POINT OF VIEW

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Why is *Coccinella septempunctata* so successful? (A point-of-view)

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Abstract. Factors were examined that could be responsible for the predominance of *Coccinella septempunctata* (C7) in most habitats of the Palaearctic and for its successful invasion of the Nearctic Region. C7 is euryphagous, but less polyphagous than *Harmonia axyridis* or *Coleomegilla maculata* in that it cannot develop or reproduce on non-aphid food. The intraguild status of C7 is intermediate. Although adult size is large, preimaginal stages are palatable to those of *H. axyridis* and *Adalia bipunctata*, whereas it is not an intraguild predator of these species. Although these traits appear to be neutral or negative, many aspects of population plasticity are advantageous for C7, often acting in concert with a bet-hedging strategy. Given its high mobility and eurytopy, the inhibition of oviposition in the presence of conspecific larval trails represents an adaptive advantage that favors increased egg dispersal and lowers the risk of offspring mortality due to cannibalism. The ability to temporarily suspend oviposition, combined with heterogenous voltinism and diapause tendencies, enable a portion of C7 populations to feed and reproduce on unpredictably occurring aphid populations. An absence of reproductive diapause in males and pre-hibernation mating are other significant adaptations, along with the tendency to produce offspring in excess of the carrying capacity of local food resources. We suggest that one explanation for the broad geographic success of C7 resides in an ecological plasticity that is based on both genetic and phenotypic polymorphisms.

1. INTRODUCTION

Although *Coccinella septempunctata* (C7) was the most studied coccinellid species in the period 1995–2004 (Sloggett, 2005), various aspects of its ecology and behavior are not yet completely understood. These lacunae in knowledge have fostered contradictory views regarding its associations with aphid prey. However, it has achieved high abundance and a dominant role among Palaearctic coccinellids in particular habitats (e.g. Honěk & Hodek, 1996; Ricci et al., 2005) and has been implicated in the displacement of native coccinellid species, particularly of *Coccinella novemnotata* (Wheeler & Hoebeke, 1995; Snyder & Evans, 2006; Frank & McCoy, 2007; Harmon et al., 2007) following its invasion of the Nearctic (Elliott et al., 1996; Reitz & Trumble, 2002). In general, most introduced species fail to become established (Mack et al., 2000). The successful establishment of C7 across extensive regions of the USA and Canada (e.g. Krafsur et al., 2005) indicates its ecological flexibility, even if its distribution in the western USA was enhanced by additional releases following the invasion of *Diuraphis noxia* (Louda et al., 2003). The invasive success of C7 in North America contrasts with the inability of *Adalia bipunctata* to expand its distribution in Japan after its establishment near Osaka in 1994 (Sakuratani et al., 2000; Kajita et al., 2006).

While some authors prefer to treat aphidophagous coccinellids as a rather uniform group ecologically (Dixon, 2000), we emphasize the need to study traits specific to individual species. Aphidophagous coccinellids differ in prey and habitat specificity, voltinism tendencies, migratory behavior, and life histories (Hodek & Honěk, 1996a). Individual species vary considerably in their impact on aphid population dynamics. Recent studies have suggested that conservation biological control strategies should focus more on key predator species than on overall abundance of predators. For example, *Coccinella* species, including C7, were recorded as key aphid predators in a study in potato fields in the state of Washington, USA (Straub & Snyder, 2006). A survey of characteristics of dominant ladybird species thus appears badly needed. The ecology of *Harmonia axyridis* has already been reviewed (Koch, 2003; Lucas et al., 2007) and it seems appropriate to examine C7 as another dominant species.

Observations of the eurytopy and euryphagy of C7 (Hodek & Honěk, 1996a) suggest it is a generalist with a broadly flexible life history. We suggest that these characteristics provide substantial advantages over more specialized species in the exploitation of diverse and inherently ephemeral prey. This essay reviews those characteristics of C7 that we suspect contribute to its “achievements”. A broad comparison of traits with other aphidophagous coccinellids is not feasible here due to space limitations and the lack of detailed field studies on most other ladybirds (Sloggett, 2005). Thus, it is possible that some traits, attributed here as specific to C7, are not exclusive to this species; future studies might reveal them also in other ladybirds. For example, the plasticity of reproductive activity observed in C7 has recently been reported in another common species, *Hippodamia convergens* (Michaud & Qureshi, 2006). Here we focus on comparisons of C7 with *A. bipunctata*, *H. axyridis* and *Coleomegilla maculata*.

In contrast to many coccinellids that are less abundant and more specialized, C7 shows traits consistent with a “risk-prone” existence (Hodek, 1966). More often then other species, C7 shows a tendency to produce offspring in excess of the carrying capacity of the local food resources. Due to the ephemerality of aphid prey and general environmental uncertainties, a proportion of progeny (sometimes rather large) may be placed at high risk of mortality. For example, it has regularly been observed in summer that millions of hungry C7 swarm, eventually to fall into seas or lakes and become washed ashore (Hodek, 1960, 1996a; Hagen, 1962; Klausnitzer, 1989; Majerus, 1994; Turnock & Wise, 2004). However, the high fecundity of C7 and bet-hedging oviposition tactics lead to a wide distribution of eggs in both time and space. Thus many oviposition decisions that appear maladaptive for offspring in specific contexts may nevertheless yield the highest maternal fitness when averaged over time. Similarly, population level phenomena that appear strongly maladaptive when viewed in isolation may yield benefits under different ecological conditions.

In the last part of this essay, we try to resolve some perceived misunderstandings regarding the ‘usefulness’ of aphidophagous coccinellids by stressing the principal difference between the classical approach to biological control and other forms, particularly conservation biological control.

2. FOOD SPECIFICITY

C7 is not as widely polyphagous as other species, e.g., *Coleomegilla maculata* or *Harmonia axyridis*, that can develop and/or reproduce successfully when fed non-aphid food such as pollen, moth eggs or drone bee powder (Smith, 1960; Hodek et al., 1978; Niijima et al., 1986). The list of essential prey recorded to date for C7, (i.e. those supporting both development and reproduction), is nevertheless extensive, comprising at least 24 aphid species, if we include species of relatively low suitability such as *Aphis fabae* and *Megoura viciae* (Hodek, 1996b, p. 171). However, several aphids have been reported as deleterious to C7, e.g. *Aphis sambuci* (Hodek, 1956) and *Macrosiphum albifrons* (Gruppe & Roemer, 1988). More examples can be found in Hodek (1996b, pp. 159–165).

While C7 can be considered a somewhat narrow generalist with respect to essential prey species, it is broadly euryphagous in its alternative or supplementary food sources and this can provide important advantages during periods when mere survival is more important than successful reproduction. Soon after emergence from dormancy shelters, the overwintered beetles feed on plant nectaries, e.g. of *Prunus spinosa*, and in the prediapause period, when aphids are scarce, on pollen of Compositae and Umbelliferae and on fungal spores. These foods are used to accumulate energy reserves in fat bodies that enable adults to survive long periods without access to essential prey (Ricci et al., 2005).

It can be concluded that C7 is a euryphagous coccinellid capable of exploiting many aphid species and supplementary food sources over the growing season in diverse, although primarily herbaceous, habitats. Nevertheless, C7 appears to be less polyphagous than *H. axyridis* and *A. bipunctata*, species than can utilize far greater numbers of aphid species as essential prey (Koch, 2003; Hodek 1996b, p. 170).

3. FORAGING BEHAVIOR

3.1 Habitat specificity

Although *A. bipunctata* may be more polyphagous than C7 (Hodek, 1956; Blackman, 1967a, b), it is a narrower habitat generalist, occurring preferentially in arboreal habitats (Mills, 1979; Honěk & Hodek, 1996; Iperti, 1999, p. 335; Sakuratani et al., 2000; Sato et al., 2005; Eigenbrode et al., 2008). This stenotopy is associated with a morphological adaptation, a well developed anal disc in *A. bipunctata* larvae that is useful for adhering to plant surfaces. This is particularly important for larvae that develop on a tree or shrub, since these host plants are more difficult for dislodged larvae to regain compared to herbaceous vegetation. When comparing the attachment forces of five species of coccinellid larvae to pea plants, *Pisum sativum*, with crystalline epicuticular waxes Eigenbrode et al. (2008) recorded very high values for *A. bipunctata* larvae. On clean glass the attachment force of *A. bipunctata* was much greater (6.3 mN) than that of C7, *C. transversoguttata* or *H. convergens* (2.6–2.8 mN). Only *H. axyridis*, another arboreal species, generated greater values (11.4 mN). The stenotopy of *A. bipunctata* is also associated with reduced mobility of adults; they disperse less often over the steppe-like central European landscape than do the more eurytopic C7 adults (Honěk & Hodek, 1996, pp. 128–144).

In contrast to *A. bipunctata*, C7 is a typical inhabitant of grasslands and fields (Osawa, 2000; Honěk & Martinková, 2005), although it has also been observed to breed in other habitats that include apple orchards (Honěk & Hodek 1996, p. 130), shrubs (Mills, 1981; Holloway et al., 1991), and even Scots pine (*Pinus sylvestris*) (Majerus, 1994). Such eurytopy was observed also after the invasion of C7 to the Nearctic region, when it was found on poplar, *Populus* spp., in addition to field crops and weeds (Maredia et al., 1992; Brown & Miller, 1998). Until recently, the rural landscape of central Europe was quite hospitable for C7, although this situation could be changing given the decline in cereal production in favor of cruciferous crops such as rape (*Brassica napus*) (Honěk & Martinková, 2005) that host primarily *Brevicoryne brassicae*, a rather unsuitable prey for ladybirds because of its waxy secretions (Hodek, 1996b).

The complexity of cues utilized by adults in orienting to specific habitats is not yet well understood, but may involve semiochemicals of both plant and insect origin. For example, Zhu & Park (2005) showed that adult C7 were strongly attracted to traps baited with methyl salicylate, a volatile released by soybean (*Glycine* sp.) plants infested with *Aphis glycines*, whereas *H. axyridis* adults did not respond, despite the fact they are also an abundant predator of this aphid in the soybean agroecosystem (Fox et al., 2004). These results are indicative that different host plant-aphid combinations can be differentially attractive to various coccinellid species. In other cases, particular plants may be attractive to many coccinellid species because they supply valuable resources in the absence of prey. Examples include the attraction of *C. maculata* to maize (*Zea mays*) in the absence of aphid infestation, and the attraction of numerous coccinellid species to the extra-floral nectaries of sunflower, *Helianthus annuus* (Michaud & Qureshi, 2005). When the density of aphids is low in alfalfa (*Medicago sativa*), C7 adults aggregate in local concentrations of the alfalfa weevil (*Hypera postica*), although weevil larvae serve only as supplemental food (Evans & Toller, 2007). Two native *Hippodamia* spp. did not respond the same way to this alternative prey, leading the authors to suggest that this difference may account in part for the displacement of native ladybirds from alfalfa by C7.

Majerus (1994) considered both *A. bipunctata* and C7 to behave as generalists in England, and reported them as abundant in a wide range of herbaceous and arboreal habitats, mentioning umbellifers, nettles and grain crops. In Belgium, Hemptinne (1989) collected *A. bipunctata* on apple trees, nettles and wheat (*Triticum* sp.). The notable differences between records from England (and Belgium) and most other data from central, southern and eastern Europe (Honěk & Hodek, 1996) are still lacking explanation. The generally higher humidity in England might favor the retention of *A. bipunctata* in non-arboreal habitats there, but comparative studies on humidity relations of these two species are lacking. Alternatively, genetic divergence of geographically separated populations may sometimes lead to novel habitat associations.

3.2 Seasonal availability of aphids

Many aphids produce their peak populations in spring. In central Europe, cereal aphids, and *A. fabae* on sugar beet (*Beta vulgaris*), usually increase in numbers exponentially in late May and June. However, many aphid species can occur also in summer and early autumn, albeit in low abundance. Examples include *Myzus persicae* in mid August in Germany (Unger & Mueller, 1954), *Microlophium carnosum* in September in England (Perrin, 1976), *Euceraphis punctipennis* in mid September in England (Wratten, 1974), *Eucallipterus tiliae* in some years in late August and early September in UK (Dixon, 1971), and various aphids on *Cirsium*, *Rumex* and *Urtica* spp. weeds in July and August in northern Italy (Burgio et al., 2006). These authors also list weeds that serve as late season refuge hosts for aphids in other habitats after arable crops are harvested. On some crops, such as beans (*Vicia faba*), hops (*Humulus lupulus*) and alfalfa (*M. sativa*), aphids are present in late summer and early autumn in central Europe. The same is true for aphids on weeds (e.g. *Aphis cirsii, Uromelan aeneus, Cavariella* spp.). In France, in Low Normandy, many species occur throughout winter (Remaudière et al., 1980). Similarly, *Schizaphis graminum* can survive in active stages under snow cover in Oklahoma (K. Giles, pers. commun.). In individual years, the abundance of aphids depends on environmental factors, particularly precipitation and temperature, and is thus often unpredictable. The notorious ephemerality of aphid prey may have led to the evolution of plastic and variable reproductive behavior in populations of C7 and other aphidophagous coccinellids.

3.3 Relation to aphid parasitoids

Aphid parasitoids have been shown to avoid leaves previously visited by adult coccinellids. The avoidance response of two *Aphidius* spp. to C7 trails was stronger than to those of *A. bipunctata*. It was found that the hydrocarbons n-pentacosane and n-heptacosane occur in significantly greater amounts in C7 trails compared to *A. bipunctata* (Nakashima et al., 2006). This response may preserve food resources for both C7 adults and their offspring and disperse aphid parasitism more widely among aphid patches. Although several authors have pointed out the potential negative impact of coccinellid predation on aphid parasitoids within their hosts (Ferguson & Stiling, 1996; Colfer & Rosenheim, 2001), little attention has been given to the consequences for coccinellids when they prey on parasitized aphids.

3.4 Movement among habitats

Due to their eurytopy and high vagility, C7 adults range widely over large expanses of landscape and feed and reproduce in many habitats. Their offspring are thus also widely dispersed, and the deterrent effect of larval tracks on oviposition (see 4.1) prevents the clumping of preimaginal stages in the richest patches of prey, reducing intraspecific competition. The vagility of C7 was noted by Elliott et al. (1998) who observed that the more vagile C7 and *H. convergens* were more affected by broader scale variation in landscape structure compared to the less vagile species *Coleomegilla maculata* and *Hippodamia parenthesis*. (See also Brewer & Elliott, 2004.) Evans (2004) reported that in Utah, USA, alfalfa fields, C7 females are more attracted to low density *Acyrthosiphon pisum* populations than are native ladybird species. Snyder et al. (2004a) suggested that the early arrival of C7 in developing aphid colonies, and their earlier oviposition there, gave larvae a size advantage over the later-developing offspring of native species.

Use of alternative habitats by C7 was followed in detail over two seasons in Michigan, USA by Maredia et al. (1992). A diverse agroecosystem composed of a mosaic of habitats supported C7 populations from late April till the end of August feeding on various aphid species hosted by annual and perennial crops (wheat, maize, soybean and alfalfa), poplar and weeds. In northern Italy, Burgio et al. (2006) observed seasonal movements of *Hippodamia variegata*, C7 and *Propylea quatuordecimpunctata* among arable crops, fallow and vegetable crops and weedy field margins.

A heterogeneous landscape presents a mosaic of patches within which C7 adults can select those that happen to be suitable at a given time. Evidence is still lacking with respect to the sensory cues employed by C7 adults to locate profitable patches, although there are records of olfactory responses of adult coccinellids to aphids at short distances (Sengonca & Liu, 1994; Mondor & Roitberg, 2000; Acar et al., 2001). Thus, many have suggested (Ives et al., 1993; Osawa, 2000; van der Werf et al., 2000) that flying adults arrive in patches at random and then make decisions to stay or leave based on the presence or abundance of prey as well as signals left by conspecific larvae. It has been estimated (Frazer, 1988) that as many as 50% of ladybirds emigrate from a patch every day only to be replaced by immigrants. Thus the abundance of adult coccinellids in a patch reflects the net balance between rates of immigration and emigration. Empirical evidence indicates that there is greater emigration from patches of lower quality than from patches of higher quality (Kareiva, 1990; Osawa, 2000). Notably, a recent study showed that predator emigration from a patch decreased with increasing aphid abundance (Cardinale et al., 2006). Further detailed studies on the emigration behaviour of ladybirds are warranted and should focus on the effects of different levels of adult satiation, as suggested by Evans (2003).

Kindlmann & Dixon (1993) introduced the concept of an "oviposition window" – a critical period of time in the development of an aphid colony when coccinellid eggs should be laid in order to ensure sufficient food to support completed larval development. However, suitable sites for C7 oviposition do not appear simultaneously on different species of plants or aphids, or even on the same plants under different environmental conditions, and thus may appear and disappear almost continuously when a large, heterogeneous landscape is considered. This scenario of continuous movement (accompanied by feeding and oviposition) among patches in an open system of heterogenous habitats does not favor, in our opinion, any mechanism that would limit C7 oviposition to a narrow time window. We suggest that this concept is valid when isolated aphid patches are considered, but has few population consequences for highly mobile ladybirds. In reality, there may be other aphid patches in the landscape with different phenological windows that are within the reach of ladybird females. The "window" assumption might be more applicable to strictly stenotopic or less mobile species. When one patch becomes unfavorable for oviposition, C7 females can disperse to other patches where the "window is still open" and repeat this behavior many times throughout the season.

3.5 Fall migration

In late autumn, when most aphids have disappeared from crops and weeds and migrated to their primary woody hosts, the aphid-coccinellid dynamic ends. In central Europe, C7 starts aggregating in hibernation sites in August, while *Ceratomegilla* (= *Semiadalia*) *undecimnotata* arrives there in early/mid July (Hodek, 1960, 1962, 1996b; Honěk, 1989; Nedvěd et al., 2001). As adult ladybirds gradually migrate to their hibernation sites, most feed on alternative food sources (pollen, fungal spores) and also on the remnants of aphid populations that sometimes exploit senescent plants (Ricci et al., 2005).

4. OVIPOSITION BEHAVIOR

C7 females oviposit in patches where they find and consume sufficient quantities of essential prey. Nevertheless, ovipositing females possess an inherent dispersal tendency even in the presence of suitable prey and in the absence of conspecific or intraguild competitors in the patch (Frazer & Raworth, 1985; Hodek & Honěk, 1996b; Evans, 2003). This tendency was demonstrated in experiments where aphids were freshly introduced onto plants and the ladybirds directly observed (Ives et al., 1993). Secondly, residues of C7 larvae deposited by the anal disk are deterrent to ovipositing conspecific females as they are indicative of a high risk of egg cannibalism in the patch.

4.1 Oviposition deterrence

The observation that *A. bipunctata* females did not oviposit in patches where conspecific larvae were encountered led at first to an erroneous assumption that physical contact of the female with the larva is needed to produce the inhibition (Hemptinne et al., 1992). Subsequent research has revealed that the tracks of crawling aphidophagous larvae deter oviposition by females of the same species (Růžička, 1994, 1997; Doumbia et al., 1998), and sometimes those of other species as well (Michaud & Jyoti, 2007).

Deterrence based on semiochemicals is obviously more efficient than deterrence in response to physical contact. Although robust comparisons are not yet possible, the deterrency of conspecific larval tracks seems strongest in smaller coccinellid species (Růžička, 2001). Although operational in C7 this deterrent mechanism is weaker than in other species, e.g. *Ceratomegilla (Semiadalia) undecimnotata* (Růžička, 2001). These semiochemicals in the residues left by coccinellid and chrysopid larvae vary among species in their environmental persistence. Whereas the residues of *Cycloneda limbifer* remain deterrent even after 30 days, those of *C. undecimnotata* last five days, and those of C7 only one day (Růžička, 2002). In experiments with *A. bipunctata* the deterrence lasted 10 days (Hemptinne et al., 2001). C7 females are also remarkable in their relatively low sensitivity to larval tracks of heterospecific larvae (Růžička, 2001). This relatively low sensitivity to signals deterrent to other species may indicate that C7 is less sensitive to the risk of intraguild predation compared to other coccinellids.

Despite a low sensitivity to oviposition-deterring semiochemicals, C7 females still recognize them and may seek other plants or habitats. The distribution of offspring among numerous prey patches may reduce intraspecific competition and cannibalism, and spread risks of offspring mortality among multiple patches.

4.2 Oocyte resorption

Female C7 may temporarily discontinue maturation of oocytes and cease oviposition when suitable prey are in short supply, and subsequently resume reproduction when conditions improve (Zaslavsky & Vaghina, 1996). This reproductive strategy occurs in other generalist coccinellid species such as *H. axyridis* (Osawa, 2005), *C.* (*S.*) *undecimnotata* (Katsoyannos et al., 2005) and *H. convergens* (Michaud & Qureshi, 2006) and may consist either of a simple delay in oocyte maturation, or involve the active resorption of eggs. Sloggett (2005) pointed out that oosorption was not studied in coccinellids until very recently and considered it a characteristic of generalist species that may be absent in more specialised ones, such as *Adalia decempunctata*.

5. DIAPAUSE AND VOLTINISM

5.1 Voltinism

Diapause in C7 has been studied mostly in regions with temperate climates where populations show heterogeneous voltinism tendencies. Typically, a greater part of a population tends toward an obligatory univoltine cycle, while a smaller proportion (differing across geographical regions and individual years; 13–20% in a study executed in central Europe) is facultatively polyvoltine (Hodek, 1962, 1996b). After establishment of C7 in the Nearctic region, similar population variation in diapause tendency was reported from New Jersey, USA (Angalet et al., 1979) and New York (Obrycki & Tauber, 1981). The great plasticity of C7 is evident also in two geographical populations of the subspecies *C. septempunctata brucki* in Japan. In Hokkaido in the north, hibernal diapause is induced by short days, whereas the population in central Honshu enters estivation diapause under long days and hibernates in quiescence (Sakurai et al., 1981; Okuda & Hodek, 1983; Hodek et al., 1984; Ohashi et al., 2003). Another case of plasticity in *C. s. brucki* has been reported recently: some adults may produce an additional generation by taking advantage of artificial substrates warmed by direct exposure to sunlight (metal cans, paper, pieces of wood) at ambient temperatures otherwise too low to permit the development of eggs and pupae (Ohashi et al., 2005).

5.2 Diapause induction

Hagen (1962) used the term “semi-estivo-hibernation” to describe the early onset of diapause in C7. In central Europe, the first individuals of the univoltine fraction of the population enter hibernation sites in early August, while those of the multivoltine fraction in the same region continue to feed through September and early October on aphid-infested weeds, and may possess eggs or vitellinized oocytes in the ovaries (Hodek, 1962, 1996b). In central Italy, pollen and spores of fungi were found in the guts of pre-diapause C7 adults in addition to aphids (Ricci et al., 2005). Variable voltinism and plastic reproductive behaviour generate overlapping generations and enable portions of the C7 populations to take advantage of various supplemental food resources that become available late in the season to augment their nutritional reserves for hibernation.

5.3 Gonads

Whereas females typically arrive at hibernation shelters with undeveloped ovaries, the testicular follicles of males remain active during the early warm period of dormancy, until the temperature falls below about 12°C (Hodek & Landa, 1971), and at least some males are able to mate. About 50% of C7 females dispose of the sperm in their spermathecae in September, whereas females of *Coccinella quinquepunctata* and *Ceratomegilla* (= *Semiadalia*) *undecimnotata* are not fertilized until the spring (Hodek & Ceryngier, 2000; Ceryngier et al., 2004). Sperm disposal by females increases intrasexual competition among males and should select for repeated matings in pre-hibernation aggregations.

5.4 Hibernation shelters

C7 populations vary in dormancy behavior and display a broad eurytopy with respect to hibernation habitats and microhabitats (Hodek, 1996a, p. 274). The adults overwinter most often in the litter, in grass tussocks, near the base of plants, or under small stones. They prefer to overwinter on a prominent landscape elevation, such as a knoll or hill, especially if these are near the breeding habitat; overwintering C7 were found in the mountains of France, Czech Republic and Poland at about 1500 m elevation (Hodek et al., 1977; Honěk, 1989; Ceryngier, 2000). If the landscape is not hilly, dormancy sites are usually selected along forest edges, in windbreaks, or in undulating portions of the terrain. The diversity of potentially suitable overwintering habitats for C7 further contributes to its broad eurytopy in both breeding and dormancy.

Population-level plasticity in life-history traits was documented in four C7 populations collected from France, Ukraine and the USA (Iowa, Delaware), by Phoofolo & Obrycki (1995, 2000), who corroborated findings from central Europe in the 1960’s and 1970’s (Hodek, 1996b). Phoofolo & Obrycki (1995, 2000) considered C7’s phenotypic variation in life-history traits as “evidence of either genetically based bet-hedging or phenotypic plasticity, or a combination of these strategies” and implied that these characteristics are among those responsible for the “success” of C7 in non-native regions.

5.5 Termination of hibernation

Diapause ends about halfway through the dormancy period and, by spring time, adults are simply in thermal quiescence. Adults emerge from hibernation in response to rising temperatures. Depending on thermal gradients within hibernation shelters (typically due to varying degrees of insolation), more than one month may elapse between departures of the first and last individuals from a particular site (Hodek, 1960). Variance in age at onset of reproduction was considered by Lewontin (1965) to be an important characteristic associated with colonizing ability, and Michaud & Qureshi (2006) concluded it was a key life history character contributing to the dominance of *H. convergens* in the High Plains region of the central

USA, a comparatively inhospitable habitat for aphidophagous coccinellids. This variation comprises a form of insurance policy for the population whenever it faces uncertainty in the timing of aphid abundance. Various dormancy phenomena thus contribute to the overall plasticity of C7 populations, particularly the variation among individuals in voltinism, diapause and timing of emergence from hibernation.

6. INTRAGUILD RELATIONS

Intraguild predation (IGP) has recently become a popular topic in biological control and conflicting views have been published. Some authors suggest that the net effect of IGP is often disruptive to an aphidophagous guild, e.g. ladybirds disturb foraging parasitoid adults and eat parasitized aphids (Dixon, 2000). Ferguson & Stiling (1996) concluded from a field cage study that the effects of IGP were non-additive; parasitoids reduced aphid populations (*Uroleucon* sp.) more effectively in the absence of coccinellids. In contrast, recent glasshouse experiments indicated that *H. axyridis* complemented biocontrol of *Macrosiphum euphorbiae* by the parasitoid *Aphelinus asychis* (Snyder et al., 2004b) despite consumption of mummies. Others have concluded that even high rates of IGP by coccinellids on parasitoids can have little effect on the outcome of biological control under open field conditions (Colfer & Rosenheim, 2001). Kindlmann & Houdková (2006) concluded from other outdoor experiments that IGP is often unimportant in the field and warn that the results of laboratory IGP experiments should be interpreted with caution. Yano's (2006) review suggests that IGP may be even less important to biological control in protected culture than in the field.

Here we address only one aspect of IGP, interactions among aphidophagous ladybird species. The larvae of C7 lack morphological features such as spines or waxy coverings that may defend some ladybird species from predation (Volkl & Vohland, 1996; Agarwala & Yasuda, 2001; Michaud & Grant, 2003). It has been suggested that the most efficient way for defenceless young larvae to escape the attacks of older larvae or those of more aggressive species (e.g. *H. axyridis***)** is by dropping from plants (Sato et al., 2003, 2005), much as some aphids escape their parasitoids (Chau & Mackauer, 1997). In experiments, where larvae were deprived of this escape route, the results of intraguild interactions are typically biased in favour of the more aggressive competitor (Michaud & Grant, 2003).

Under conditions of low prey availability in small cages, larvae of C7 were favored in competitive interactions with larvae of *C. maculata* (Obrycki et al., 1998). The authors suggested that the effect was due to the greater size of C7 larvae compared to similar-aged *C. maculata* larvae.

When IG interactions were examined between two native North American species (*H. convergens* and *C. transversoguttata*) and two introduced species (C7 and *H. axyridis*) in microhabitats consisting of pea (*Pisum* sp.) plants and aphids, both introduced species were superior to the natives (Snyder et al., 2004a). IG predation was frequently observed between the two introduced species, but neither had a consistent advantage over the other. Nevertheless, *H. axyridis* appeared more successful in preying on the two native species than did C7 and various mechanisms have been proposed to explain why *H. axyridis* larvae may be especially effective IG predators. These include the presence of short spines on the dorsal surface (Michaud, 2002), adhesive tarsi and chemical defence (S. Eigenbrode, W. Snyder and G. Clevenger, pers. commun.), and a generally high level of aggression that yields 'first strike' advantages (Michaud & Grant, 2003). Cardinale et al. (2006) reported dominance of C7 in behavioral interactions between adults, not only with *C. maculata*, but also with *H. axyridis*. In contrast, the IG superiority of *H. axyridis* larvae over C7 larvae was revealed indirectly in a study focused on *A. bipunctata* in Japan (Kajita et al., 2006) in which the survival of *A. bipunctata* larvae was reduced in the presence of *H. axyridis* larvae, but not those of C7.

Harmonia axyridis began invading the United States in 1988 (Chapin & Brou, 1991) and, by the late 1990s, had successfully invaded the citrus groves in Florida where it displaced *Cycloneda sanguinea* as the dominant coccinellid predator of *Toxoptera citricida* (Michaud, 2002). In a similar time frame, *H. axyridis* invaded the apple orchards of West Virginia where it quickly became the dominant coccinellid predator of *Aphis spiraecola*, replacing the formerly dominant C7 (Brown, 2003). In field crops of the High Plains region of the central United States, however, *H. axyridis* has not become a prominent coccinellid, although it has been present there for more than a decade (Michaud & Qureshi, 2006). The difference may be due to either the arid climate or a certain preference of *H. axyridis* for arboreal habitats (Lucas et al., 1997), although its willingness to enter fields of corn (*Zea mays*) (Lundgren et al., 2004; Galvan et al., 2005) and soybean (*Glycine* sp.) (Fox et al., 2004; Mignault et al., 2006) appears rather anomalous in this perspective. A recent prediction (van Rijn et al., 2006) is that *H. axyridis* will not replace the less aggressive C7 in certain habitats because of its relatively high level of cannibalism. Because of its relatively large size compared to most ladybirds native to Europe and the Nearctic region, C7 might be expected to be a formidable predator in IG interactions**.** Experiments showed, however, that feeding on IG competitors, such as larvae of *H. axyridis,* can cause high mortality in C7 larvae, whereas the reverse is not true (Yasuda & Ohnuma, 1999). Also, feeding on eggs of *A. bipunctata* is detrimental for C7 development (Agarwala & Dixon, 1992) and fourth instar larvae are reluctant to do so (Hemptinne et al., 2000).

Thus, in spite of its size, C7 appears to be a less formidable IG predator than *H. axyridis*. It will be informative to observe the outcome of current competitions between C7 and *H. axyridis* in habitats of the Nearctic region, and later in the Palaearctic region. The current era of IG superiority of C7 in many habitats may be short-lived in the face of range expansion by the more competitive *H. axy-*

ridis. Those habitats in which C7 resists displacement by *H. axyridis* may provide important clues to environmental factors that are ecologically favorable to C7.

7. SUCCESSFUL – BUT NOT USEFUL?

The main focus of this essay is not applied biological control, but our discussion of C7 ecology is relevant to the debate about the potential impact of aphidophagous ladybirds on aphid population dynamics. Aphids often achieve elevated and damaging populations on crops despite the presence of numerous coccinellids. However, we should not underestimate the biological control potential of aphidophagous insects, including coccinellids, simply because they do not always regulate populations of aphids to our satisfaction. It is well recognized that coccinellids are important agents of natural (spontaneous) biological control and it would be unwise to neglect their potential (e.g. Smith & Hagen, 1966; Rice & Wilde, 1988; Obrycki & Kring, 1998; Michaud, 2004; Kriz et al., 2006). Their potential has often become evident when predators were eliminated by pesticides, or when a cold spring favored the reproduction of aphids but inhibited the activity of coccinellids. It should also be recognized that large and damaging aphid infestations are rare in natural ecosystems and mostly confined to agricultural crops where they may arise largely as a function of agricultural practices that favor their population increase over that of their natural enemies.

Coccinellids have been successfully used as components of biological control within a framework of integrated pest management and in augmentative programs as early as the 1950s, e.g. against alfalfa aphids (Stern et al., 1959). Conservation approaches, such as intercropping (Fye & Carranza, 1972; Patt et al., 1997) and other modifications of agriculture practices and landscape use patterns, are promising ways to encourage native coccinellids to enter managed ecosystems and increase their impact on aphid populations (Hodek & Honěk, 1996b, pp. 370–389; Obrycki & Kring, 1998; Landis et al., 2000). In this sense, we do not concur with rather pessimist views (e.g. Dixon, 2000, p. 217) that assume negligible impact is inevitable. We agree with Hirose (2006), who recommends a focus on conservation biological control utilizing mobile natural enemies of aphids with high reproductive potential. C7 seems eminently well-suited to comply with this requirement.

Symondson et al. (2002) stated that according to "a review of manipulative field studies, in ~75% cases generalist predators (single species or species assemblages) significantly reduced pest numbers". Together with a parasitoid and two heteropterans, C7 and *H. convergens* exerted significant control of *Myzus persicae* and *Brevicoryne brassicae* in recent cage experiments that showed the role of biodiversity in aphid suppression on collard (*Brassica oleracea*) (Snyder et al., 2006). Very recently, C7, *C. maculata* and *H. axyridis* have all been reported as important components of the suite of natural enemies controlling pea aphid populations in Wisconsin (Cardinale et al., 2006). The recent emergence of *H. axyridis* as a key predator of *Aphis glycines* in soybean (*Glycine* sp.) fields of the American Midwest is another example (Gardiner & Landis, 2007).

Contrasting views have emerged on the impact of aphidophagous coccinellids on the population dynamics of aphids and their potential role in biological control of aphids for several reasons. First, observations on individual species have sometimes been generalized across all aphidophagous coccinellids. Our emphasis in the present essay is that individual species have very specific ecological traits, despite sharing the common habit of aphidophagy. Furthermore, judgements on the usefulness of aphidophagous ladybirds are often made in reference to biological control in general, without discrimination between its different forms. Results of classical biological control efforts with aphidophagous coccinellids may rightly generate a pessimist view with regard to efficacy, but this view is not necessarily valid for the role of ladybeetles in other types of biocontrol.

When compared with coccidophagous coccinellids, aphidophagous ladybirds are much less suitable for the so called "classical" approach in which, after establishment, the imported natural enemies are expected to regulate/control the target insect without any further "assistance" or continuing human inputs, i.e., automatically. This occurred when *Rodolia cardinalis* was introduced to California against the coccid *Icerya purchasi* inadvertently introduced earlier (De Bach, 1964). Such a success was possible because "the rate of increase ratio between the predator and prey was in favor of the coccinellid" (Hodek, 1973, p. 215; Hodek & Honěk, 1996b, p. 352). A similar explanation was given by Hagen (1974) and can be simplified by saying that the success of an introduced natural enemy depends mainly on its generation time relative to that of the target pest. The crucial relationship between predator and prey was already understood in a very early analysis of the "*Rodolia* miracle", when Thorpe (1930, p. 937) explained the success by stressing that *Rodolia* "has, roughly, three generations to one of its prey". This classic wisdom has recently been revived under the term "generation time ratio" (Kindlmann & Dixon 1999, Dixon 2000).

In contrast, only one or two generations of aphidophagous coccinellids have to face many annual aphid generations. Because this reversed situation strongly favours the aphids, aphidophagous coccinellids are ill suited for classical biological control through introductions.

Due to recent recognition of many non-target impacts of invasive ladybirds, most government agencies in the USA have stopped introducing and distributing alien coccinellid species (Louda et al., 2003). Thus, the emphasis in biological control has been shifting away from classical biological control and toward conservation and augmentation utilizing native or already established introduced species (Barbosa, 1998; van Lenteren et al., 2006). This emphasis will require more intensive research on intraguild interactions and a concentration on prominent, widely distributed aphidophagous species such as

C7. Only detailed knowledge of their ecology and ethology will permit rational human interventions to increase coccinellid impact on target aphid species through appropriate management and modification of cultural practices. For example, even the timing and height of mowing, not only of crop fields, but also field margins, may influence coccinellid abundance and efficacy via effects on food availability and dispersal behavior (Boller et al., 2004; Burgio et al., 2006).

8. CONCLUSIONS

Factors were examined that could be responsible for the predominance of C7 in various coccinellid communities of the Palaearctic and for its successful invasion of the Nearctic Region.

Differences in life-history parameters (rate of development, intrinsic rate of increase, etc.) do not indicate any particular advantage for C7 over other aphidophagous coccinellid species – even some of those recently displaced by C7 in North America. C7 is a euryphagous ladybird, perhaps even generalist, but it cannot reproduce without suitable aphid prey, which might represent an important disadvantage under marginal conditions. One might expect C7 to be favoured by its large size in intraguild interactions with many coccinellid species, but this is not always the case. Species such as *A. bipunctata* and *H. axyridis* may be favoured over C7 due to their immature stages being unpalatable or otherwise defended.

While the above mentioned attributes appear either neutral or negative with respect to the ecological success of C7, various aspects of population-level plasticity appear advantageous. Oviposition by C7 females is inhibited in the presence of conspecific larval trails, although less so in comparison with other coccinellid species. In the context of C7's high mobility and eurytopy, the avoidance of such sites can have important adaptive consequences. Egg distribution over greater spatial scales may lower the overall risk of mortality for offspring due to cannibalism and starvation and reduce the population impact of localized events that inflict density-independent mortality. Distribution of offspring in time is facilitated by temporal variation in onset of oviposition. The ability to resorb oocytes under conditions of food limitation conserves reproductive effort until such time as resources are available to support successful development of progeny.

Heterogenous voltinism and diapause enable a portion of C7 populations to exploit aphids well into late summer and fall. Such life history plasticity may be a key factor in the species' success, particularly in arid regions where midsummer conditions may be too hot or dry for aphid population development, whereas late summers become favorable once again. An absence of reproductive diapause in males, pre-hibernation mating, and the storage of sperm by females through winter months, are other traits consistent with an overall strategy of ecological opportunism.

Although apparently favoured over C7 (and many other coccinellids) in aggressive interactions, *H. axyridis* does not invariably displace C7 in all habitats and both species still coexist in certain habitats in USA, as in Japan. The continuing intraguild interactions between C7 and *H. axyridis* in numerous novel habitats are thus worthy of continued observation to determine final outcomes and infer ecological correlates, as both species are strong competitors and highly successful invasive species.

In conclusion, we suggest that the notorious success of C7 in both native and introduced habitats probably arises from its general ecological plasticity that is based on high levels of individual variation within populations and great phenotypic flexibility in the expression of traits by individuals. The characteristics enumerated above, and the tendency of C7 to reproduce beyond the carrying capacity of habitats, represent effective adaptations to the ephemeral and unpredictable nature of its aphid prey, adaptations that may be more highly evolved in C7 than in many other aphidophagous species.

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