

Cyclic Colonization in Predictably Ephemeral Habitats: A Template for Biological Control in Annual Crop Systems

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Biological control strategies that were developed for orchards and forests have had limited success in controlling pests in annual crop systems (ACSs). In this paper I will argue that an accurate characterization of the habitat template of ACSs will be a key feature for developing new strategies of biological control for field crops. I argue that ACSs are "predictably ephemeral" habitats that present a selective environment that is different from that commonly envisioned for disturbed or early successional habitats. By drawing on examples from natural ecosystems that are predictably ephemeral, I characterize the types of life cycles and life-history traits that are common in insects that thrive in these types of environments. "Fugitive" or "colonizing" species that evolve in unpredictably disturbed environments usually allocate resources to numerous dormant or vagile propagules at the expense of parental survival. In contrast, many insects that exploit predictably ephemeral habitats respond to disturbance by dispersing to permanent refugia where they delay reproduction, overwinter, and then recolonize the following year. I refer to this strategy as "cyclic colonization" and document its ubiquity in natural and agroecosystems. Cyclic colonizers typically exhibit between-generation developmental flexibility in life-history traits. In many species, "establishment generations" have small or no wings, are behaviorally sedentary, grow rapidly, reproduce at an early age, and have high fecundities. In contrast, "overwintering generations" are well adapted for dispersal to and from permanent habitats (long wings, behavioral tendency for flight, reproductively immature) and for winter survival. Cyclic colonizers are not, necessarily "r-selected," but rather have generations that alternate between relatively r- and K-selected life-history traits. Cyclic colonization explicitly relies on spatial heterogeneity, and therefore, effective biological control strategies in ACSs must include a landscape ethic that provides an abundance of permanent habitats that can act as reservoirs for indigenous and introduced enemies. The development of an optimal agricultural landscape for biological control in ACSs

will require a metapopulation approach that focuses on annual cycles of colonization between permanent refugia and a patchwork of crop fields. Finally, given the ubiquity of cyclic colonization in ACSs, it seems that effective biological control will depend on an increased information base about the seasonal cycles, dispersal behavior, and overwintering ecology of indigenous and introduced natural enemies. © 1997 Academic Press

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INTRODUCTION

Biological control has enjoyed greater successes in agroforests and orchards than in annual crop systems (Ehler and Miller, 1978; Hall and Ehler, 1979; Nechols and Obrycki, 1989; Hall *et al.*, 1980; Greathead, 1988; Waage and Greathead, 1988; Waage and Mills, 1992; Ehler, 1995; Corbett and Rosenheim, 1996). One difference between these crop systems is habitat stability, and Southwood (1977) has argued that natural enemies should be more effective in controlling pests in stable than in unstable habitats. Although intuitively pleasing, the empirical basis for this idea is poorly documented, and ecological theory does not make a clear prediction about how temporal variation in the environment affects the stability of predator-prey interactions (Reeve, 1988; Murdoch and Walde, 1989; Murdoch, 1990; Sabelis *et al.*, 1991; May and Watts, 1992). An alternative explanation for the limited success of biological control in annual crop systems (ACSs) is that the life-history attributes of the natural enemies (predators, parasites, parasitoids, diseases, etc.) that have proven successful in perennial systems are inappropriate for the habitat template (*sensu* Southwood, 1977, 1988) of ACSs. Ehler and Miller (1978) were among the first to emphasize that an effective biological control program in any agroecosystem should be based on careful consideration of the correspondence between

life history and habitat template. They suggest that "r-selected" pests will thrive in ACSs and that these pests are more likely to be controlled by "r-selected" predators than by the "K-selected" species that have historically been effective in orchard systems (see also Price, 1991). More recently, Tauber and Tauber (1993) illustrate the importance of choosing a control agent whose life-history adaptations are compatible with the habitat template of the target agroecosystem (see also Branson and Krysan, 1981; Ruberson *et al.*, 1989; Waage, 1990a).

The purpose of this paper is to focus specifically on the habitat template of ACSs and life-history adaptations of insects that colonize such habitats. I argue that the dominant mode of colonization in ACSs and comparable natural ecosystems is different from that typically envisioned for colonizing, "r-selected" species, and I discuss the implications of this for effective biological control in ACSs. Colonization in this paper is approached at the landscape level. Subsequent papers in this issue focus on within-field predator movements related to patch use and aggregative responses to patchiness in prey abundance.

WHAT IS THE APPROPRIATE HABITAT TEMPLATE FOR ACSs?

In characterizing the components of habitat template, Southwood (1977) distinguished between durational stability and temporal variability. I will refer to these components as ephemerality and predictability, respectively. These terms emphasize the distinction between ephemerality *per se* and the degree to which that ephemerality is predictable. Tauber and Tauber (1993) suggest that the scale (e.g., diel vs. seasonal) and magnitude (harshness of Southwood (1977)) of temporal change in the environment should also be included in an analysis of habitat template.

In temperate climates, all agroecosystems (agroforests, orchards, cover crops, row crops) have a seasonally ephemeral resource base, and the predictability and magnitude of this seasonality in resources depend more on local climate than on type of agroecosystem. However, the degree to which habitat structure is ephemeral will differ among types of agroecosystems. In agroforests and in many orchards (depending on management strategy, e.g., Murphy *et al.*, 1996), habitat structure is relatively permanent, and thus, suitable overwintering sites are often available for pests and natural enemies (e.g., Pschorn-Walcher, 1977; Brown, 1993; Roland, 1994; Corbett and Rosenheim, 1996). In contrast, habitat structure in fields of annual crops is strikingly ephemeral. Habitat structure breaks down catastrophically during harvest and/or from soil manipulation, and the harsh, inhospitable conditions between crops are often not conducive for the overwinter-

ing of natural enemies. The breakdown in habitat structure in these ACSs is extremely predictable compared to disturbances in most natural ecosystems (Tauber and Tauber, 1993).

Ideally, one would like to review the life-history literature on insects that live in a variety of terrestrial ecosystems that, like ACSs, are "predictably ephemeral" in order to characterize the life-history strategies of insects that thrive in such habitats (Ehler and Miller, 1978). Unfortunately, the obvious terrestrial choices for comparison are procrustean in their fit to the habitat template of ACSs. For example, in temperate grasslands, habitat structure changes each autumn, but the change is less severe than in crop fields so that both herbivores and their natural enemies can overwinter in the accumulated thatch and upper soil horizons (e.g., Stinner and Abrahamson, 1979; McCrea and Abrahamson, 1987; also see Stanton, 1988). The catastrophic breakdown of habitat structure in crop fields is more akin to natural disasters (fires, avalanches, floods, storms) that influence life histories in "disturbance-maintained" ecosystems (e.g., Sousa, 1984; Knapp, 1985; Wallace and Collins, 1990). However, natural catastrophes are not nearly as predictable in time and space as the harvest and soil manipulation schedules in annual crop fields (Tauber and Tauber, 1993). Thus, native grasslands and other disturbance-maintained ecosystems do not provide an appropriate model for the pattern of disturbance in ACSs.

COLONIZATION OF EPHEMERAL AQUATIC HABITATS AS A MODEL FOR COLONIZATION OF ACSs

Ephemerality in aquatic habitats is relatively easy to assess because the boundaries are often discrete and because deterioration in habitat quality is easily observed (i.e., when they dry). Aquatic ecologists have spent considerable time categorizing habitat ephemerality and the corresponding life-history adaptations of aquatic organisms (see reviews by Wiggins *et al.*, 1980; Williams and Hynes, 1977; Boulton and Sutter, 1986; Williams, 1987; Batzer and Wissinger, 1996; Wissinger and Gallagher, in press). Of the different types of ephemeral aquatic habitats in temperate climates, headwater streams and vernal ponds seem to be most comparable to ACSs. These habitats are always wet in spring, but nearly always dry later in summer. As with the habitat template of ACSs, this predictable disturbance involves an annual breakdown in the structural integrity of the habitat.

Species that live in predictably ephemeral aquatic habitats exhibit two general colonization strategies (Batzer and Wissinger, 1996). The first is desiccation resistance which is best documented in flightless organisms (protists, rotifers, crustacean zooplankton, molluscs) that depend on a resistant, dormant stage in the

substrate (e.g., Gilbert, 1974; Hildrew, 1985; Hairston *et al.*, 1990). Although there are examples of desiccation resistance in aquatic insects, this strategy seems to be most common in harsh and/or unpredictable habitats (e.g., desert streams, rainpools, treeholes, temporary saline ponds) (Wiggins *et al.*, 1980; Williams, 1985, 1987). In predictably ephemeral waters, aquatic insects use a second colonization strategy that involves migration to and from the habitat during the wet and dry phases of the hydroperiod. I refer to this strategy as "cyclic colonization" (Batzer and Wissinger, 1996), and in aquatic habitats, it usually involves either (1) local dispersal between temporary and permanent waters, (2) timed metamorphosis with an adult stage that diapauses in the surrounding terrestrial environment during the dry phase of the wetland or stream, and/or (3) annual long distance migrations.

The most frequent mode of cyclic colonization by aquatic insects appears to involve local movements between temporary and permanent habitats. For example, the colonizers of headwater streams immigrate from permanent downstream reaches of the stream (or from adjacent standing waters) or spend the dry phase of the hydroperiod as terrestrial, diapausing adults (e.g., Boulton and Sutter, 1986; Delucchi and Peckarsky, 1989, and references therein; Westermann, 1993). A similar scenario characterizes the life cycle strategies of aquatic insects that exploit temporary lentic systems. For example, in wetlands that are flooded annually to provide habitat for migratory waterfowl, the dominant aquatic insects (two species of multivoltine chironomids, two dytiscid beetles, and a corixid bug) are all cyclic colonizers (Batzer and Resh, 1991, 1992; Batzer *et al.*, 1993). Adults immigrate from nearby permanent habitats and complete one to several generations before emigrating back to permanently inundated habitats (Batzer, personal communication). Similarly, in the subalpine wetlands that I study, aquatic Coleoptera and Hemiptera annually colonize temporary basins from their winter refugia in permanent basins. In addition, several species of caddisflies (Trichoptera) exploit these temporary ponds by spending the dry phase of the hydroperiod as diapausing adults in the surrounding forest (Wissinger *et al.*, 1996; Wissinger and Brown, unpublished). Long-distance cyclic colonization of temporary habitats by aquatic insects appears to be a less common strategy and is only well-described for large, migratory species of dragonflies (Odonata; e.g., *Tamea*, *Pantala*, *Anax*) that migrate latitudinally (Trotter, 1966, 1967; Walker and Corbet, 1975; Wissinger, 1989).

EVIDENCE FOR CYCLIC COLONIZATION IN ACSs

Cyclic colonization appears to be a common strategy for insects that thrive in terrestrial annual habitats

(see reviews by Southwood, 1962a,b; Dingle, 1972, 1978; Denno and Dingle, 1981; Taylor and Taylor, 1985; Rankin, 1985a,b; Dixon *et al.*, 1993). A cursory venture into the literature of agricultural entomology suggests that many predatory insects and other arthropods cyclically migrate between crop fields and permanent habitats (e.g., linyphiid spiders, aphids, Heteroptera, Homoptera, Neuroptera, braconid parasitoids; coccinellid, carabid, staphylinid Coleoptera) (Pimentel and Wheeler, 1973; Price, 1976; Ehler, 1977; den Boer *et al.*, 1980; Bechinski and Pedogo, 1981; Lesiewics *et al.*, 1983; Bryan and Wratten, 1984; Wratten *et al.*, 1984; Kennedy and Margolies, 1985; Coombes and Sotherton, 1986; Sunderland *et al.*, 1986, 1987; Decae, 1987; Vorley and Wratten, 1985; Good and Giller, 1988, 1990; O'Neil and Wiedenmann, 1990; Wiedenmann and O'Neil, 1991; Wiedenmann *et al.*, 1991; Tauber and Tauber, 1993; Carter and Rypstra, 1995; Frampton *et al.*, 1995). Most of these cases describe local migrations between adjacent habitats, but several involve long distance dispersal (see reviews by Dingle, 1982; Rankin 1985a,b; Taylor and Taylor, 1985; Woiwood and Stewart, 1990). Unidirectional colonization, such as the "pied-piper" migrations described for several crop pests, does not appear to be a common strategy for natural enemies (Davidson and Lyon, 1987; Mitchell, 1981; Dingle, 1982). Similarly, although some pests at low latitudes are able to overwinter in fields, this too does not appear to be a common strategy for predators (see Davidson and Lyon, 1987). Thus, the dominant theme that emerges from the terrestrial insect ecology literature is that many, if not most, of the predatory insects that are potential natural enemies in ACSs migrate cyclically between fields and surrounding permanent habitats (hedgerows, woodlots, and other field boundaries).

The widespread occurrence of cyclic colonization in ACS landscapes suggests that (1) many taxa have evolved rapidly in response to agriculture, and/or (2) cyclic migration was an ecological strategy, at least in some populations, in the native landscape. Cyclic colonization in a preagricultural landscape would have been most likely in subpopulations near local landscape boundaries (e.g., riparian woodlands in prairie) or along the major ecotone between native grassland and forest ecosystems (Petranka and McPherson, 1979; Grimm, 1983; Jacobson and Grimm, 1986). Populations of forest insects that were adapted to the complex habitat mosaic at that ecotone would have been at a selective advantage during transformation to an agricultural landscape. Tauber and Tauber's (1986, 1987, 1993) work on the physiology, genetics, and ecology of the natural enemy, *Chrysoperla carnea*, provides an example of the type of genetic diversity that would facilitate this transformation from native ecotone to agricultural landscape. In addition to several forest

biotypes, they have identified a biotype of *C. carnea* that completes several summer generations in fields before retreating to forest edges in fall (Tauber and Tauber, 1993).

CYCLIC VS UNIDIRECTIONAL PARADIGMS OF COLONIZATION

Cyclic colonization, as described above, is conceptually different from the unidirectional movements described by the major ecological and evolutionary paradigms of dispersal, migration, and colonization. Many of the earliest ideas about colonization stem from plant ecology and models of secondary succession. In these models, disturbance is envisioned to be followed by the invasion of vagile species which quickly colonize such habitats, but are later replaced by less vagile species (Connell and Slayter, 1977; Davis, 1986; Grubb, 1986; Miles, 1987). Although disturbances can be cyclic (e.g., fire), and there are a number of hypotheses about the mechanisms that underlie community change during

succession, the dispersal of "pioneer" species from one open habitat to the next is viewed as being unidirectional. Similarly, in disturbance-maintained habitats, community composition is thought to revert unpredictably to the most vagile species, and colonization is viewed as a unidirectional process of propagule dispersal (Connell, 1978; Sousa, 1979) (Fig. 1).

Other paradigms that have historically shaped ecological thinking about colonization and colonizing species also emphasize unidirectional rather than cyclic movements of species between habitats. Migration is typically unidirectional in (1) the theory of island biogeography (MacArthur and Wilson, 1967; see also, Robinson and Quinn, 1988), (2) population genetics models of gene flow (e.g., Lewontin, 1965; Parsons, 1982, 1983), (3) models of habitat choice (e.g., Brown and Pavlovic, 1993), (4) models for juvenile dispersal (e.g., Waser, 1985; Othmer *et al.*, 1988), (5) source-sink models (Pulliam, 1988; Pulliam and Danielson, 1988; Danielson, 1991, 1992), and (6) metapopulation models for spatially structured populations (reviews by Gilpin

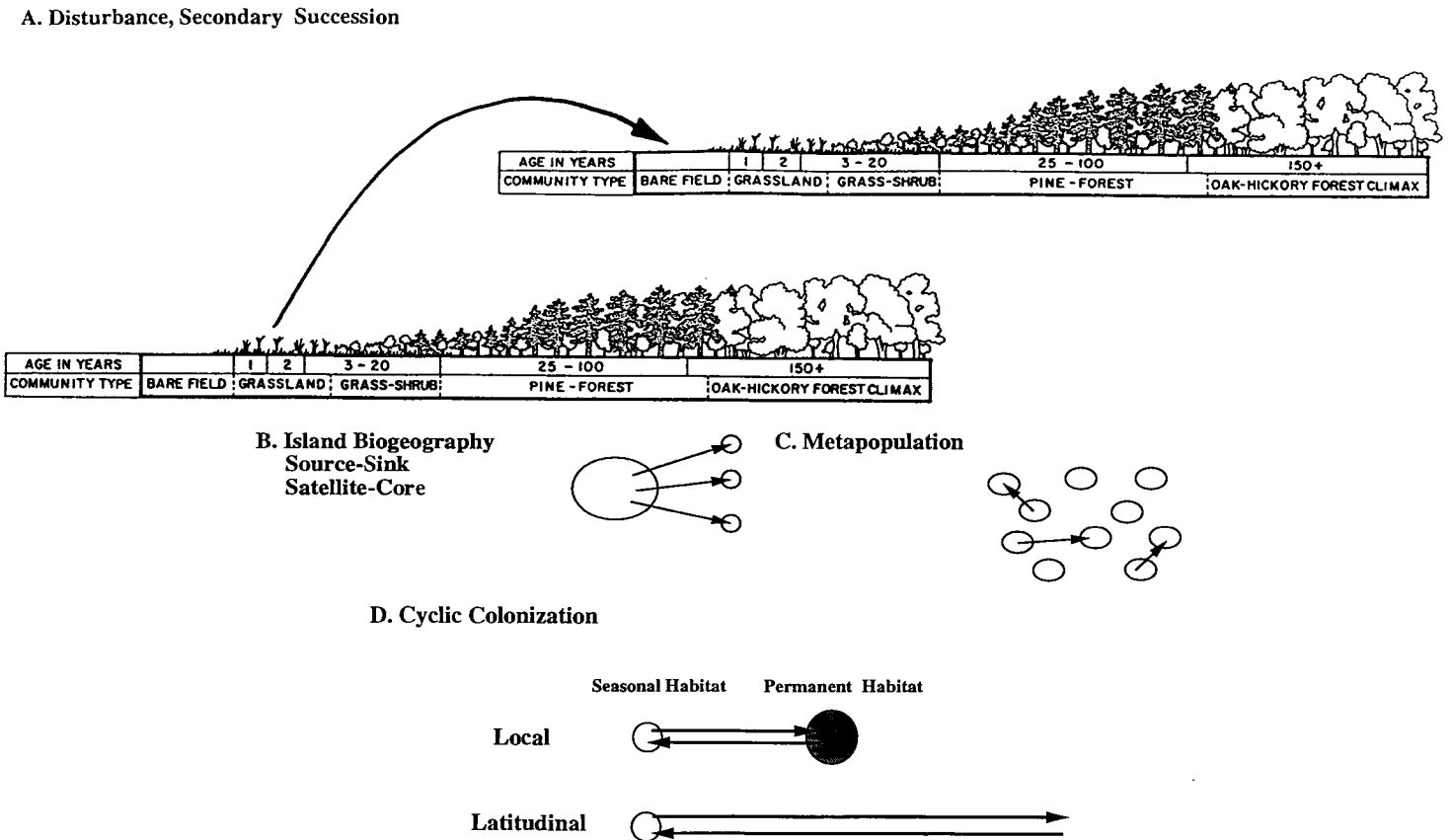


FIG. 1. (A) In models of disturbance and secondary succession, vagile species are early colonists and are eventually replaced (mechanism not presumed) by less vagile but superior competitors (modified from DeSanto, 1978). (B) In models of community assembly and island colonization, dispersal from mainland, source, or core populations is balanced or exceeded by extinction rates in the colonized habitats. (C) In heterogeneous landscapes, low rates of dispersal counteract local population extinction and result in persistence of the metapopulation. (D) In contrast to the unidirectional dispersal in A-C, dispersal in ACSs and other predictably ephemeral habitats involves cycles of immigration and emigration, either between adjacent permanent and ephemeral habitats, or as a result of long-distance migration.

and Hanski, 1991; Hanski and Thomas, 1994) (Fig. 1). To my knowledge, Cohen's (1967) model for host-alternating aphids represents the only population dynamics model that is based on cyclic colonization. My point is that colonization of ACSs by natural enemies is not unidirectional, and therefore, current ecological and evolutionary paradigms about colonization and colonizing species should be applied cautiously to the development of strategies for biological control in ACSs.

LIFE HISTORY AND OTHER ECOLOGICAL CHARACTERISTICS OF CYCLIC COLONIZERS

In general, colonizing species should exhibit adaptations that enhance both dispersal and establishment (Simberloff, 1981). For cyclic colonizers in particular, these adaptations should reflect selection for (1) dispersal from permanent or overwintering refugia, (2) establishment in the ephemeral habitat (microhabitat selection, host location, mating, rapid reproduction leading to multiple generations; see Hopper and Roush, 1993), (3) emigration back to overwintering habitats, and (4) survival in winter refugia.

The aquatic adults of Hemiptera (families Corixidae, Gerridae, Veliidae, Notonectidae) and Coleoptera (families Dytiscidae, Hydrophilidae) are among the best cyclic colonizers of ephemeral waters and exemplify the adaptations for this lifestyle (reviewed by Vepsäläinen, 1978; Jarvinen and Vepsäläinen, 1976; Zera, 1985; Nilsson, 1986). In general, among different species within a genus, inhabitants of permanent waters (with little need for dispersal) tend to be monomorphically wingless or short-winged, whereas species that inhabit harsh or unpredictable habitats are typically long-winged and always capable of dispersing. Those that move back and forth seasonally between permanent and temporary habitats are usually polymorphic for wing presence/size (see below). A second generalization that should be of interest to biological control specialists is that species whose life cycles are dominated by dispersal (long or polymorphic wings) tend to have larger body sizes than sedentary species that live in permanent habitats. The positive relationship between dispersal and body size in aquatic insects has also been recognized in terrestrial insects (reviewed by Harrison, 1980; Dingle, 1982) where it is hypothesized to result from selection for (1) larger wings and/or flight muscles, (2) higher fecundities, and/or (3) energy storage.

Most of our information on the life-history correlates of cyclic colonization has resulted from the study of species with flight polymorphisms (i.e., discrete intra-specific differences in wing size, wing musculature, flight behaviors, etc. (reviews by Harrison, 1980; Dingle, 1985; Roff, 1986, 1994; Tauber *et al.*, 1986)). The association of flight polymorphism and cyclic colonization is perhaps best understood for water striders (Hemiptera:

Gerridae) that exhibit wing-length polyphenism (i.e., polymorphism that results from developmental flexibility; also see Tauber *et al.*, 1986). Typically, long-winged adults overwinter in permanent waters or in surrounding terrestrial habitats, and then fly to temporary ponds or streams in spring. When the long-winged adults arrive in spring, wing musculature histolyzes in the females and the developing ovaries expand into the vacated thoracic space. Depending on the length of the wet phase of the hydroperiod, one or more short-winged or wingless generations are completed during summer. As habitats dry, or as autumn approaches, long-winged individuals with immature gonads emigrate and return to winter refugia. Photoperiod and temperature act as developmental cues and appear to influence wing development during the penultimate nymphal instar (see reviews by Jarvinen and Vepsäläinen, 1976; Vepsäläinen, 1978; Zera, 1985).

This sequence of life cycle events is also found in numerous terrestrial insects including aphids, leafhoppers (family Delphacidae), seed-eating bugs (family Lygaeidae and Pyrrhocoridae), crickets (family Gryllidae), numerous butterflies, and a variety of beetles (families Carabidae, Staphylinidae, Coccinellidae) (Harrison, 1980; Rankin, 1985a,b; Wratten and Thomas, 1990; Sabelis, 1992; Novotny, 1994a,b; Aukema, 1995). Common features of the life cycles of these insects include (1) dispersal from overwintering sites prior to reproduction; (2) onset of reproductive development and loss of flight ability after migration (usually via wing muscle histolysis); (3) one to several generations of highly fecund, but sedentary, individuals; and (4) an emigrating, winged generation with delayed reproduction. Although cyclic colonizers do not necessarily exhibit wing dimorphisms, they do alternate between delayed reproduction and a tendency for dispersal in one generation and reproductive maturation and sedentary behavior in subsequent generations (i.e., the flight-oogenesis syndrome of Johnson (1966, 1969)).

The concurrent changes in reproductive state, wing morphology, and tendency to fly that are integral to this "adaptive syndrome" emphasize that cyclic colonization involves a suite of physiological, morphological, and behavioral coadaptations (Solbreck, 1978, 1985, 1995; den Boer *et al.*, 1980; Harrison, 1980; Rankin and Rankin, 1980a,b; Dingle, 1985; Palmer and Dingle, 1986; Tauber and Tauber, 1993; Han and Gatehouse, 1993; Fairbairn, 1994). Physiological studies with *Hippodamia convergens* (Coleoptera: Coccinellidae), *Oncopeltus fasciatus* (Hemiptera: Lygaeidae), and *Gryllus rubens* (Orthoptera: Gryllidae) suggest that changes in flight behavior, reproductive state, and wing histolysis in cyclic colonizers are coordinated by a common set of neuro-endocrinological events related to the production of juvenile hormone (Rankin and Rankin, 1980a,b; Rankin, 1985a,b; Zera and Tiebel, 1988; Zera and Tobe,

1990). An energetic tradeoff between higher survival and dispersal in the "overwintering generation," and higher reproductive effort (including faster maturation and higher fecundities) in the "establishment generation(s)" has been suggested for many insects (reviewed by Dixon *et al.*, 1993). Recently, Mole and Zera (1993; Zera and Mole, 1994) have explicitly demonstrated an energetic tradeoff between flight muscle maintenance and ovarian development.

Experimental genetics with polymorphic species have played an important role in uncovering life history adaptations of cyclic colonizers. For example, through selection experiments, Zera (1981, 1984, 1985; Zera *et al.*, 1983) found that long-winged phenotypes have undeveloped ovaries and higher overwintering survival rates than short-winged conspecifics, whereas short-winged individuals complete nymphal development faster and have higher fecundities than long-winged individuals. It appears that for polymorphic species in general, diapause, wing form, and migration tendency are under polygenic control and are genetically linked (Dingle, 1978; Istock, 1981; Dingle *et al.*, 1988; Palmer and Dingle, 1986, 1989). Thus, selection on one trait will result in correlated changes in others (Palmer and Dingle, 1986)!

Finally, there is evidence that many cyclic colonizers are generalist predators. Aquatic taxa that are best known as cyclic colonizers (e.g., Hemiptera, Coleoptera, Odonata) are often polyphagous with a proclivity for cannibalism and intraguild predation (Polis *et al.*, 1989; Wissinger and McGrady, 1993; Wissinger *et al.*, 1996). Cannibalism and intraguild predation also appear to be common interactions among terrestrial cyclic colonizers (e.g., Sunderland and Vickerman, 1980; Coombs and Sotherton, 1986; Hurd and Eisenburg, 1990; Agarwala and Dixon, 1992; Rosenheim *et al.*, 1993; Carcamo *et al.*, 1995; Rosenheim *et al.*, 1995). Although these interactions should enhance the establishment or persistence of natural enemies at low pest densities, they may also decrease the net effectiveness of predator guilds in controlling pest species as shared prey (Ehler, 1990; Rosenheim *et al.*, 1995).

CYCLIC COLONIZERS—r- OR K-SELECTED?

I have avoided characterizing cyclic colonizers in the context of r- and K-selection because I think that this paradigm constrains, rather than facilitates, the quest for effective biological control in ACSs. The r- and K-selection model, as proposed by MacArthur and Wilson (1967) is not a theory of life histories, but a model of density-dependent natural selection. Mortality is thought to be relatively density-dependent in stable habitats (K-selection), and relatively density-independent in frequently disturbed habitats (r-selection). Lists of supposed life-history correlates of r- and

K-selection (e.g., Pianka, 1970) are only loosely related to the theory and many species exhibit both r and K-selected traits (e.g., Hart and Begon, 1982; see reviews by Boyce, 1984; Begon, 1985). Although the model certainly has life-history implications, ecologists can rarely isolate the effects of habitat stability from other selective forces that act upon life-history traits. For example, Tallamy and Denno (1981) compared the life histories of lacebugs (Hemiptera: Tingidae) including several species that cyclically colonize hosts in early successional habitats. They found that traits such as age of first reproduction, egg size, clutch size, and number of clutches differ markedly between species living in the same fields. Differences in the life-history traits of these species were related to stage-specific differences in predation rather than to habitat stability. Tallamy and Denno's results emphasize that constraints other than habitat template (e.g. predation) can influence r- and K-selected life-history correlates.

Because ACSs are frequently disturbed, previous authors have suggested that biological control should focus on natural enemies with r-selected life-history traits (Force, 1972; Ehler and Miller, 1978; Price and Waldbauer, 1982). The general idea is that because mortality in disturbed habitats is often density- and size-independent, species should allocate resources to current reproductive effort and vagile propagules, rather than to growth, survival, and future reproductive success (Begon, 1985; Stearns, 1989). However, many natural enemies in ACSs respond to disturbance by dispersing to permanent habitats where they delay reproduction and enter a physiological state that increases survival (K-selected traits). Disturbance in ACSs creates the potential for density- and size-independent mortality, but the predictability of that disturbance has apparently led to the evolution of life cycles with timed dispersal and diapause (Taylor, 1986). Furthermore, colonizing insects tend to be larger in body size than congeners living in permanent habitats (another K-selected trait) (Dingle, 1982). Thus, while cyclic colonizers are good dispersers and summer generations will have some r-selected traits (high fecundity, rapid development, early reproduction), the overall life history is mixed with respect to the r-K paradigm (see also Drea and Hendrickson, 1986). If pressed to place cyclic colonizers within a r-K context, I would argue that they are species that alternate between K-selected traits in the overwintering generation and r-selected traits in the colonizing and establishment generation(s).

CYCLIC COLONIZATION AND BIOLOGICAL CONTROL IN ACSs

Above I argue that cyclic colonization is the dominant strategy that insects use to exploit predictably ephem-

eral habitats including ACSs. Thus, the success of biological control programs will depend on cultural practices that encourage relatively permanent habitats (e.g., hedgerows, woodlots, riparian borders, fallow fields, intercropped perennials) that can serve as reservoirs of natural enemies (Batra, 1992). Although such habitats will not affect colonization by long-distance migrants (e.g., some species of lady beetles), most examples of cyclic colonization by natural enemies appear to involve migration between local habitats. Thus, the degree to which natural enemies will be effective in controlling pests in ACSs will depend on (1) the quality and quantity of these overwintering sites, (2) the size to edge ratio of fields relative to overwintering sites (dispersal into the centers of large fields can delay effective control), (3) tradeoffs between the benefits (shelter, overwintering, refuge from pesticides) and costs (reduced dispersal among fields) of field boundaries, and (4) the degree to which broad-spectrum pesticides eliminate natural enemies once they have colonized in spring (Kareiva, 1990; Wratten and Thomas, 1990; Frampton *et al.*, 1995; Wratten *et al.*, 1995). There is evidence in support of points 1–3 from experimental studies that involve manipulating the size and spatial configuration of refugia for natural enemies and from mark-recapture studies of within- and between-field movements. For example, the addition of long, narrow strips of native vegetation in crop fields dramatically increases the densities of predatory beetles that disperse throughout the fields in spring (Thomas and Wratten, 1988; Thomas *et al.*, 1992; Wratten *et al.*, 1995). With respect to point 4 above, pesticide application strategies that have a minimal impact on natural enemies both in fields and in adjacent refugia will no doubt play an important role in developing an effective control strategy for ACSs (reviewed by Burns, 1988; Jepson, 1989a,b; Waage, 1989). Heterogeneous landscapes provide refugia for the behavioral avoidance of pesticides by natural enemies and serve as reservoirs of susceptible pest genotypes, thus, slowing the evolution of resistance (see Roush and Tabashnik, 1990; Sherratt and Jepson, 1993).

Specifying the particular cultural changes that will encourage the most stable and diverse assemblages of natural enemies in ACSs will require a landscape approach to agriculture (Bunce and Howard, 1990; Batra, 1992). Metapopulation theory is one such approach (Levins, 1980; den Boer, 1981), and one prediction of this theory is that in a heterogeneous landscape, populations can persist, and population interactions (competitive, predator-prey) can be stable even when they are not at the local population level (see reviews by Hanski, 1991; Harrison, 1991; Chesson and Rosenzweig, 1991; Hanski and Thomas, 1994). Unfortunately, current models assume unidirectional, rather than cyclic, dispersal dynamics (Hansson, 1991; Ebenhard,

1991; Hanski, 1994) and do not clearly distinguish between within-field and between-field effects. Landscape-level approaches to host-parasitoid and prey-predator interactions in agroecosystems suggest that these interactions can be stabilized by habitat patchiness (Reeve, 1988, 1990; Pacala *et al.*, 1990; Sabelis *et al.*, 1991); yet, within-field habitat patchiness can be destabilizing and can promote prey outbreaks (Kareiva, 1987; Kareiva and Odell, 1987). Differences in scale also appear to underlie contradicting evidence for the response of natural enemies to vegetational diversity (reviewed by Corbett and Plant, 1993). A hierarchical approach (see Levin, 1992; Drake *et al.*, 1993) that integrates colonization at the landscape level (as addressed in this paper) with the dispersal dynamics of natural enemies within fields will no doubt be most productive. At the landscape level, the results presented in this paper suggest that models for encouraging natural enemies for ACSs should focus on annual dispersal cycles between winter refugia and a patchwork of fields. Because of crop rotation cycles, the overwintering pool of emigrants in the fall from previous crops will provide the source of immigrants to adjacent fields in the following year (Fig. 2).

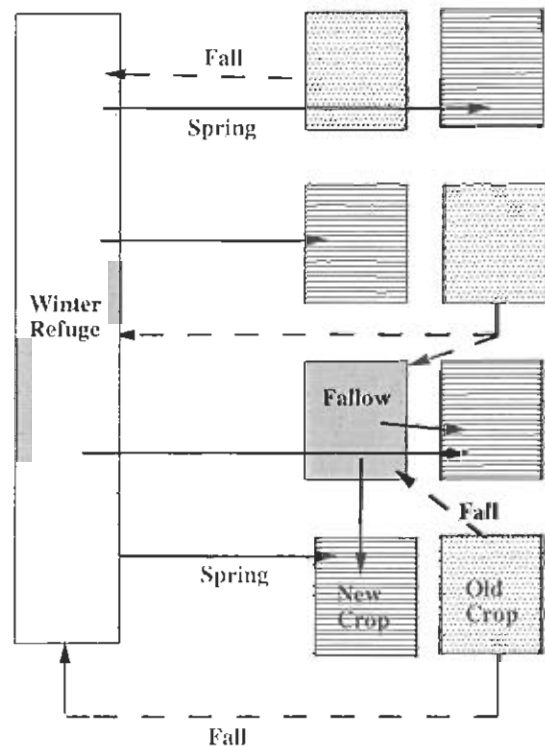


FIG. 2. Cyclic colonization in ACSs will rely on a heterogeneous agricultural landscape and specifically on the quality and quantity of winter refugia (e.g., hedgerows, woodlots, riparian borders, fallow fields). Metapopulation theory that predicts the conditions for the persistence of natural enemies in such a landscape will need to account for crop rotation such that emigrants from fields in fall will provide the colonists for adjacent fields in spring.

The widespread occurrence of cyclic colonization in ACSs also has ramifications for choosing introduced species for pest control (see reviews by Ehler, 1990; Waage, 1990a). Effective species should have life histories that are developmentally flexible, alternating between rapid maturation, early age of first reproduction, and high fecundity in the establishment generation(s); and delayed reproduction, high survival, and adaptations for dispersal in the overwintering generation. Selection experiments with polymorphic and polyphenic insects suggest that there is a wealth of additive genetic variance associated with the morphological, physiological, and behavioral correlates of dispersal ability with selection on one trait leading to correlated changes in other traits (Palmer and Dingle, 1986, 1989; Dingle *et al.*, 1988; Han and Gatehouse, 1993; Tauber and Tauber, 1993; Fairbairn, 1994). Thus, there may be considerable potential for the development of genetic lines and biotypes with seasonal life cycles that are tailored to the seasonal breakdown in habitat structure that occurs in ACSs (see also Roush, 1990). However, the persistence of introduced species and the success of introduction strategies other than annual inundative releases will be limited by the quality and quantity of overwintering sites. Clearly, the success of biological control programs in ACSs will ultimately depend on (1) cultural practices that encourage the development of a heterogeneous agricultural landscape and (2) an increased information base about the seasonal cycles, dispersal behavior, and life histories of introduced and natural enemies.

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