during a production season may provide for increased pest suppression by coccinellids. These refuges must initially be attractive to

coccinellids but could act as traps if the predators are attracted more to the refuge than the target crop. The basis for refuge development is a reliance on coccinellids' use of host cues to locate the host habitat as well as to encourage reproduction. For example, aphid presence cues oviposition in *C. septempunctata* and reduces female movement, which increases the likelihood that they will place eggs near prey (58). Females will also deposit eggs more readily in the absence of conspecific larvae (108). Strips of weeds within crops may harbor significant populations of alternate prey and beneficial insects (including coccinellids); this practice has reduced pest aphid populations in apple (261) and has been suggested for use in a number of other agricultural crops (3). Reduction of cotton pest (*Lygus* spp.) populations in early spring, using weed management, has been proposed because predators (including coccinellids) are emigrating when pest densities are increasing (64). Selection of a ground cover under an arboreal crop may or may not influence coccinellid populations in the crop (155). Ground covers in pecan orchards harboring large aphid populations (not pecan pest species) were a refuge for coccinellids, but the presence of the covers had no measurable effect on pests in pecan (18, 238).

Coccinellids may be abundant in refuges at various times of the year, particularly where large numbers of overwintering adults are common, e.g. *H. convergens* and *Harmonia axyridis* (89, 155). However, populations of coccinellids occur in numerous habitats seasonally, and a refuge may be considered to be any area other than the focus crop or field. Careful attention of overwintering sites and banded herbicide applications conserve *Stethorus punctum punctum* populations in apples without enhancing refugia for the pest (tufted apple bud moth) (61, 62). Avoiding corn stubble destruction reduces mortality of overwintering coccinellids, but such a practice would not be practical in areas where pests (especially lepidopterous borers) also use these sites (206).

Landscape Design

Given the broad host range and high mobility of adult coccinellids, scientists have had great difficulties clearly partitioning mortality caused by coccinellids in any given ecosystem. Indeed, only evaluation of the population dynamics of a target coccinellid species at the landscape level is likely to provide reliable predictions of coccinellid impacts in any target system. The use of barriers to prevent interplot movement of insects demonstrates the necessity of using large plots when comparing cultural systems (e.g. monocultures vs polycultures) (12). The tendency for *C. maculata* to aggregate in maize during pollen shed and tasseling demonstrates the volatility of its populations in surrounding systems (87). In central Mexico, two *Hippodamia* species were more prevalent in maize-faba bean polycultures than in corn monocultures, presumably because of the availability of extrafloral nectaries in faba beans (252). Conversely, in the

United States, *C. maculata* was more common and consumed more European corn borers in maize monocultures than in two polycultures, a fact attributed to increased aphid densities and spatially distributed corn pollen in the monoculture (6). Increased foraging time (and lower predation efficiency) in polycultures has been attributed to increased plant densities typical of polycultures (217). When designing a landscape, the plant structure or architecture of the selected crop(s) may influence foraging behavior of predaceous coccinellids (21, 141); however, this is unlikely to be given high priority in crop management. However, the general benefits derived from diversification of agricultural systems (217) warrant increased consideration of landscape planning.

Food Supplements

Applications of various sugars and/or proteins (e.g. “artificial honeydew”) to a field consistently result in increased numbers of coccinellids (60, 91, 92). The ecological basis for these applications is that emigrating coccinellids will “correct” the predator-pest ratios by accelerating the increase of the predators (91). For example, *C. maculata* and/or *Hippodamia* spp. are increased in plots sprayed with food supplements in alfalfa (60, 91), corn (20), and cotton (187). Not only do coccinellid densities increase as a result of food sprays, but populations are observed in target areas earlier, although they quickly disperse when prey become scarce (232). Localized increases in predator populations are likely to result in coccinellid reproduction and increased pest reduction, particularly if prey are abundant (20, 91). Given the frequent positive results obtained from studies investigating food sprays, there appears to be considerable promise for their use, although the behavioral basis for their action is not well understood (92).

IMPORTATION

Following the successful biological control of the cottony-cushion scale primarily by the vedalia beetle, *Rodolia cardinalis*, importation programs focused on Coccinellidae—which is described as the “ladybird fantasy” period (19, 90). Only 4 of over 40 species introduced during this period were established. Thus questions were raised regarding the colonizing ability of coccinellids (19), although selected species (e.g. *R. cardinalis*, *Chilocorus nigritus*, *C. septempunctata*) are considered good colonizers (19, 210, 224, 229). Since 1900, 4 exotic coccinellid species have been recorded from the United Kingdom (163) and 18 of 179 species intentionally introduced are now established in North America (43, 82, 128). Attempts to establish some species were made over several decades. For example, *C. septempunctata* was released from 1957 to 1973 in 11 states (7), and *Menochilus sexmaculatus* (= *Cheilomenes sexmaculata*) was

released seven times from 1910 to 1976 in 6 states (23, 82). The estimated establishment rate for coccinellids into North America (0.10) is lower than a worldwide estimate (0.34) for all biological control programs (85). Unfortunately, factors influencing establishment have been examined for relatively few coccinellid species. Insecticides and winter prey scarcity prevented establishment of *Stethorus nigripes* in California (125). As is the case for all importation programs (85), most successful importations of coccinellids are in orchards or perennial habitats. Aphidophagous species have not been purposefully established in annually disturbed agricultural habitats, but several species have adventively established in North America (43, 118).

Evaluation of Candidate Species

Selecting coccinellid species for importation is typically based on field observations of predation on the target pest and/or on consistent associations of the coccinellid and prey species in their native range. Although this is a logical first step, observed predation does not necessarily mean that the prey is suitable for coccinellid development and reproduction (90, 114, 249). As a result, understanding prey specificity of coccinellids continues to be a critical research area (92, 100, 117, 163, 243). Prey specificity is based on a knowledge of the phylogeny and morphology of predator and prey, and on the proximate ecological factors that influence prey selection (4, 117, 121, 136, 212, 228, 242). Records of prey selection have predictive value for species released in new environments (28, 48, 68, 69, 114, 163); however, many predator-prey records have a bias towards agricultural habitats. Nontarget insect prey, microorganisms associated with certain prey, or nonanimal food items (fungi, pollen, nectar) may be required by an introduced coccinellid species (92, 93, 192). As a likely result, several nonspecific aphidophagous coccinellids have not readily established (82, 89, 93). Field exposure of exotic pests and serological techniques may aid in the determination of prey selection by predators (86, 95, 239, 244).

Releasing climatically matched species or biotypes, including those adapted to local temperature conditions, has been considered critical for biological control (222, 226). Thermal pre-adaptation may have had a role in the establishment and rapid increase in abundance of *Coccinella undecimpunctata* in British Columbia (67). Effects of temperature on introduced coccinellids and comparisons with indigenous species have been extensively determined (67, 170, 173, 174, 182, 194). Thermal requirements for many multivoltine aphidophagous species, including coccinellids, show a high degree of consistency over wide geographic areas (122, 193, 203, 246), which may be related to the prey's thermal responses (156). Understanding coccinellid thermal responses helps in evaluation of seasonal phenology relative to native species and is a basis for predator-prey models (9, 88). Beyond this, the value of these

studies in selection of coccinellids for use in biological control programs remains to be demonstrated.

The relationship between genetic diversity of natural enemies and importation biological control continues to be discussed (31, 123, 221), although examination of gene diversity has focused primarily on parasitic Hymenoptera (209). Recent studies have determined allozyme loci diversity in several coccinellid species: e.g. *A. bipunctata* (148), *C. septempunctata* (150), *C. maculata* (37, 152, 240), *Curinus coeruleus* (65), *H. axyridis* (147), *H. variegata* (151), and *Propylea quatuordecimpunctata* (149). These studies provide an analysis of gene diversity in four Palearctic species established in North America: *C. septempunctata*, *H. variegata*, *H. axyridis*, and *P. quatuordecimpunctata*. No evidence was found that genetic diversity was a basis for establishment of these species in North America.

Disruption of Biological Control

Most coccinellid species feed on more than one prey species; thus, disruption of existing biological control by introduced coccinellids and the potential for indigenous coccinellid species to disrupt introductions needs to be considered (220). For example, because coccinellids feed on parasitized aphids (mummies) (36, 63, 257), the introduction of a coccinellid species may affect existing aphid parasitoids. Conversely, indigenous coccinellids may reduce the likelihood of establishing an introduced aphid parasitoid, although neither case has been documented (66). Coccinellid predation of phytophagous species feeding on alligatorweed, lantana, and prickly pear cacti has been reported (75, 79). The potential for significant egg mortality of *Galerucella* spp. released for biological control of the weed *Lythrum salicaria* by indigenous *C. maculata* has been demonstrated (184). *C. septempunctata* may disrupt biological control of the alfalfa weevil, *Hypera postica*, in Utah by reducing aphid densities that produce honeydew used by *Bathyplectus* parasitoids of *H. postica* larvae (59). However, adult *C. septempunctata* also feed directly on alfalfa weevil larvae, and there is no evidence for disruption of biological control of the alfalfa weevil by *C. septempunctata* in Iowa (73, 74).

Quarantine

Several species of parasitic Hymenoptera, Diptera, Nematoda, and Acari attack Coccinellidae (5, 48, 114, 117a, 133, 163, 197, 216, 230). More detailed examination of introduced coccinellids for insect pathogens (e.g. *Nosema* spp., *B. bassiana*, and *Hesperomyces virescens*) may be warranted (114, 159, 162, 163, 237, 251, 256). Also, emphasis in quarantine needs to be placed on screening for maternally transmitted bacteria that alter sex ratios (131) and sexually transmitted diseases that may be vectored by parasitic mites (132).

Coccinellids released from quarantine free of parasitoids and pathogens may be attacked by indigenous species. For example, *Dinocampus coccinellae* (Hym. Braconidae) attacks introduced *C. septempunctata*, *P. quatuordecimpunctata*, and *H. variegata* (22, 191, 200); *Aprostocetus neglectus* (Hym. Eulophidae) attacks immature stages of *Chilocorus kuwanae* in North Carolina (180); and the tachinid *Strongygaster triangulifera* attacks *H. axyridis* (181).

Rearing and Release Methods

One focus for rearing imported coccinellids has been on the effects of temperature and prey on development and reproduction (e.g. 44, 172, 255). Symbiotic microorganisms may cause female-biased sex ratios in coccinellids (131). Effects of inbreeding during rearing also need to be considered relative to establishment (123).

Importation programs using coccinellids have historically released as many adults as were available from quarantine and rearing. Introductions of large numbers of predaceous adults in a single location may cause density-dependent movement. Furthermore, many coccinellid species are cannibalistic, and competition for prey may occur following release. The importance of environmental factors or physiological states of released adults (e.g. reproductive vs diapausing adults) for establishment has seldom been evaluated (e.g. 7, 23, 125).

Data for relatively few coccinellid species compare releases of immatures and adults. Adult *C. kuwanae* dispersed after release, and eggs desiccated or were preyed upon, whereas larvae resulted in local establishment (47). Conversely, the adult stage of three *Chilocorus* spp. was best for release against high densities of red scale, *Aonidiella aurantii* (99, 227). When *C. nigrinus* adults were released on scales infesting bamboo adjacent to citrus orchards, they moved into citrus orchards to prey on red scale (99).

Diapausing adults were presumably the colonizing stage of several coccinellid species fortuitously established in North America (43). Diapausing adult *C. septempunctata* were released into overwintering habitats in the United States (7, 107). The release of laboratory-reared aphidophagous coccinellid species has been suggested to be a nonviable approach for importation of these species (43).

Evaluation

Use of genetic markers to distinguish among released populations of coccinellid species has been attempted (218). Relatively few quantitative evaluations of introduced coccinellid species have been conducted [e.g. *Diomus pumilio* (50)]. Evaluations have historically been qualitative; for example, in the late 1890s following release of *R. cardinalis* in southern California, *Icerya purchasi* densities declined and orange production increased (19). Not until the late 1960s were

detailed evaluation studies of *R. cardinalis* conducted in California (210). However, the underlying mechanisms of biological control of *I. purchasi* through the interaction of *R. cardinalis* and the parasitic fly *Cryptochaetum iceryae* continue to be studied (250).

An additional aspect to the evaluation of an introduced coccinellid species is its potential effects on indigenous coccinellid species and nontarget species (236). The establishment of *Chilocorus cacti* and *C. nigrinus* has not caused a decrease in populations of indigenous *Chilocorus* spp. in South Africa (98, 101). Conversely, based upon trends in sampling data in North America, the spread of *C. septempunctata* is correlated with a decline in the indigenous species *Coccinella novemnotata* (258). The effects of *C. septempunctata* on indigenous coccinellid species have been documented in an 18-year study in South Dakota (53, 54, 143). Densities of *A. bipunctata* and *Coccinella transversoguttata* in South Dakota were reduced following the spread of *C. septempunctata* (55). The addition of *C. septempunctata* did not increase coccinellid abundance, and presumably no increase in biological control of aphids in corn, alfalfa, or small grains resulted (55). Mechanisms underlying the interactions among *C. septempunctata* and indigenous Nearctic predators have been examined (25). No differences in 48-h weight gain were observed when a *H. convergens* larva was paired with a conspecific or *C. septempunctata* larva in the presence of abundant prey (57). Interspecific interactions at low prey densities reduced preimaginal survival of *C. maculata* compared to *C. septempunctata* (14 vs 66%) owing to competition for aphids or intraguild predation (199). In a two-year field cage study using *Myzus persicae*-infested potato plants, no negative interspecific interactions were observed between *C. septempunctata* and *C. maculata* larvae (199).

Case Histories

WHITEFLY Over 50 species of Coccinellidae attack eggs and immature stages of whitefly pests (69, 183). Some of these polyphagous predators are mobile as larvae seeking out prey, whereas others are sedentary and complete preimaginal development on one leaf (69). Because of the pest status of *Bemisia* spp., interest in importation biological control of this pest has increased (71). *Bemisia* spp. are preyed on by 13 coccinellid species (68, 189), and 3 species are undergoing evaluation for possible release in the United States: *Serangium parcesetosum* from India (158), *Serangium* n. sp. from Malaysia, and *Clitostethus arcuatus* from Spain (70).

SCALES Coccinellid species have been used in several historically significant and successful projects for biological control of scale (45, 48). The coccinellids *R. cardinalis* (19), *Cryptognatha nodiceps* (32, 90, 247), *C. kuwanae* (= *C.*

similis) (32, 47, 90, 180), *Hyperaspis pantherina* (14), *Rhyzobius lophanthae* (121), and *C. nigrinus* and *Chilocorus bipustulatus* [100, 224 (includes a prey list), 226, 227] provide biological control of scale pests.

PSYLLIDS AND APHIDS Nine coccinellid species were released in the western United States for biological control of the pear psyllid, *Cacopsylla pyricola* (253). Three of these species, released for other Homopteran pests, are now established in the western United States: *H. axyridis*, *C. septempunctata*, and *D. pumilio*. *Harmonia conformis* is established in Hawaii and *D. pumilio* in California for biological control of the acacia psyllid (11, 50). Relatively few aphidophagous coccinellids have been established through importation programs (43, 82, 118). *H. convergens* from California released in South America presumably established because of similar geography that fit its migratory and overwintering behaviors (93). During the twentieth century, eight aphidophagous coccinellid species have established and spread in North America (43, 84, 118), although none likely established as a result of intentional releases: *C. undecimpunctata* (231), *C. septempunctata* (7, 59, 214, 229), *Harmonia dimidiata* (82), *H. axyridis* (27, 82, 166, 248), *Harmonia quadripunctata* (118, 254), *H. variegata* (43, 82, 83, 259), *P. quatuordecimpunctata* (26, 43, 259, 262), and *Scymnus (Pullus) suturalis* (82, 118). The first collections of *H. axyridis* in North America in 1988 and 1991 were 8 to 10 years after releases in Louisiana and Georgia and hundreds of kilometers from release sites (27, 248). This species is now widely distributed in North America (33, 51, 142, 155). High levels of gene diversity indicate that no bottlenecks occurred during establishment; differences among *H. axyridis* populations indicate multiple establishments (147).

C. septempunctata, *P. quatuordecimpunctata*, and *H. axyridis* may have been accidentally introduced through seaports (e.g. Saint Lawrence Seaway, New York, and New Orleans) (43, 262). Based upon overwintering and dispersal behaviors (107, 116), this type of introduction is plausible (229). Because attempts to establish *C. septempunctata* and *H. axyridis* were also underway, the origins of these two species in North America remain questionable (43, 181, 229, 248). Allozyme studies did not resolve the origins of *C. septempunctata* or *H. axyridis* in North America (147, 150). Presumably, seaport introductions of coccinellids could be tested with sampling on transoceanic ships or in harbors. Spatially separated and temporally delayed post-release establishment of introduced aphidophagous species may be the pattern for this type of coccinellid (7, 84, 147, 155). Although this delay may be caused by a lack of sampling or undetectable densities of introduced species, continuous sampling following releases of *H. axyridis* in Louisiana and Georgia failed to detect colonization (27, 248).

AUGMENTATION

Historically, augmentation has involved release of reared adults (e.g. *Cryptolaemus montrouzieri*, *Rodolia cardinalis*, *Stethorus picipes*) or adults collected from overwintering sites (e.g. *H. convergens*, *Brumus* spp., and *Semiadalia undecimnotata*) (44, 89, 90, 93, 167, 168). Even though there is no evidence for the effectiveness of the latter type of release, *H. convergens* from California continues to be collected and released. *Cryptolaemus montrouzieri* was the first species used to demonstrate an inoculative approach for augmentative biological control (90). Commercial availability of coccinellids depends on the cost of collecting or rearing and, in some instances, on the effectiveness of releases (40, 129). Augmentative biological control in greenhouses has been documented for mealybugs using *C. montrouzieri* (134) and for *Bemisia* spp. with *D. pusillus* (102, 103).

Candidate Selection

Coccinellid species used for augmentation range from those easily collected and stored as adults, without rearing (e.g. *H. convergens*), to species that must be reared but show effectiveness in greenhouse and field environments (e.g. *Cryptolaemus*, *Stethorus*, *Delphastus*). Mass production of *Stethorus* spp. and effectiveness of *S. picipes* releases against the avocado brown mite have been documented (28, 167, 234). However, because of the relatively high rearing costs for this predator compared to predaceous phytoseiid mites, releases of *S. picipes* are not made (167).

Rearing and Release Methods

Numerous methods exist for rearing coccinellids on prey (44, 48, 92), e.g. *Stethorus* spp. (234) and *C. montrouzieri* (145). Cannibalism by larvae and adults is a persistent problem in mass rearing of many coccinellid species (1, 163, 175). Nutritional requirements for coccinellids, similar to other predatory groups, are very specific (34, 255). Thus, artificial diets that support normal rates of coccinellid egg production are not commercially available (e.g. 92, 211). Honeybee products or brood have been used for semi-artificial diets (92).

Generally, egg production on artificial diets has been observed for species with pinkish or pale colored adults [e.g. *C. maculata* (8) *Harmonia*, *Olla*] (92). *C. montrouzieri* has been reared on a meridic (partially defined) diet (30), and *R. cardinalis* has been reared and produces eggs on a holidic (chemically defined) diet (165). Females of aphidophagous species with orange-red adults (e.g. *Coccinella*, *Hippodamia*) do not produce eggs on artificial diets without supplemental feeding on aphids (92). The correlation between pale adult coloration and egg production may indicate that carotenoids and carotenes, most likely from aphid prey (16), are essential factors for fecundity (92).

Adults are the stage typically released in augmentation programs (one exception is *C. nigrinus* eggs released on polyester fiber pads for control of red scale in South Africa) (99, 224). Dispersal of adults from field releases is not limited to *H. convergens* collected from California overwintering sites (41). Adult *H. convergens*, *Hippodamia tredecimpunctata*, and *Hippodamia parenthesis* collected in South Dakota and released in aphid-infested fields dispersed within four days (144). Dispersal of *H. convergens* has been reduced by de-winging adults (135). Based on laboratory studies, Giroux et al (78) suggested that third instar *C. maculata* be released against *Leptinotarsa decemlineata* eggs and first instars. Releases of *C. septempunctata* and *C. transversoguttata* eggs and larvae for aphid suppression on potatoes in Maine resulted in highly variable numbers of coccinellids in the release plots and variable effects on aphid densities (235).

Evaluation

Evaluations of augmentative releases of coccinellids have focused on immediate reductions of target pest densities, thus intensive sampling and field cages are used frequently (94, 161). Nontarget effects have not been examined following augmentative releases of coccinellid species. Egg and larval cannibalism has been observed in several coccinellid species, and this behavior varies with prey density (1, 163, 201, 245). The concentration of large numbers of coccinellids in augmentative releases is likely to increase cannibalism and intraguild predation (220). However, augmentative releases of *H. convergens*, *D. pusillus*, and *C. nigrinus*, predators known to feed on parasitized hosts, have improved levels of biological control (36, 120, 225).

A similar nontarget concern for augmentative releases of other generalist predators (e.g. Chrysopidae, Pentatomidae) is their effect on existing coccinellid populations. The hemipteran predator *Podisus maculiventris* feeds on five coccinellid species, although the possibility of intraguild predation in the field is considered low (124, 169). Similarly, species of Chrysopidae feed on coccinellid larvae, which suggests that inundative releases of chrysopids in California vineyards may affect coccinellid species in that agroecosystem (39, 48). Microbial insecticides, e.g. entomogenous fungi and entomopathogenic nematodes, may have negative effects on coccinellids in an agroecosystem, although this has not been documented (137, 179, 205, 251).

Case Histories

DELPHASTUS PUSILLUS This species is distributed across southern North America and into South America (82) and preys on several whitefly species, including *Bemisia* spp. (29, 81, 189). Field and greenhouse releases of *D. pusillus* have been evaluated, including its interactions with whitefly parasitoids and resistant plant cultivars (102–106, 119, 120). This species is available from

over 25 commercial sources (40, 129) and has been considered the best commercially available predator of *Bemisia* spp. (15).

HIPPODAMIA CONVERGENS Several billion *H. convergens* are collected annually from overwintering sites in California and sold (49) despite numerous studies showing the ineffectiveness of field releases of *H. convergens* for aphid suppression because of adult dispersal (41, 42, 44, 89, 144, 223). Releases of *H. convergens* may reduce aphid densities in greenhouses or provide 1- to 3-day reductions in high aphid densities on potted plants (49, 213). We fail to see the value of these field releases and conclude, as have numerous biological control workers, that there is no biological basis for the release of overwintering *H. convergens* for aphid suppression. Augmentative releases of *H. convergens* may be appropriate in enclosed structures such as greenhouses or interior landscapes where movement is restricted. Beyond the lack of effectiveness, the collection and release of *H. convergens* is not a sound biological control practice for two reasons: (a) Removal of *H. convergens* from California overwintering sites may have adverse effects on local populations, and (b) the distribution of *H. convergens* from California distributes a parasitoid, *D. coccinellae*, and a microsporidian pathogen, *Nosema hippodamiae* (160, 223, 237). Finally, because adult *H. convergens* can serve as vectors of fungal pathogens [e.g. dogwood anthracnose fungus (35)], increasing numbers of highly dispersive adults from augmentative releases could increase vectoring of plant pathogens.

CONCLUSIONS AND FUTURE DIRECTIONS

Coccinellids will continue to play a role in naturally occurring and human-assisted biological control, and they will be considered as possible natural enemies for importation whenever a homopteran pest invades a new region. Their role in insect pest management can be greatly enhanced with a return to the conceptual framework of integrated control (241). Quantitative sampling methods have been described for many agricultural systems, and their use is needed to incorporate mortality because of coccinellids in insecticide treatment decisions. Although there has been an increase in the number of experimental evaluations describing the efficacy of coccinellids in pest management systems, documentation of the impact of coccinellids is lacking in most systems (113). Methods to evaluate the effect of pesticides on coccinellids must be standardized to provide comparable results among species and locations.

The key impediments to implementation of conservation and augmentation programs are the same as those described more than 30 years ago (44, 126). Insecticides remain the single most detrimental factor to the survival of coccinellids in agroecosystems. Conservation techniques are needed to enhance

the effectiveness of naturally occurring and released coccinellids. Use of food sprays in commercial production fields warrants continued evaluation. In importation programs, rather than maximizing the number of individuals released, focus is warranted on seasonal dispersal behaviors, overwintering requirements, suitability of alternate prey, and breeding structure. Genetic analysis of introduced coccinellids should be a part of all introduction programs. The establishment of several Palearctic coccinellid species in North America provides an opportunity to examine the effect of these exotic species on resident populations and communities. Only through long-term quantitative studies (55) can questions about the benefits and risks of importing Coccinellidae (236) be scientifically addressed. Several coccinellid species are appropriate for use in augmentation programs, e.g. *Cryptolaemus*, *Stethorus*, and *Delphastus* spp.; however, the most widely released species, *H. convergens*, is not. Biological control has been enhanced by conservation, importation, and augmentation of coccinellids in numerous agroecosystems, but further application and refinement of these technologies is needed.

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