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Exotics as host plants of the California butterfly fauna

Sherri D. Graves[a,*], Arthur M. Shapiro[b]

[a]*1430 Castec Drive, Sacramento, CA 95864, USA*
[b]*Center for Population Biology, University of California, Davis, CA 95616, USA*

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Abstract

Introduced species may impact native species and communities in many ways. One which has received relatively little attention is by serving as resources for natives, thereby altering their ecology. We address such impacts on the California butterfly fauna as currently understood. Eighty-two of California's approximately 236 butterfly species (34%) are reported as ovipositing or feeding on introduced plant taxa. Many more utilize introduced plants as nectar sources. Interactions with introduced plant taxa are not distributed evenly among butterfly species. Alpine and desert butterflies interact with relatively few introduced plants because few exotic plant species have reached and successfully colonized these habitats. Other California butterfly species are specialists on particular plant families or genera with no exotic representatives in California and have thus far failed to recognize any introduced plants as potential foodplants. Some California butterflies have expanded their geographic ranges and/or extended their flight seasons by feeding on exotic plants. However, negative impacts of exotic plant species can also occur. At least three of the state's butterfly species currently lay eggs on introduced taxa that are toxic to larvae. Impacts of introduced plant taxa on California's butterflies are expected to increase as both habitat conversion and alien introductions accelerate.

Keywords: Naturalized plants; Weeds; Floristics; California Floristic Province

1. Introduction

Exotic plant species are increasingly recognized as having broad scale effects on the structure and function of biotic communities across the world (Cronk and Fuller, 1995; Mack et al., 2000). California now has at least 1057 naturalized plant species; these exotics are a prominent feature of many California ecosystems and completely dominate native plants in some habitats (Rejmanek et al., 1991; Heady, 1995).

Although much of the research on invasive plants has focused on competitive effects, there are many other ways in which introduced plants can alter ecosystems. Invasion of an area by an introduced plant can have large direct and indirect effects on native herbivores, particularly those species for which the plant serves as a potential foodplant (see Bowers et al., 1992, and Nagy et al., 1998, for examples). The effects of rangeland weeds on livestock have been relatively well studied for economic reasons (Lorenz and Dewey, 1988; James et al., 1991). However, effects of exotic plants on herbivorous insects have the potential to be much greater due to the greater specificity and limited mobility of most insects, especially in the larval stages.

Introduced plants may promote oviposition by native herbivorous insects even if they are toxic to larvae, preventing development to adulthood (Remington, 1952; Straatman, 1962; Sevastopulo, 1964; Bowden, 1971; Chew, 1977). For larvae with limited capacity for movement in the early instars, this situation can lead to complete mortality for eggs deposited on such a plant. In the long term, we expect natural selection to produce either physiological adaptations for feeding on the plant by larvae or changes in oviposition preferences of adult females resulting in avoidance of the plant for oviposition. However, in the short term, a toxic introduced plant that promotes oviposition can serve as a population sink, resulting in decreases in population size and possible extinction, especially of small, vulnerable populations (Courant et al., 1994; Porter, 1994). Introduced hosts could also facilitate hybridization between specialist insects, resulting in loss of genetic diversity

* Corresponding author. Tel.: +1-916-486-0919.
E-mail address: sdgphc@jps.net (S.D. Graves).

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(see Rhymer and Simberloff, 1996; this may be occurring in the butterfly *Glaucopsyche lygdamus* in the northeastern USA; Dirig and Cryan, 1991).

On the other hand, some introduced plants that promote oviposition may be high quality host plants for native insects and result in the expansion of the local host plant range. This can occur if native insects are preadapted to feed on the plant or when they overcome the initial toxicity or low palatability of introduced plants via natural selection (Thomas et al., 1987; Bowers et al., 1992; Karowe, 1990; Singer et al., 1993; Courant et al., 1994). The addition of a novel plant to the host plant range can buffer the insect population from fluctuations in availability of native host species and/or allow it to maintain itself in disturbed and urban areas when native host populations decline or go locally extinct (Shapiro, 2002). In the case of crop plant monocultures, the increase in biomass of acceptable host plants may permit much larger populations of a species in a particular area than was possible prior to cultivation (Shapiro, 1979; Tabashnik, 1983). If the introduced host plant has a different phenology than the ancestral host species, incorporation of the novel plant into the host plant range may permit the evolution of increased multivoltinism (Shapiro, 1975a, 1995; Shapiro and Masuda, 1980). Phytophagous insects are often limited by the geographic range of their hosts (Bernays and Chapman, 1994; Loxdale and Lushai, 1999). Introduced hosts, having a broader geographic range than native hosts, may permit the expansion of the insect population geographically. This may result in rapid evolution of local adaptation (Carroll et al., 1998; Groman and Pellmyr, 2000). In some cases, introduced hosts may serve as refuges from parasitoids and/or predators if these natural enemies use different cues for locating host plants of insect prey/hosts than the cues used by the herbivores themselves (Fox and Eisenbach, 1992; Gratton and Welter, 1999) and may also alter or reduce exposure to pathogens (Jaenike, 1990). The most extreme consequence of adopting an introduced host is speciation, as claimed for the apple maggot *Rhagoletis* (Feder, 1998).

The goal of this paper is to examine the actual and potential impacts of introduced plant species on one element of California's native insect fauna: the butterflies. Butterflies are well suited for such an analysis since they are large and conspicuous compared to most other insects and are studied by large numbers of both professional and amateur lepidopterists. We are thus more likely to have data on recent use of introduced plants by butterflies than for most other insect taxa. It is hoped that this paper will serve both to kindle interest in the impacts of exotic plant species on phytophagous insects in general and to accelerate and encourage the collection of this type of data for butterflies and other herbivores.

2. Methods

Introduced plants naturalized in the state were identified by using The Jepson Manual (Hickman, 1993) with a couple of exceptions. The plant *Rorippa nasturtium-aquaticum* (also called *Nasturtium officinale*) is recognized as introduced (Munz, 1968) though it is not so recorded in The Jepson Manual. This was assumed to be an oversight, and this plant was considered introduced in the state (Rejmanek and Randall, 1994). Information on distribution and country of origin was also based on designations in The Jepson Manual, and all plant names used in the paper are based on this reference. Information on ornamental and cultivated plants came from the Sunset Western Garden Book (Hogan, 1988). We omitted a few plants, such as *Phyla* (= *Lippia*) *nodiflora*, usually considered aliens, but whose status as such is in doubt (Rejmanek and Randall, 1994). We also treated *Helianthus annuus* var. *macrocarpus*, the cultivated sunflower, as introduced, although The Jepson Manual treats the species as native.

Data on use of introduced plants by California butterflies were obtained by searching both the primary and the secondary literature for references and by contacting California lepidopterists. Some sources of information covered a broader geographic area than the state of California. Most secondary sources, such as field guides, simply compile lists of hosts without specifying geographic sources or specific publications. Many of these "records" are probably erroneous and the vast majority cannot be tracked down. In these cases, all references for butterfly use of introduced taxa known to be naturalized in California were recorded though it was recognized that some of these records undoubtedly came from outside the state and some were based on misidentifications. Attempts were made to find the original sources for these records and/or to corroborate them with California data. If this could not be done, the records were analyzed based on geographic overlap (Stanford and Opler, 1993; Hickman, 1993; Whitson, 1996) and broad habitat affinities of the plant and butterfly taxa within the state. Those records that seemed extremely unlikely to have come from California were eliminated from the data set. Those that seemed reasonable were retained as possible California records. Some records indicated that larvae were taken from one plant and reared on another—these rearing records were not included in our data set.

Some host plant designations were given at the level of the genus instead of the species. In these cases, it was assumed that records were for native plant taxa if those were available. Records at the level of the genus were included in the data set only when all species in the genus in California are introduced. The most recent field guide (Opler and Wright, 1999) rarely identifies

host taxa in detail, instead using broad descriptors like "rock cresses" or "wild buckwheats." We did not attempt to translate these into Latin binomials.

All records of California butterflies using introduced taxa were ranked as to the level of confidence in that record. Of interest was whether the butterfly naturally uses the plant in California, even if rarely. Combinations ranked as "High" were considered well documented in the state. A "Moderate" ranking was given to combinations that seemed reasonable given known foodplants of the butterfly and distributions of both butterfly and plant in the state; these records represent good possibilities but need confirmation. Records of butterflies on plants that seemed possible though unlikely for this state given the distributions and habitat affinities of the plant and butterfly species in California were ranked as having "Low" confidence. Some records were considered valid for oviposition but unlikely as actual foodplants of the butterfly listed; these were ranked as "Oviposition Only." If the plant was known to be toxic to larvae, the designation"Lethal" was added as well. A few plants seemed unlikely not only for California but for the particular butterfly taxa in general; these were noted as "Unlikely."

3. The California butterfly fauna

California has approximately two hundred thirty six species of butterflies (Garth and Tilden, 1986) in nine to eleven butterfly families, depending on accepted taxonomy (Comstock, 1927; Emmel and Emmel, 1973). The butterfly fauna is primarily derived from three elements: Holarctic taxa that share affinities with many temperate Eurasian butterflies, Sonoran taxa typical of the western United States and northern Mexico, and more tropical taxa that tend to enter California only in the southern half of the state (Garth and Tilden, 1986). Although the butterfly fauna itself is considered well-known, there are still species for which life history and host plant data are lacking. For example, early stages and specific host plant data remain unknown for many of the Hesperiid skippers that feed on unidentified grasses. In addition, although the broad outlines of butterfly species' distributions in the state are well characterized, there remain many remote, often montane areas that are little collected. This is especially the case in months outside the prime flight season for local butterflies. Largely because of this, new local records and significant range extensions continue to be documented. However, the geographic locations where our knowledge of butterfly hostplants is most lacking tend to be remote, high altitude areas little impacted by introduced plant taxa (Frenkel, 1977), so the holes in our data are less significant for this paper than they might at first appear.

4. Introduced plants in California

The development of California's rich alien flora has been reviewed recently by Randall et al. (1998). It is estimated that 16 exotic plant species became established during the Mission period (1769–1825), 63 more during the Mexican period (1825–1848), and an additional 55 during the Gold Rush period (1849–1860) (Rejmanek et al., 1991).

The rate of exotic introductions increased significantly in the twentieth century. Jepson reported 292 naturalized species in 1925, Robbins et al. (1951) reported 497 "weeds" in California, Munz and Keck reported 797 introduced species in 1957, updated by Munz to 975 in 1968 (Rejmanek et al., 1991). The recently published Jepson Manual of Higher Plants of California lists 1057 species as naturalized in the state (Hickman, 1993). These figures fail to include many crop plants (California Department of Food and Agriculture, 1996) and garden ornamentals (Hogan, 1988) planted in California since they fail to propagate themselves outside of cultivation, a distinction that probably means little to phytophagous insects. The actual number of exotic plant species to which the butterflies of the state might be exposed is thus actually much greater than these numbers imply, and most of the interactions have begun in the very recent past.

Exotic plant species are not distributed uniformly across the state. In California, the presence of introduced species tends to drop off with increasing altitude (Frenkel, 1977; Schwartz et al., 1996). More than 30% of the 1057 introduced species of plants listed in The Jepson Manual (Hickman, 1993) are found only at elevations below 300 m and more than fifty percent are found only below 500 m. Only approximately six percent of all introduced species are found above 2000 m and less than two percent are found above 2500 m (Fig. 1). Fig. 2 demonstrates that this trend is well-distributed across both large and small plant families as represented in the California flora. Therefore, the extent of exposure to exotic plant species varies greatly depending on the geographic distribution of particular butterfly taxa. In California, maximum butterfly faunal richness occurs at mid-elevation (1500–2500 m) on the west slope of the Sierra Nevada and in the Trinity Alps and High North Coast Ranges (Shapiro 1996; Stanford and Opler, 1993; Shapiro and Richerson, unpublished), with a second center of diversity in the deserts of the southeastern part of the state. Low-elevation butterfly faunas west of the Sierra–Cascade axis are relatively undiverse. However, most of the records reported here are from these low-elevation faunas.

The distribution of introduced plant taxa differs greatly by region as well as elevation. In general, exotic species tend to be more common in disturbed areas and along transportation corridors that facilitate their

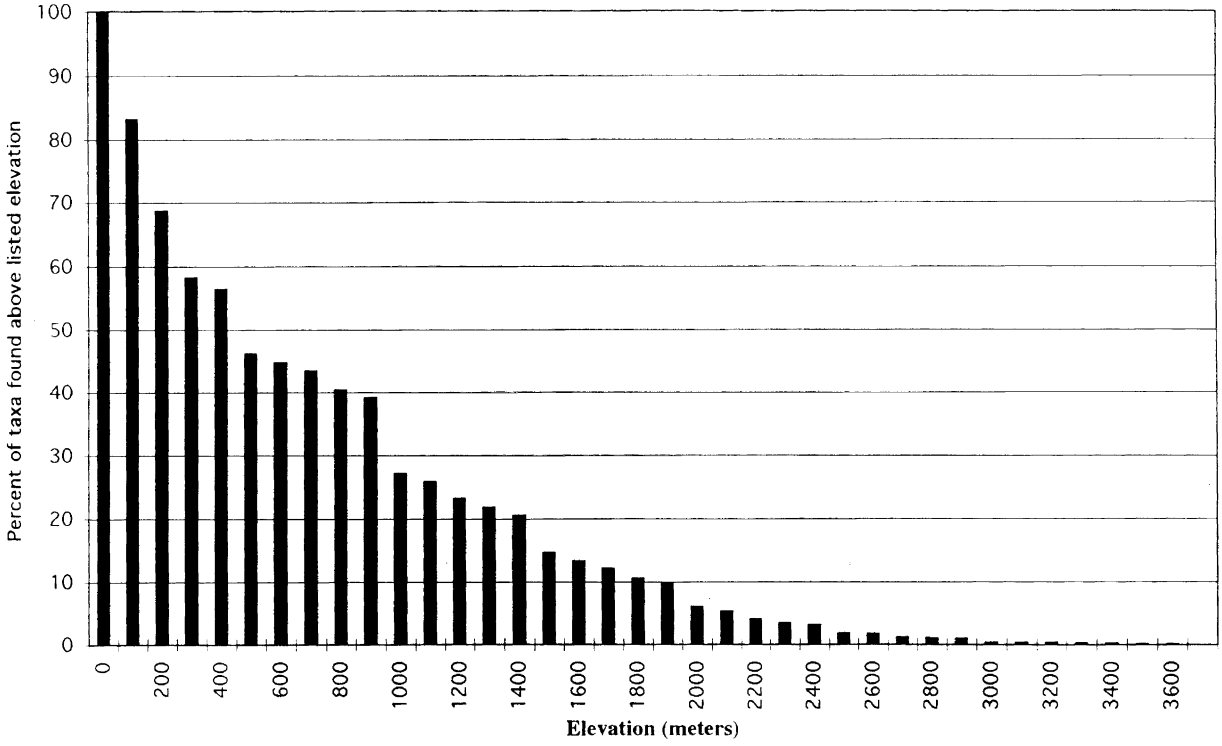

Fig. 1. Elevational distribution of California's introduced plant taxa; date from Hickman (1993).

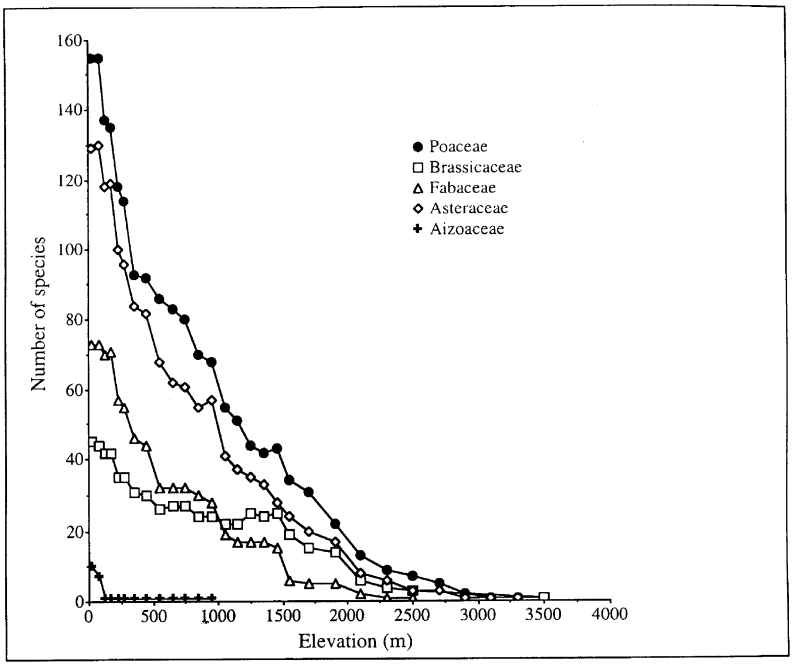

Fig. 2. Numbers of introduced plant species of five families as distributed by altitude in California (data courtesy M. Rejmanek).

spread. Approximately 5% (51/1057) of California's introduced taxa (data from Hickman, 1993) are broadly distributed across the state; another 15 percent are found in all or most of the California Floristic Province. Coastal regions of the state are particularly rich in introduced taxa; this narrow strip of land running the length of the state and supporting truly coastal plant communities harbors 73% of the exotic plant species found in California (Fig. 3) (see Hickman, 1993, for more detailed descriptions of the geographic subdivisions of the state). The coastal fog belt harbors several endemic butterfly taxa, but overall has a relatively

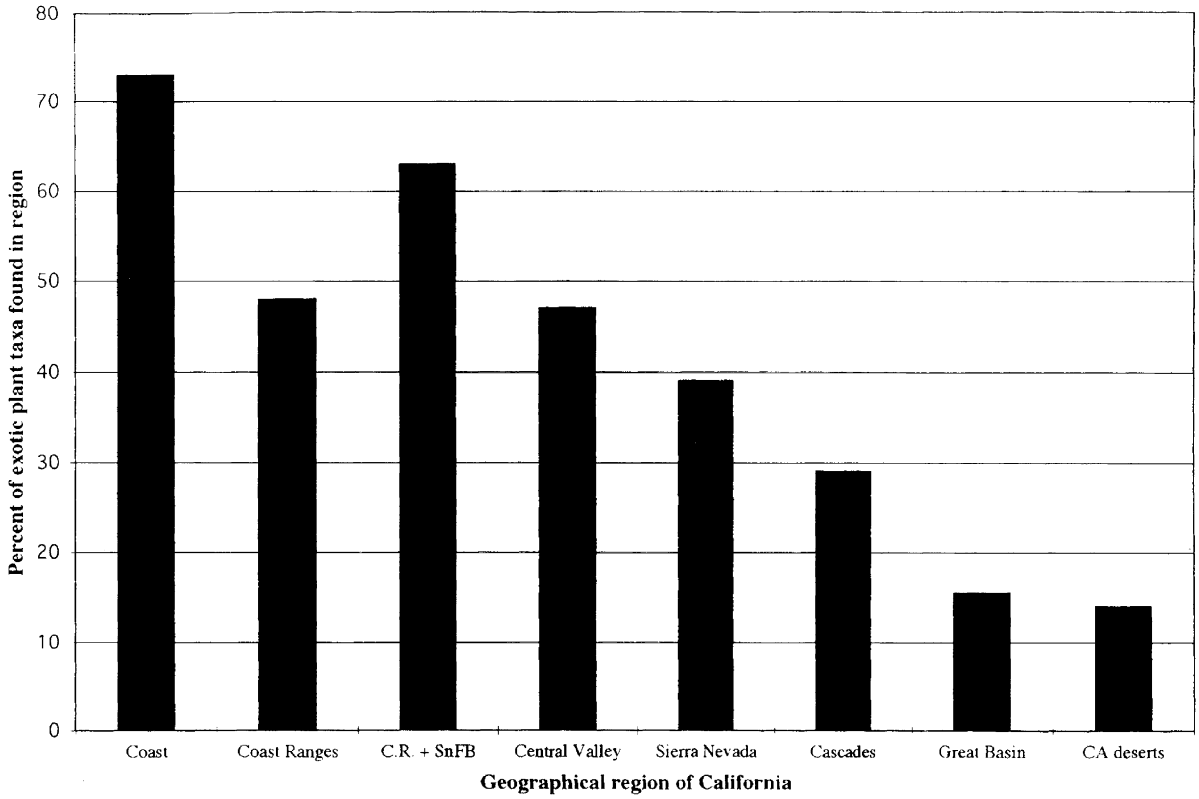

Fig. 3. Distribution of exotic plant species in California by region. The numbers for individual areas include plant species distributed more widely. Data and regional designations are from Hickman (1993). (C.R. and SnFB = Coast Ranges + San Francisco Bay area.)

undiverse fauna, as is typical of cool, cloudy areas. The Bay Area urban fauna is very heavily associated with introduced host plants, however. California's Central Valley is home to almost half (47%) of the state's introduced plant taxa. Although it has relatively few butterfly species, most of them are associated with introduced hosts (Shapiro, 1974a,b, 1984). This is particularly true in "valley grassland" (Heady, 1995) where native hosts are largely extirpated. Both the Sierra Nevada and the Cascade ranges harbor approximately 39 percent of the state's exotic plant taxa though the numbers drop off as one increases in altitude. Desert regions (14%) and the Great Basin Province (15%) have fewer exotic plant taxa (Fig. 3).

5. Butterfly–exotic plant interactions

California's butterflies interact with introduced plants in a variety of ways. For example, yellow star thistle, *Centaurea solstitialis*, is considered one of the state's worst weeds, but now serves as a major nectar source for many Central Valley and foothill butterflies. Migrating monarch butterflies, *Danaus plexippus*, now predominantly utilize introduced *Eucalyptus* trees as communal winter roosting sites along the California coast (Lane, 1993). This is due to a scarcity of large native trees (decimated by logging and development) near the coast and possibly because Eucalyptus trees provide both shelter and a source of nectar for the butterflies (Westman, 1990). However, the major direct impact of introduced plant species on California's butterflies occurs when butterfly taxa recognize these exotic plants as potential larval hosts.

We have compiled records of 82 species of California butterflies feeding on exotic plant species in the state. Of these, 59 species (61%) have records that are well documented in the state (a ranking of high in Table 1) and 70 (85%) have records for which we have either moderate or high confidence. The remaining 12 species have records in which we have low confidence and may, upon further examination, be invalid. The number of exotic plant species reported to be used by different butterflies varies greatly from a single species for 26 of the butterflies to a high of 42 species for the painted lady, *Vanessa cardui* (Fig. 4).

At least nine California butterfly species, and probably more, have increased their geographic range by colonizing exotic host plants. Three of these evidently entered the state only after the introduction of exotic host plants. *Agraulis vanillae*, the Gulf Fritillary, is the state's only representative of the tropical butterfly family Heliconiidae. In California, it feeds solely on introduced passionflower species (*Passiflora*) planted as

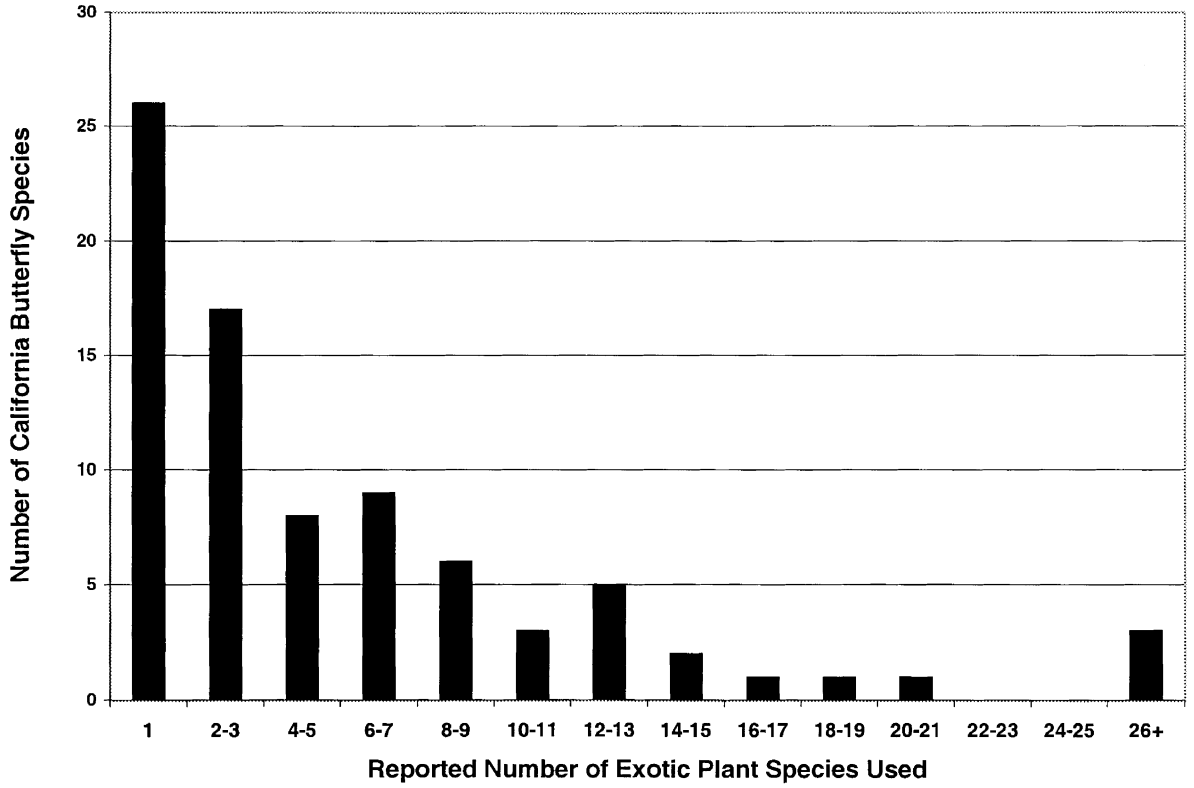

Fig. 4. Numbers of exotic hosts reported to be utilized by those California butterfly species reported to utilize exotics.

oramentals in urban and suburban areas (Copp and Davenport, 1978). *Papilio cresphontes*, the Giant Swallowtail, is found across most of the eastern United States and ranges south to Colombia (Scott, 1986). It was first recorded in California in 1963 (Emmel and Emmel, 1973) where it feeds exclusively on planted *Citrus* species, occasionally causing economic damage. *Calpodes ethlius*, the Brazilian Skipper, invades California from Mexico and breeds on ornamental *Canna* species (Orsak, 1978). Although *C. ethlius* has been collected on a number of occasions in southern California, it does not seem to have established a permanent breeding population in the state.

In at least two and possibly many cases, the use of exotic hosts has enabled butterfly species in California to extend their breeding seasons, resulting in more generations each year, in addition to extending their geographic ranges. *Papilio zelicaon,* the anise swallowtail, typically has one to two generations in the mountains and foothills of California where it feeds on native apiaceous hosts. However, along the coast, in the San Francisco Bay Area and the urbanized south coastal plains and in the Central Valley, *P. zelicaon* feeds on introduced sweet fennel, *Foeniculum vulgare*, and produces four to six or more generations each year. It is not known if or to what extent *P. zelicaon* was present in the Central Valley prior to the introduction of these plants. It also breeds on cultivated *Citrus* in both southern California and a small area at the north end of the Central Valley (Shapiro, 1995). Although there are currently no native summer hosts in the valley, it is possible that *P. zelicaon* used native species associated with previously widespread tule marsh communities (Shapiro, 1995). In any case, the use of exotics has greatly extended the range of *P. zelicaon* in lowland California.

In a similar case, *Pieris napi* is generally univoltine in the Sierra Nevada foothills but becomes bivoltine in these habitats by breeding on *Rorippa nasturtium-aquaticum*, a perennial aquatic plant introduced from Europe (Shapiro, 1975a). The aquatic habit of *R. nasturtium-aquaticum* results in it remaining green and succulent long after most other vegetation has dried out. Using *R. nasturtium-aquaticum* has allowed both *P. napi* and the introduced *P. rapae* to extend their ranges into areas of the foothills that previously had no brassicaceous hosts in summer (Shapiro, 1975a). The recently established, very aggressive weed *Lepidium latifolium* has facilitated a massive invasion of *P. rapae* into riparian zones in the western Great Basin, where it was formerly rare or absent (Shapiro, personal observation).

Shapiro (2002) hypothesizes that many of the weedy multivoltine butterflies now associated with exotic hosts in disturbed habitats in California originated in the (now much reduced) marshlands, where they had native hosts that remained usable for breeding in the otherwise hot, dry summer. If this is correct, introduced hosts

related to their ancestral native ones may have been the critical factor allowing these taxa to maintain populations in the lowlands after the marshlands were decimated by development. Shapiro (2002) also provides data demonstrating that in Davis, Yolo County, in California's Central Valley, 29/32 butterfly species breed on introduced plants and 13 have no known native hosts in Davis at all. Introduced taxa have thus become a critical component of the habitat within the city; this is probably representative of the California urban and suburban fauna overall.

Cultivated alfalfa, *Medicago sativa*, has proven to be an attractive exotic host for a number of California butterflies and its abundance has permitted increased population size in addition to range expansion for some, if not all, of them. California alfalfa fields can usually be spotted at a distance in summer by the yellow swarms of *Colias eurytheme*. Essig (1915) reported that in 1913, less than 50 years after the introduction of alfalfa, thousands of *C. eurytheme* were present over every acre of alfalfa in cultivation from Imperial County near the Mexican border to Modoc County in far northeastern California. Use of alfalfa in California has also been reported for *Colias alexandra* (questionably), *Colias philodice, Erynnis funeralis, Hemiargus ceraunus gyas, Leptotes marina, Lycaeides melissa, Strymon melinus, Thorbyes pylades,* and *Vanessa cardui* (Table 1). Alfalfa commonly escapes to roadsides and waste ground, and some of these butterflies may "follow" it there, sometimes far from cultivation. The alfalfa-feeding *L. melissa* constitutes a recently evolved ecotype or ecological race (C. Nice et al., 2002). It can now be found breeding on "feral" alfalfa along roadsides throughout northeastern California.

An apparently new ecotype of *Glaucopsyche lygdamus* feeding on naturalized annual vetches has spread rapidly along highway embankments in both the Central Valley and adjacent foothills since 1970 and is now penetrating foothill habitats where native perennial hosts are still used. A parallel phenomenon in the same species in New York state since the 1960s potentially threatens the genetic integrity of a rare, endemic subspecies (Dirig and Cryan, 1991).

The invasion of an area by an introduced plant species can have negative consequences for butterfly taxa that recognize the plant as a potential host. *Papilio zelicaon* is currently laying eggs on *Ammi visnaga*, an introduced apiaceous plant, in California's Sacramento Valley. Larvae of *P. zelicaon* from these populations are unable to survive on *A. visnaga* and usually die before reaching the third instar (Graves, 1997). Eggs laid on this plant in the field are thus wasted, and continued oviposition on this plant has the potential to reduce population numbers, though there is no evidence this is currently occurring. A similar phenomenon was noted for *Pieris napi macdunnoughii* and *P. occidentalis* on the exotic *Thlaspi arvense* in Colorado (Chew, 1977). Although *P. napi* occurs in different habitats than the plant in California, both *P. occidentalis* and *P. protodice* lay on *T. arvense* here despite the fact that it is lethal to larvae (AMS, personal observation). Overall, *T. arvense* is less common in California than in Colorado.

California butterfly species are differentially exposed to introduced potential host plants. The state's 14 alpine butterfly species have very little, if any, exposure to introduced plant taxa due to their restriction to high altitudes. None of these species is recorded as feeding on introduced taxa in California; records in Scott (1986) for *Lycaena phlaeas* on the introduced taxa *Rumex acetosella* and *Rumex crispus* are almost certainly for the eastern subspecies, which may itself be introduced from Europe. Desert taxa are also exposed to fewer exotic taxa than most. Of the 27 butterfly species that are largely confined to the desert regions of the state, only three (11%) are recorded to feed on introduced taxa. These interactions have been facilitated by irrigated agriculture in desert areas and the towns that accompany agriculture. All three of these taxa feed on plants associated with cultivation and/or urban areas: *Phoebis agarithe* on ornamental Senna (*Cassia*) species, *Hemiargus ceraunus gyas* on cultivated alfalfa, and *Copaeodes aurantiaca* on bermuda grass (*Cynodon dactylon*), commonly grown in lawns.

Other butterfly taxa are exposed to few, if any, good potential introduced hosts due to their specialization on particular plant lineages with no exotic members in California. Absence of phylogenetically-related plants, while not necessarily a barrier to colonization of exotics—especially if a secondary-chemical "bridge" unites them (Ehrlich and Raven, 1964)—does make such colonization less likely. There are 25 species in the California butterfly fauna (10.6%) that are specialists on plant families that, according to the Jepson Manual, have no naturalized exotics present in the state (Table 2). Of these, only two, *Nymphalis californica*, the California tortoise-shell, and *Erynnis tristis*, the mournful dusky-wing, are recorded on introduced hosts. In the case of *N. californica*, the record, on cultivated alfalfa, is from a single source and is considered somewhat unlikely. The other species, *E. tristis*, feeds on the ornamental cork oak, *Quercus suber*, a member of the same plant family as its native hosts, on the University of California Davis campus where it is widely planted (Shapiro, 1974b) and thus falls outside our criteria for this group. This case, like that of *Agraulis vanillae* on ornamental passionflowers, does illustrate, however, that localized ornamental plantings of exotics cannot be ignored in terms of potential impacts on native insects even if these plants fail to become naturalized. While there are no recorded exotic host plants for the pine-feeders *Incisalia eryphon* or *Neophasia menapia* in California, *I. eryphon* has colonized planted Monterey pine, a native plant on

Table 1
Records of California butterflies on non-native host plants (some of these records may not be from California—see Section 2 in text)

Butterfly species	Plant species	Confidence level	Source
Agraulis vanillae	*Passiflora alato-caerulea*	High	Copp and Davenport, 1978
Agraulis vanillae	*Passiflora incarnata*	High	AMS, personal observation
Agraulis vanillae	*Passiflora caerulea*	High	Copp and Davenport, 1978
Agraulis vanillae	*Passiflora manicata*	High	Copp and Davenport, 1978
Agraulis vanillae	*Passiflora* spp.	High	Emmel and Emmel, 1973; Garth and Tilden, 1986
Amblyscirtes vialis	*Poa pratensis*	Low	Tietz, 1972
Anthocharis lanceolata	*Sisymbrium officinale*	Moderate	Tietz, 1972; Scott, 1986
Anthocharis sara	*Barbarea verna*	High	Shapiro, 1980; Scott, 1986
Anthocharis sara	*Barbarea vulgaris*	High	Opler, 1967; Emmel and Emmel, 1973; Scott, 1986
Anthocharis sara	*Brassica napus*	High	Shapiro, 1974b; Scott, 1986
Anthocharis sara	*Brassica nigra*	High	Garth and Tilden, 1986; Scott, 1986; Brown et al., 1992
Anthocharis sara	*Brassica rapa*	Moderate	Tietz, 1972; Garth and Tilden, 1986; Scott, 1986
Anthocharis sara	*Capsella bursa-pastoris*	Unlikely	Scott, 1986
Anthocharis sara	*Hirschfeldia incana*	High	Shapiro, 1974b; Scott, 1986
Anthocharis sara	*Tropaeolum* spp.	Low	Scott, 1986
Anthocharis sara	*Raphanus sativus*	High	Shapiro, 1974b; Scott, 1986
Anthocharis sara	*Sinapis alba*	Moderate	Tietz, 1972; Scott, 1986
Anthocharis sara	*Sinapis arvensis*	High	Opler, 1967; Emmel and Emmel, 1973; Garth and Tilden, 1986; Scott, 1986
Anthocharis sara	*Sisymbrium officinale*	High	Opler, 1967; Tietz, 1972; Emmel and Emmel, 1973; Garth and Tilden, 1986; Scott, 1986
Atalopedes campestris	*Cynodon dactylon*	High	Tietz, 1972; Shapiro, 1974b; Garth and Tilden, 1986; Scott 1986
Atalopedes campestris	*Digitaria sanguinalis*	Moderate	Tietz, 1972; Scott, 1986
Atalopedes campestris	*Eleusine indica*	Moderate	Scott, 1986
Atalopedes campestris	*Paspalum dilatatum*	High	AMS, personal observation
Atalopedes campestris	*Poa pratensis*	Moderate	Garth and Tilden, 1986
Atalopedes campestris	*Stenotaphrum secundatum*	Moderate	Garth and Tilden, 1986; Scott, 1986
Brephidium exilis	*Atriplex rosea*	High	Shapiro, 1973, 1974a, 1974a, 1974b; Scott, 1986
Brephidium exilis	*Atriplex semibaccata*	High	Tietz, 1972; Emmel and Emmel, 1973; Shapiro, 1973, 1974a, 1974b; Garth and Tilden, 1986; Scott, 1986
Brephidium exilis	*Chenopodium album*	Low	Tietz, 1972; Garth and Tilden, 1986; Scott, 1986
Brephidium exilis	*Salsola iberica/complex tragus*	High	Shapiro, 1974b; Orsak, 1978; Scott, 1986; Haeger, 1988
Brephidium exilis	*Tetragonia tetragoniodes*	High	AMS, personal observation
Calpodes ethlius	*Canna* spp.	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Orsak, 1978; Scott, 1986; Brown et al., 1992
Celastrina arigolus echo	*Ilex* spp.	Low	Scott, 1986
Celastrina arigolus echo	*Leucanthemum vulgare*	Low	Scott, 1986
Celastrina arigolus echo	*Malus pumila*	Low	Scott, 1986
Celastrina arigolus echo	*Melilotus officinalis*	Low	Scott, 1986
Celastrina arigolus echo	*Prunus serotina*	Low	Scott, 1986
Cercyonis pegala	*Avena fatua*	Low	Scott, 1986
Chlosyne lacinia	*Helianthus ciliaris*	Low	Tietz, 1972, Scott, 1986
Chlosyne lacinia	*Verbesina enceloides*	Low	Scott, 1986
Coenonympha tullia	*Poa pratensis*	Low	Tietz, 1972; Scott, 1986
Colias alexandra	*Medicago sativa*	Low	Garth and Tilden, 1986; Scott, 1986
Colias alexandra	*Trifolium pratense*	Moderate	Scott, 1986
Colias alexandra	*Trifolium repens*	Moderate	Tietz, 1972; Garth and Tilden, 1986
Colias eurytheme	*Lotus corniculatus*	High	AMS, personal observation
Colias eurytheme	*Medicago lupulina*	Moderate	Scott, 1986
Colias eurytheme	*Medicago polymorpha*	Moderate	Tietz, 1972
Colias eurytheme	*Medicago sativa*	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Shapiro, 1974b, Scott, 1986; Garth and Tilden, 1986; Brown et al., 1992
Colias eurytheme	*Melilotus alba*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Colias eurytheme	*Melilotus officinalis*	High	Scott, 1986; AMS, personal observation
Colias eurytheme	*Phaseolus vulgare*	Low	Scott, 1986
Colias eurytheme	*Pisum sativum*	Low	Tietz, 1972; Scott, 1986
Colias eurytheme	*Trifolium pratense*	High	Scott, 1986; AMS, personal observation
Colias eurytheme	*Trifolium repens*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Colias eurytheme	*Vicia benghalensis*	High	AMS, personal observation

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Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Colias eurytheme	*Vicia cracca*	High	Shapiro, 1974b; Scott, 1986
Colias eurytheme	*Vicia sativa*	High	Tietz, 1972; Shapiro, 1974a, 1974b; Scott, 1986
Colias eurytheme	*Vicia villosa*	High	Shapiro, 1974b
Colias harfordii	*Trifolium repens*	Low	Tietz, 1972
Colias occidentalis	*Melilotus alba*	Low	Scott, 1986
Colias philodice	*Cytisus* spp.	Unlikely	Scott, 1986
Colias philodice	*Medicago hispida*	Low	Scott, 1986
Colias philodice	*Medicago sativa*	High	Tietz, 1972; Emmel and Emmel, 1973; Scott, 1986; Garth and Tilden, 1986
Colias philodice	*Melilotus alba*	Moderate	Scott, 1986
Colias philodice	*Trifolium hybridum*	Moderate	Scott, 1986
Colias philodice	*Trifolium pratense*	Moderate	Scott, 1986
Colias philodice	*Trifolium repens*	Moderate	Scott, 1986
Colias philodice	*Vicia cracca*	Moderate	Tietz, 1972, Scott, 1986
Copaeodes aurantiaca	*Cynodon dactylon*	Moderate	Tietz, 1972; Garth and Tilden, 1986; Scott, 1986
Danaus gilippus strigosus	*Asclepias curassavica*	High	Sakai, 1992; Scott, 1986
Danaus gilippus strigosus	*Nerium oleander*	High	Sakai, 1992
Danaus plexippus	*Asclepias curassavica*	High	Scott, 1986; SDG, personal observation
Epargyreus clarus	*Acacia* spp.	Low	Scott, 1986
Epargyreus clarus	*Phaseolus vulgaris*	Low	Scott, 1986
Epargyreus clarus	*Robinia pseudoacacia*	High	Tietz, 1972; Shapiro, 1974b; Scott, 1986
Epargyreus clarus	*Wisteria*	High	Comstock, 1927; Emmel and Emmel, 1973
Erynnis funeralis	*Medicago hispida*	Moderate	Tietz, 1972; Scott, 1986
Erynnis funeralis	*Medicago sativa*	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Orsak, 1978; Garth and Tilden, 1986; Scott, 1986
Erynnis funeralis	*Medicago* spp.	Moderate	Comstock, 1927
Erynnis tristis	*Quercus suber*	High	Shapiro, 1974b; Garth and Tilden, 1986
Euchloe ausonides	*Brassica napus*	High	Shapiro, 1974b; Scott, 1986
Euchloe ausonides	*Brassica nigra*	High	Shapiro, 1974a, b; Garth and Tilden, 1986; Scott, 1986
Euchloe ausonides	*Brassica rapa*	Moderate	Garth and Tilden, 1986; Scott, 1986
Euchloe ausonides	*Hirschfeldia incana*	Moderate	Scott, 1986
Euchloe ausonides	*Isatis tinctoria*	Moderate	Scott, 1986
Euchloe ausonides	*Raphanus sativus*	High	Shapiro, 1974a, b; Scott, 1986
Euchloe ausonides	*Sinapis arvensis*	Moderate	Scott, 1986
Euchloe ausonides	*Sisymbrium altissimum*	Moderate	Scott, 1986
Euchloe ausonides	*Sisymbrium officinale*	Moderate	Scott, 1986
Euchloe ausonides	*Sisymbrium* spp.	Moderate	Garth and Tilden, 1986
Euchloe hyantis	*Isatis tinctoria*	Moderate	Scott, 1986
Euchloe hyantis	*Sisymbrium altissimum*	Moderate	Scott, 1986
Euphydryas chalcedona	*Buddleja davidii*	Low	Scott, 1986
Euphydryas chalcedona	*Cymbalaria muralis*	Moderate	Scott, 1986
Euphydryas chalcedona	*Leucanthemum maximum*	Unlikely	Tietz, 1972
Euphydryas chalcedona	*Lonicera* spp.	High	Emmel and Emmel, 1973; Scott, 1986
Euphydryas chalcedona	*Plantago lanceolata*	High	Emmel and Emmel, 1973; Scott, 1986
Euphydryas chalcedona	*Plantago major*	Moderate	Scott, 1986
Euphydryas chalcedona	*Verbascum thapsus*	Moderate	Scott, 1986
Euphydryas chalcedona	*Veronica anagallis- aquatica*	Low	Scott, 1986
Euphydryas editha	*Plantago lanceolata*	High	White and Singer, 1974; Scott 1986
Euphydryas editha	*Plantago pusilla*	Low	Scott, 1986
Euphydryas editha	*Valerianella* spp.	Moderate	Scott, 1986
Eurema nicippe	Ornamental *Cassia* spp. (''Senna'')	High	Comstock, 1927; Emmel and Emmel, 1973; Scott, 1986; Garth and Tilden, 1986
Everes comyntas	*Lotus corniculatus*	High	AMS, personal observation
Everes comyntas	*Medicago lupulina*	Moderate	Scott, 1986
Everes comyntas	*Melilotus alba*	High	AMS, personal observation
Everes comyntas	*Melilotus indica*	Moderate	Scott, 1986
Everes comyntas	*Melilotus officinalis*	Moderate	Scott, 1986
Everes comyntas	*Trifolium hybridum*	Moderate	Scott, 1986
Everes comyntas	*Trifolium pratense*	Moderate	Scott, 1986
Everes comyntas	*Trifolium repens*	Moderate	Scott, 1986
Everes comyntas	*Vicia benghalensis*	High	AMS, personal observation
Everes comyntas	*Vicia cracca*	High	Shapiro, 1974b; Scott, 1986

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Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Everes comyntas	*Vicia sativa*	High	Shapiro, 1974a, b; Scott, 1986
Everes comyntas	*Vicia villosa*	High	Shapiro, 1974b; Scott, 1986
Glaucopsyche lygdamus	*Medicago sativa*	Low	Scott, 1986
Glaucopsyche lygdamus	*Melilotus alba*	Low	Scott, 1986
Glaucopsyche lygdamus	*Vicia benghalensis*	High	AMS, personal observation
Glaucopsyche lygdamus	*Vicia cracca*	Moderate	Tietz, 1972; Scott, 1986
Glaucopsyche lygdamus	*Vicia sativa*	High	Shapiro, 1974b; Scott, 1986
Glaucopsyche lygdamus	*Vicia villosa*	High	Shapiro, 1974b; Scott, 1986
Heliopetes ericetorum	*Alcea rosea*	Moderate	Tietz, 1972; Garth and Tilden, 1986; Scott, 1986
Heliopetes ericetorum	*Malva nicaeenis*	Moderate	Scott, 1986
Heliopetes ericetorum	*Malva* spp.	Moderate	Garth and Tilden, 1986; Brown et al., 1992
Hemiargus ceraunus gyas	*Medicago sativa*	High	Tietz, 1972; Emmel and Emmel, 1973; Garth and Tilden, 1986; Scott, 1986
Hemiargus isola	*Medicago sativa*	High	Shapiro, 1974b; Scott, 1986
Hemiargus isola	*Melilotus alba*	High	Shapiro, 1974b; Scott, 1986
Hemiargus isola	*Melilotus indica*	Moderate	Scott, 1986
Hemiargus isola	*Melilotus officinalis*	Moderate	Scott, 1986
Hemiargus isola	*Trifolium fragiferum*	Low	Scott, 1986
Hemiargus isola	*Trifolium repens*	Moderate	Scott, 1986
Hesperia comma	*Lolium* spp.	Moderate	MacNeill, 1964; Garth and Tilden, 1986; Scott, 1986
Hesperia comma	*Phleum pratense*	Moderate	Tietz, 1972
Hesperia comma	*Poa pratensis*	Low	Tietz, 1972
Hesperia juba	*Poa pratensis*	Low	Scott, 1986
Hesperia lindseyi	*Phalaris aquatica*	High	AMS, personal observation
Hylephila phyleus	*Cynodon dactylon*	High	Comstock, 1927; Emmel and Emmel, 1973; Shapiro, 1974b; Garth and Tilden, 1986; Scott, 1986
Hylephila phyleus	*Paspalum dilatatum*	High	AMS, personal observation
Hylephila phyleus	*Pennisetum clendestinum*	High	AMS, personal observation
Hylephila phyleus	*Poa pratensis*	Moderate	Tietz, 1972; Scott, 1986
Hylephila phyleus	*Stenotaphrum secundatum*	Moderate	Scott, 1986
Hylephila phyleus	*Digitaria sanguinalis*	Moderate	Tietz, 1972
Junonia coenia	*Antirrhinum majus*	High	Emmel and Emmel, 1973; Shapiro, 1978; Garth and Tilden, 1986; Scott, 1986
Junonia coenia	*Cymbalaria muralis*	Moderate	Scott, 1986
Junonia coenia	*Digitalis* spp.	Moderate	Scott, 1986
Junonia coenia	*Kickxia elatine*	High	AMS, personal observation
Junonia coenia	*Kickxia spuria*	High	Shapiro, 1978; Scott, 1986; Camara 1997
Junonia coenia	*Linaria marocanna*	Moderate	Scott, 1986
Junonia coenia	*Linaria vulgaris*	Moderate	Scott, 1986
Junonia coenia	*Plantago coronopus*	High	Shapiro, 1974a; Scott, 1986
Junonia coenia	*Plantago lanceolata*	High	Tietz, 1972; Emmel and Emmel, 1973; Shapiro, 1974a, b; Garth and Tilden, 1986, Scott, 1986; SDG, personal observation
Junonia coenia	*Plantago major*	High	Garth and Tilden, 1986; Scott, 1986
Junonia coenia	*Plantago virginica*	Moderate	Scott, 1986
Junonia coenia	*Veronica anagallis- aquatica*	Moderate	Scott, 1986
Junonia coenia	*Veronica catenata*	Moderate	Scott, 1986
Leptotes marina	*Lathyrus odoratus*	High	Emmel and Emmel, 1973; Scott 1986
Leptotes marina	*Medicago sativa*	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Orsak, 1978; Garth and Tilden, 1986; Scott, 1986
Leptotes marina	*Melilotus alba*	High	Shapiro, 1974b
Leptotes marina	*Plumbago capensis*	High	AMS, personal observation
Leptotes marina	*Plumbago* spp. (*Leadwort*)	High	Comstock, 1927; Emmel and Emmel, 1973; Orsak, 1978
Leptotes marina	*Wisteria*	Moderate	Comstock, 1927
Lerodea eufala	*Cynodon dactylon*	High	Shapiro, 1974a, b; Garth and Tilden, 1986; Scott, 1986
Lerodea eufala	*Echinochloa crus-galli*	High	Shapiro, 1974a, b; Scott, 1986
Lerodea eufala	*Oryza sativa*	High	Shapiro, 1974b; Scott, 1986
Lerodea eufala	*Paspalum ciliatifolium*	High	AMS, personal observation
Lerodea eufala	*Setaria verticillata*	High	Shapiro, 1974b; Scott, 1986
Lerodea eufala	*Sorghum bicolor*	High	Shapiro, 1974b; Scott, 1986
Lerodea eufala	*Sorghum halepense*	High	Shapiro, 1974a, b; Scott, 1986
Lerodea eufala	*Poa pratensis*	Moderate	Tietz, 1972

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Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Limenitis lorquini	*Cotoneaster* spp.	Low	Scott, 1986
Limenitis lorquini	*Malus pumila*	Low	Tietz, 1972; Scott, 1986
Limenitis lorquini	*Malus sylvestris-apple*	Low	Garth and Tilden, 1986
Limenitis lorquini	*Prunus cerasifera-plum*	Low	Garth and Tilden, 1986
Limenitis lorquini	*Prunus cerasus-cherry*	Low	Garth and Tilden, 1986
Limenitis lorquini	*Prunus domestica*	Low	Tietz, 1972; Scott, 1986
Lycaeides melissa	*Medicago sativa*	High	Scott, 1986
Lycaena cupreus	*Rumex acetosella*	High	Emmel and Emmel, 1974; Scott, 1986; AMS, personal observation
Lycaena cupreus	*Rumex* spp.	High	Comstock, 1927
Lycaena editha	*Rumex acetosella*	High	Emmel and Emmel, 1974 (ovip.); Scott, 1986; AMS, personal observation
Lycaena helloides	*Polygonum arenastrum*	High	Comstock, 1927; Tietz, 1972; Shapiro, 1974a, b; Scott, 1986
Lycaena helloides	*Polygonum persicaria*	High	Shapiro, 1974b; Scott, 1986
Lycaena helloides	*Rumex acetosella*	Moderate	Scott, 1986
Lycaena helloides	*Rumex conglomeratus*	Moderate	Scott, 1986
Lycaena helloides	*Rumex crispus*	High	Shapiro, 1974a, b; Scott, 1986
Lycaena rubidus	*Rumex crispus*	Moderate	Scott, 1986
Lycaena xanthoides	*Rumex conglomeratus*	High	Shapiro, 1974b; Scott, 1986
Lycaena xanthoides	*Rumex crispus*	High	Shapiro 1974a, b; Garth and Tilden, 1986; Scott, 1979(80), 1986
Lycaena xanthoides	*Rumex pulcher*	High	Emmel and Emmel, 1973, Garth and Tilden, 1986; Scott, 1986
Nathalis iole	*Bidens pilosa*	High	Emmel and Emmel, 1973; Orsak, 1978; Garth and Tilden, 1986; Scott, 1986
Nathalis iole	*Cosmos*	Moderate	Scott, 1986
Nathalis iole	*Erodium circutarum*	Ovip. only	Scott, 1986
Nathalis iole	*Mollugo verticillata*	Ovip. only	Scott, 1986
Nathalis iole	*Stellaria media*	Ovip. only	Scott, 1986
Nathalis iole	*Tagetes erecta*	High	Garth and Tilden, 1986
Nathalis iole	*Tagetes* spp.	High	Emmel and Emmel, 1973; Scott, 1986
Nymphalis antiopa	*Celtis australis*	High	AMS, personal observation
Nymphalis antiopa	*Celtis occidentalis*	High	AMS, personal observation
Nymphalis antiopa	*Celtis sinensis*	High	AMS, personal observation
Nymphalis antiopa	*Populus alba*	Moderate	Scott, 1986
Nymphalis antiopa	*Rumex acetosella*	Low	Scott, 1986
Nymphalis antiopa	*Salix babylonica*	High	Shapiro 1974b; Scott, 1986
Nymphalis antiopa	*Ulmus americana*	High	AMS, personal observation
Nymphalis antiopa	*Ulmus parviflora*	High	Emmel and Emmel, 1973; Orsak, 1978
Nymphalis antiopa	*Ulmus pumila*	Moderate	Scott, 1986
Nymphalis californica	*Medicago sativa*	Low	Tietz, 1972
Nymphalis milberti	*Urtica urens*	High	Shapiro, 1975b
Ochlodes sylvanoides	*Cynodon dactylon*	Moderate	Scott, 1986
Panoquina panoquinoides errans	*Cynodon dactylon*	Moderate	Tietz, 1972
Papilio cresphontes	*Citrus grandis*	Moderate	Tietz, 1972; Scott, 1986
Papilio cresphontes	*Citrus limon*	High	Tietz, 1972; Emmel and Emmel, 1973; Scott, 1986
Papilio cresphontes	*Citrus sinensis*	High	Tietz, 1972; Emmel and Emmel, 1973; Scott, 1986
Papilio cresphontes	*Citrus* spp.	High	Garth and Tilden, 1986
Papilio eurymedon	*Malus pumila*	Moderate	Scott, 1986
Papilio eurymedon	*Melilotus alba*	Ovip. only	AMS, personal observation
Papilio eurymedon	*Prunus domestica*	Moderate	Scott, 1986
Papilio eurymedon	*Prunus persica*	High	Emmel and Emmel, 1973; Scott, 1986
Papilio multicaudatus	*Fraxinus* spp.	High	AMS, personal observation
Papilio multicaudatus	*Platanus* spp.	High	AMS, personal observation
Papilio multicaudatus	*Prunus cerasus*	Moderate	Tietz, 1972; Scott, 1986
Papilio rutulus	*Ligustrum japonicum*	High	AMS, personal observation
Papilio rutulus	*Ligustrum lucidum*	High	AMS, personal observation
Papilio rutulus	*Malus malus-apple*	Moderate	Garth and Tilden, 1986
Papilio rutulus	*Malus pumila*	Moderate	Tietz, 1972; Scott, 1986
Papilio rutulus	*Persea americana*	Unlikely	Tietz, 1972
Papilio rutulus	*Prunus amysdalus*	High	AMS, personal observation
Papilio rutulus	*Prunus caroliniana*	High	Shapiro, 1974b; Scott, 1986

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Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Papilio rutulus	*Prunus cerasus*	Moderate	Tietz, 1972; Scott, 1986
Papilio rutulus	*Prunus domestica var. galatensis*	Moderate	Tietz, 1972; Scott, 1986
Papilio rutulus	*Prunus persica*	Moderate	Scott, 1986
Papilio rutulus	*Salix babylonica*	Moderate	Scott, 1986
Papilio rutulus	*Syringa vulgaris*	High	Shapiro, 1974b
Papilio rutulus	*Ulmus* spp.	High	Garth and Tilden, 1986; Scott, 1986
Papilio rutulus	*Platanus occidentalis*	High	AMS, personal observation
Papilio rutulus	*Platanus orientalis*	High	AMS, personal observation
Papilio rutulus	*Fraxinus velutina*	High	AMS, personal observation
Papilio zelicaon	*Ammi majus*	Ovip. Only	AMS, personal observation
Papilio zelicaon	*Ammi visnaga*	Ovip. Only Lethal	SDG, personal observation; AMS, personal observation
Papilio zelicaon	*Anethum graveolens*	High	Tietz, 1972; AMS, personal observation
Papilio zelicaon	*Apium graveolens*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Papilio zelicaon	*Apium petroselinum*	Moderate	Tietz, 1972
Papilio zelicaon	*Carum carvi*	High	Scott, 1986; AMS, personal observation
Papilio zelicaon	*Carum* spp.	High	Comstock, 1927
Papilio zelicaon	*Citrus limon*	High	Comstock, 1927; Tietz, 1972; Scott, 1986
Papilio zelicaon	*Citrus limon*	High	Emmel and Shields, 1978
Papilio zelicaon	*Citrus sinensis*	High	Comstock, 1927; Tietz, 1972; Shapiro and Masuda, 1980; Scott, 1986; SDG, personal observation
Papilio zelicaon	*Citrus sinensis*	High	Shapiro and Masuda, 1980
Papilio zelicaon	*Citrus* spp.	High	Emmel and Emmel, 1973
Papilio zelicaon	*Conium maculatum*	High	Goeden and Ricker, 1982; Scott, 1986; SDG, personal observation
Papilio zelicaon	*Daucus carota*	High	Comstock, 1927; Tietz, 1972; Garth and Tilden, 1986; Scott, 1986
Papilio zelicaon	*Foeniculum vulgare*	High	Comstock, 1927; Emmel and Emmel, 1973; Shapiro, 1974a; Garth and Tilden, 1986; Scott, 1986; SDG, personal observation
Papilio zelicaon	*Pastinaca sativa*	High	Comstock, 1927; Tietz, 1972; Scott, 1986
Papilio zelicaon	*Petroselinum crispum*	High	Scott, 1986; AMS, personal observation
Papilio zelicaon	*Ruta graveolens*	High	Scott, 1986; AMS, personal observation
Paratrytone melane	*Bromus inermis*	Low	Tietz, 1972
Paratrytone melane	*Cynodon dactylon*	High	Tietz, 1972; Scott, 1986; Brown et al., 1992; Barbehenn, 1994
Paratrytone melane	*Digitaria ischaemum*	Moderate	Tietz, 1972
Paratrytone melane	*Digitaria sanguinalis*	Moderate	Tietz, 1972
Paratrytone melane	*Ehrharta erecta*	High	Barbehenn, 1994
Paratrytone melane	*Lamarkia aurea*	High	Garth and Tilden, 1986; Scott, 1986; Brown et al., 1992; Barbehenn, 1994
Paratrytone melane	*Lolium multiflorum*	High	Barbehenn, 1994
Paratrytone melane	*Paspalum dilatatum*	High	Barbehenn, 1994
Paratrytone melane	*Pennisetum clandestinum*	High	Barbehenn, 1994
Paratrytone melane	*Phyllostachys bambusoides*	High	Barbehenn, 1994
Paratrytone melane	*Sorghum bicolor*	High	Barbehenn, 1994
Paratrytone melane	*Stenotaphrum secundatum*	High	Scott, 1986; Brown et al., 1992; Barbehenn, 1994
Phoebis agarithe	Ornamental *Cassia* spp. (''Senna'')	High	Emmel and Emmel, 1973
Phoebis sennae	Ornamental *Cassia* spp. (''Senna'')	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Orsak, 1978; Scott, 1986; Garth and Tilden, 1986; Brown et al., 1992
Pholisora catullus	*Amaranthus albus*	High	Scott, 1986. Ams, personal observation
Pholisora catullus	*Amaranthus blitoides*	High	AMS, personal observation
Pholisora catullus	*Amaranthus caudatus*	Moderate	Scott, 1986
Pholisora catullus	*Amaranthus hybridus*	High	Shapiro, 1974a, 1974b; Scott, 1986
Pholisora catullus	*Amaranthus powellii*	High	AMS, personal observation
Pholisora catullus	*Amaranthus retroflexus*	High	Shapiro, 1974b; Scott, 1986
Pholisora catullus	*Amaranthus spinosus*	Low	Scott, 1986
Pholisora catullus	*Atriplex rosea*	High	Shapiro, 1974b; Scott, 1986
Pholisora catullus	*Celosia argentea*	High	AMS, personal observation
Pholisora catullus	*Celosia cristata*	High	AMS, personal observation
Pholisora catullus	*Chenopodium album*	High	Comstock, 1927; Tietz, 1972; Shapiro, 1974b; Scott, 1986
Pholisora catullus	*Chenopodium ambrodiodes*	Moderate	Scott, 1986
Pholisora catullus	*Chenopodium foliosum*	Moderate	Scott, 1986

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Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Pholisora catullus	*Chenopodium murale*	High	Shapiro, 1974b
Phyciodes mylitta	*Carduus pycnocephalus*	High	Shapiro, 1974b; Scott, 1986
Phyciodes mylitta	*Centaurea solstitialis*	High	Shapiro, 1974b; Scott 1986
Phyciodes mylitta	*Cirsium arvense*	Moderate	Scott, 1986
Phyciodes mylitta	*Cirsium vulgare*	High	Shapiro, 1974b; Scott, 1986
Phyciodes mylitta	*Silybum marianum*	High	Shapiro, 1974a, 1974b; Garth and Tilden, 1986; Scott, 1986
Pieris napi	*Barbarea verna*	High	Shapiro, 1980; Scott, 1986
Pieris napi	*Brassica nigra*	Moderate	Tietz, 1972; Scott, 1986
Pieris napi	*Brassica oleracea*	Low	Comstock, 1927; Tietz, 1972; Scott, 1986
Pieris napi	*Brassica rapa*	Low	Comstock, 1927; Tietz, 1972; Scott, 1986
Pieris napi	*Lepidium virginicum*	Moderate	Scott, 1986
Pieris napi	*Raphanus raphanistrum*	Low	Scott, 1986
Pieris napi	*Raphanus sativus*	Low	Tietz, 1972; Scott, 1986
Pieris napi	*Rorippa nasturtium-aquaticum*	High	Shapiro, 1975a; Scott, 1986
Pieris napi	*Sinapis alba*	Low	Tietz, 1972; Scott, 1986
Pieris napi	*Alyssum sp.*	High	AMS, personal observation
Pieris napi	*Sisymbrium officinale*	High	Scott, 1986; AMS, personal observation
Pieris rapae	*Armoracia rusticana*	High	AMS, personal observation
Pieris rapae	*Brassica napus*	High	Scott, 1986; AMS, personal observation
Pieris rapae	*Brassica nigra*	High	Tietz, 1972; Shapiro, 1974a, 1974b; Scott, 1986
Pieris rapae	*Brassica oleracea acephala*	High	Emmel and Emmel, 1973
Pieris rapae	*Brassica oleracea capitata*	High	Emmel and Emmel, 1973
Pieris rapae	*Brassica oleracea*	High	Tietz, 1972; Shapiro, 1974b; Scott, 1986; Garth and Tilden, 1986
Pieris rapae	*Brassica rapa*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Pieris rapae	*Brassica* spp.	High	Emmel and Emmel, 1973
Pieris rapae	*Cakile edentula*	Moderate	Tietz, 1972; Scott, 1986
Pieris rapae	*Capsella bursa-pastoris*	Unlikely	Tietz, 1972; Scott, 1986
Pieris rapae	*Cardaria draba*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Descurainia sophia*	Moderate	Scott, 1986
Pieris rapae	*Eruca vesicaria*	Moderate	Scott, 1986
Pieris rapae	*Hirschfeldia incana*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Lactuca sativa*	Unlikely	Tietz, 1972
Pieris rapae	*Lepidium campestre*	High	Scott, 1986; AMS, personal observation
Pieris rapae	*Lepidium latifolium*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Lobularia maritima*	Moderate	Scott, 1986
Pieris rapae	*Lunaria annua*	Moderate	Scott, 1986
Pieris rapae	*Matthiola incana*	Moderate	Emmel and Emmel, 1973; Scott, 1986
Pieris rapae	*Raphanus sativus*	High	Tietz, 1972; Emmel and Emel, 1973; Shapiro, 1974a, b; Scott, 1986
Pieris rapae	*Reseda odorata*	Low	Scott, 1986
Pieris rapae	*Rorippa nasturtium- aquaticum*	High	Shapiro, 1975a; Scott, 1986
Pieris rapae	*Sinapis alba*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Pieris rapae	*Sinapis arvensis*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Sisymbrium altissimum*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Sisymbrium irio*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Sisymbrium officinale*	High	Shapiro, 1974b; Scott, 1986
Pieris rapae	*Tropaeolum majus*	High	Emmel and Emmel, 1973; Garth and Tilden, 1986
Plebeius acmon	*Melilotus alba*	High	Shapiro, 1974b; Scott, 1986
Plebeius acmon	*Polygonum arenastrum*	High	Shapiro, 1974a, b; Scott, 1986
Plebejus saepiolus	*Trifolium hybridum*	Moderate	Scott, 1986
Plebejus saepiolus	*Trifolium repens*	Moderate	Scott, 1986
Plebius icariodes	*Vicia cracca*	Low	Tietz, 1972
Polites sabuleti	*Cynodon dactylon*	High	Tietz, 1972; Shapiro, 1974b; Garth and Tilden, 1986; Scott, 1986
Polites sabuleti	*Digitaria sanguinalis*	Moderate	Tietz, 1972
Polites sabuleti	*Poa pretensis*	Low	Scott, 1986
Pontia beckeri	*Brassica nigra*	High	Emmel and Emmel, 1973; Scott, 1986
Pontia beckeri	*Brassica* spp.	High	Garth and Tilden, 1986
Pontia beckeri	*Descurainia sophia*	Moderate	Scott, 1986
Pontia beckeri	*Isatis tinctoria*	High	AMS, personal observation
Pontia beckeri	*Lepidium perfoliatum*	Moderate	Scott, 1986

(*continued on next page*)

Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Pontia beckeri	*Sisymbrium altissimum*	High	Garth and Tilden, 1986; Scott, 1986; AMS, personal observation
Pontia beckeri	*Sisymbrium loeselii*	Moderate	Scott, 1986
Pontia beckeri	*Sisymbrium officinale*	Moderate	Garth and Tilden, 1986
Pontia occidentalis	*Brassica nigra*	Moderate	Scott, 1986
Pontia occidentalis	*Cardaria draba*	High	AMS, personal observation
Pontia occidentalis	*Chorispora tenella*	Low	Scott, 1986
Pontia occidentalis	*Descurainia sophia*	Moderate	Scott, 1986
Pontia occidentalis	*Lepidium campestre*	Moderate	Scott, 1986
Pontia occidentalis	*Lepidium virginicum*	High	Shapiro, 1976; Scott, 1986
Pontia occidentalis	*Sisymbrium altissimum*	High	Scott, 1986; AMS, personal observation
Pontia occidentalis	*Thlaspi arvense*	Ovip. only Lethal	Scott, 1986; AMS, personal observation
Pontia protodice	*Alyssum* spp.	High	AMS, personal observation
Pontia protodice	*Brassica nigra*	High	Shapiro, 1974b; Scott, 1986
Pontia protodice	*Brassica oleracea*	Moderate	Comstock, 1927; Tietz, 1972; Scott, 1986
Pontia protodice	*Brassica rapa*	Moderate	Scott, 1986
Pontia protodice	*Brassica* spp.	High	Emmel and Emmel, 1973; Garth and Tilden, 1986
Pontia protodice	*Cakile edentula*	Moderate	Tietz, 1972; Scott, 1986
Pontia protodice	*Capsella bursa-pastoris*	Unlikely	Tietz, 1972; Scott, 1986
Pontia protodice	*Cardaria draba*	High	Scott, 1986; AMS, personal observation
Pontia protodice	*Decurainia sophia*	Moderate	Scott, 1986
Pontia protodice	*Hirschfeldia incana*	High	Shapiro, 1974b; Scott, 1986
Pontia protodice	*Lepidium latifolium*	High	Shapiro, 1974b; Scott, 1986
Pontia protodice	*Lepidium virginicum*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Pontia protodice	*Lobularia maritima*	Moderate	Tietz, 1972; Scott, 1986
Pontia protodice	*Malcolmia africana*	Low	Scott, 1986
Pontia protodice	*Raphanus sativus*	High	Shapiro, 1974b; Scott, 1986
Pontia protodice	*Reseda* spp.	Moderate	Scott, 1986
Pontia protodice	*Sinapis arvensis*	High	Tietz, 1972; Shapiro, 1974b; Scott, 1986
Pontia protodice	*Sisymbrium altissimum*	High	Scott, 1986; AMS, personal observation
Pontia protodice	*Sisymbrium officinale*	High	Garth and Tilden, 1986; AMS, personal observation
Pontia protodice	*Sisymbrium* spp.	High	Tietz, 1972; Emmel and Emmel, 1973
Pontia protodice	*Thlaspi arvense*	Ovip. only Lethal	Scott, 1986; AMS, personal observation
Pontia sisymbrii	*Descurainia sophia*	High	AMS, personal observation, Scott, 1986
Pontia sisymbrii	*Sisymbrium officinale*	Moderate	Garth and Tilden, 1986
Pontia sisymbrii	*Sisymbrium* spp.	Moderate	Tietz, 1972; Scott, 1986
Pyrgus albescens	*Malva* spp.	High	Emmel and Emmel, 1973; Brown, et al., 1992
Pyrgus communis	*Abutilon theophrasti*	Moderate	Tietz, 1972; Scott, 1986
Pyrgus communis	*Alcea rosea*	High	Tietz, 1972; Shapiro, 1974b; Scott, 1986
Pyrgus communis	*Malva neglecta*	High	Comstock, 1927; Shapiro, 1974b; Scott, 1986
Pyrgus communis	*Malva nicaeensis*	High	Shapiro, 1974a, 1974b; Scott, 1986
Pyrgus communis	*Malva parviflora*	High	Shapiro, 1974b; Scott, 1986
Pyrgus communis	*Malva* spp.	High	Garth and Tilden, 1986
Pyrgus communis	*Malva sylvestris*	High	Shapiro, 1974b; Scott, 1986
Pyrgus communis	*Anoda* spp.	Low	Scott, 1986
Pyrgus communis	*Hibiscus trionum*	Low	Tietz, 1972; Scott, 1986
Pyrgus communis	*Modiola caroliniana*	High	Scott, 1986; AMS, personal observation
Pyrgus communis	*Sida rhombifolia*	Moderate	Scott, 1986
Pyrgus communis	*Chenopodium album*	Ovip. only	AMS, personal observation
Strymon melinus	*Callistemon* spp.	Ovip. only	AMS, personal observation
Strymon melinus	*Campanula* spp. (Ornamental)	Ovip. only	AMS, personal observation
Strymon melinus	*Citrus limon*	Low	Scott, 1986
Strymon melinus	*Echium wildpretii*	Ovip. only	AMS, personal observation
Strymon melinus	*Gossypium herbaceum*	Moderate	Tietz, 1972; Scott, 1986
Strymon melinus	*Humulus japonicus*	High	AMS, personal observation
Strymon melinus	*Humulus lupulus*	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Scott, 1986; Garth and Tilden, 1986
Strymon melinus	*Lamium amplexicaule*	Low	Scott, 1986
Strymon melinus	*Lantana macropoda*	Low	Scott, 1986
Strymon melinus	*Lotus corniculatus*	High	AMS, personal observation
Strymon melinus	*Malva neglecta*	High	Shapiro, 1974b; Scott, 1986
Strymon melinus	*Malva nicaeensis*	High	Shapiro, 1974b; Scott, 1986

(*continued on next page*)

Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Strymon melinus	*Malva parviflora*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Strymon melinus	*Malva* spp.	High	Comstock, 1927; Emmel and Emmel, 1973; Garth and Tilden, 1986; Brown et al., 1992
Strymon melinus	*Medicago sativa*	High	Scott, 1986; AMS, personal observation
Strymon melinus	*Melilotus alba*	High	Scott, 1986; AMS, personal observation
Strymon melinus	*Myoporum parvifolium*	Ovip. only	AMS, personal observation
Strymon melinus	*Phaseolus limentis*	Moderate	Tietz, 1972; Scott, 1986
Strymon melinus	*Phaseolus lunatus*	Moderate	Scott, 1986
Strymon melinus	*Phaseolus* spp.	High	Emmel and Emmel, 1973; Brown et al., 1992
Strymon melinus	*Phaseolus vulgaris*	High	Tietz, 1972; Garth and Tilden, 1986; Scott, 1986; SDG, personal observation
Strymon melinus	*Pisum sativum*	Low	Tietz, 1972; Scott, 1986
Strymon melinus	*Senna alata*	High	Orsak, 1978; Scott, 1986
Strymon melinus	*Trifolium arvense*	High	Scott, 1986; AMS, personal observation
Strymon melinus	*Trifolium repens*	High	Scott, 1986; AMS, personal observation
Strymon melinus	*Verbascum thapsus*	Moderate	Scott, 1986
Strymon melinus	*Zea mays*	Unlikely	Tietz, 1972; Scott, 1986
Thorybes pylades	*Medicago sativa*	Moderate	Garth and Tilden, 1986; Scott, 1986
Thorybes pylades	*Trifolium pratense*	Moderate	Tietz, 1972; Scott, 1986
Thorybes pylades	*Trifolium repens*	Moderate	Tietz, 1972; Scott, 1986
Thorybes pylades	*Wisteria* spp.	Moderate	Garth and Tilden, 1986
Urbanus proteus	*Phaseolus* spp.	High	Emmel and Emmel, 1973; Brown et al., 1992
Urbanus proteus	*Phaseolus vulgaris*	High	Tilden, 1976; Orsak, 1978
Urbanus proteus	*Wisteria*	High	Emmel and Emmel, 1973
Vanessa annabella	*Alcea rosea*	High	Tietz, 1972; Shapiro, 1974a, 1974b; Dimock, 1978; Garth and Tilden, 1986; Scott, 1986
Vanessa annabella	*Ligustrum* spp.	Low	Comstock, 1927
Vanessa annabella	*Malva mauritiana*	High	AMS, personal observation
Vanessa annabella	*Malva neglecta*	High	Shapiro, 1974b; Scott, 1986
Vanessa annabella	*Malva nicaeensis*	High	Shapiro, 1974a, 1974b; Scott, 1986
Vanessa annabella	*Malva parviflora*	High	Dimock, 1972, 1978; Shapiro, 1974b; Scott, 1986
Vanessa annabella	*Malva* spp.	High	Comstock, 1927; Emmel and Emmel, 1973; Brown, et al., 1992
Vanessa annabella	*Malva sylvestris*	Moderate	Scott, 1986
Vanessa annabella	*Parietaria judaica*	High	AMS, personal observation
Vanessa annabella	*Urtica urens*	High	Dimock, 1978; Scott, 1986
Vanessa atalanta	*Boehmeria* spp.	Moderate	Comstock, 1927
Vanessa atalanta	*Humulus lupulus*	High	Comstock, 1927; Tietz, 1972; Emmel and Emmel, 1973; Garth and Tilden, 1986
Vanessa atalanta	*Parietaria judaica*	High	AMS, personal observation
Vanessa atalanta	*Pilea* spp.	High	AMS, personal observation
Vanessa atalanta	*Soleirolia soleirolii*	High	Emmel and Emmel, 1973; Shapiro, 1974b, 1975b; Scott, 1986
Vanessa atalanta	*Urtica urens*	High	Scott, 1986; AMS, personal observation
Vanessa cardui	*Alcea rosea*	High	Tietz, 1972; Shaprio, 1974b; Scott 1986
Vanessa cardui	*Alcea* spp.	High	Comstock, 1927; AMS, personal observation
Vanessa cardui	*Beta* spp.	Moderate	Comstock, 1927
Vanessa cardui	*Beta vulgaris*	Moderate	Scott, 1986
Vanessa cardui	*Borago officinalis*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Vanessa cardui	*Calendula officinalis*	Moderate	Tietz, 1972; Scott, 1986
Vanessa cardui	*Carduus acanthoides*	High	Scott, 1986; AMS, personal observation
Vanessa cardui	*Carduus nutans*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Vanessa cardui	*Carduus pycnocephalus*	High	Shapiro, 1974b; Garth and Tilden, 1986
Vanessa cardui	*Centaura nigra*	Moderate	Scott, 1986
Vanessa cardui	*Centaurea solstitialis*	High	Shapiro, 1974a, b; Scott, 1986
Vanessa cardui	*Chenopodium album*	Low	Tietz, 1972; Scott, 1986
Vanessa cardui	*Chrysanthemum* spp.	Moderate	Scott, 1986
Vanessa cardui	*Cirsium arvense*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Vanessa cardui	*Cirsium undulatum*	Moderate	Scott, 1986
Vanessa cardui	*Cirsium vulgare*	High	Tietz, 1972; Shapiro, 1974b; Scott, 1986
Vanessa cardui	*Citrus sinensis*	Low	Scott, 1986
Vanessa cardui	*Cnicus benedictus*	Moderate	Scott, 1986
Vanessa cardui	*Cucumis melo*	Moderate	Scott, 1986

(*continued on next page*)

Table 1 (*continued*)

Butterfly species	Plant species	Confidence level	Source
Vanessa cardui	*Cynara scolymus*	High	Shapiro, 1974b; Orsak, 1978; Scott, 1986
Vanessa cardui	*Gossypium* spp.	High	Scott, 1986; AMS, personal observation
Vanessa cardui	*Helianthus annuus var. macropus*	High	AMS, personal observation
Vanessa cardui	*Lactuca sativa*	Moderate	Comstock, 1927
Vanessa cardui	*Lantana* spp.	Moderate	Scott, 1986
Vanessa cardui	*Malva neglecta*	High	Shapiro, 1974b; Scott, 1986
Vanessa cardui	*Malva nicaeensis*	High	Shapiro, 1974b
Vanessa cardui	*Malva parviflora*	High	Shapiro, 1974b; Scott, 1986
Vanessa cardui	*Malva* spp.	High	Comstock, 1927; Emmel and Emmel, 1973; Brown et al., 1992
Vanessa cardui	*Malva sylvestris*	Moderate	Tietz, 1972; Scott, 1986
Vanessa cardui	*Medicago sativa*	Moderate	Comstock, 1927; Scott 1986
Vanessa cardui	*Nicotiana glauca*	Moderate	Scott, 1986
Vanessa cardui	*Onopordum acanthium*	High	Tietz, 1972; Scott, 1986; AMS, personal observation
Vanessa cardui	*Petunia* spp.	Low	Scott, 1986
Vanessa cardui	*Phaseolus vulgaris*	Moderate	Tietz, 1972; Orsak, 1978; Scott, 1986
Vanessa cardui	*Pisum sativum*	Moderate	Scott, 1986
Vanessa cardui	*Plantago lanceolata*	High	Shapiro, 1974b; Scott, 1986
Vanessa cardui	*Raphanus sativus*	Low	Comstock, 1927; Scott 1986
Vanessa cardui	*Silybum marianum*	High	Tietz, 1972; Shapiro, 1974a, 1974b; Scott, 1986
Vanessa cardui	*Solanum tuberosum*	Moderate	Comstock, 1927
Vanessa cardui	*Soleirolia soleirolii*	Moderate	Scott, 1986
Vanessa cardui	*Symphytum officinale*	High	Scott, 1986; AMS, personal observation
Vanessa cardui	*Urtica urens*	High	Shapiro, 1974b; Orsak, 1978; Scott, 1986
Vanessa virginiensis	*Alcea rosea*	Low	Tietz, 1972; Scott, 1986
Vanessa virginiensis	*Carduus* spp.	Low	Scott, 1986
Vanessa virginiensis	*Cirsium arvense*	Low	Tietz, 1972; Scott, 1986
Vanessa virginiensis	*Gazania uniflora*	High	AMS, personal observation
Vanessa virginiensis	*Onopordum acanthium*	Low	Scott, 1986
Vanessa virginiensis	*Silybum marianum*	Low	Scott, 1986
Zerene eurydice	*Medicago sativa*	Low	Scott, 1986

which it was not previously reported, in the San Francisco Bay area (Powell, 1997). Many of the tree and shrub feeders in the table inhabit predominantly foothill and montane areas which have only recently become part of California's suburban landscape. As development and associated ornamental plantings become more common near the natural habitats of these butterflies, we may begin to see greater use of introduced plants by them.

Specialization on different plant taxa can extend down to the level of the genus. A number of California butterflies feed on plant species in the Polygonaceae. Many feed entirely on species in the genus *Eriogonum*, while others feed exclusively on species of *Polygonum* and *Rumex*. The genus *Eriogonum* has 111 named species in California and numerous varieties, all of them native to the state. *Polygonum* and *Rumex*, in contrast, are moderate-sized Holarctic genera comprised of mixtures of native and exotic species. Fourteen Lycaenid species are specialists on the genus *Eriogonum* in California; none of these butterflies is recorded on introduced plant taxa. In contrast, of the six Lycaenids that specialize on *Polygonum* and/or *Rumex,* four are recorded as feeding on introduced species of *Polygonum* and/or *Rumex* within California and one other is reported to feed on an introduced *Rumex* within its range in the western United States though this record is currently unconfirmed for California (Table 1).

Barring constraints imposed by specialization on plants at the level of the genus or subfamily, we would generally expect those butterflies which feed on plant families well represented by exotic species in California to be among the most likely to utilize introduced plant taxa (Connor et al., 1980). California has 176 naturalized exotic grasses (Poaceae), 153 introduced plants in the family Asteraceae, 90 in the Fabaceae, and 63 in the Brassicaceae (Hickman, 1993). Of the 34 species known to feed on grasses, 14 (41%) are recorded on exotic taxa. However, this number is likely to be an underestimate. All of the grass-feeding species are either hesperiid skippers or satyrids that remain poorly known compared to other butterfly taxa. For many of these taxa, native hosts are still undocumented. In addition, grasses themselves are notoriously difficult to identify. The lack of records for California butterflies on exotic grasses should not therefore be taken to mean that such interactions do not occur, but merely that more investigation is needed. However, most of these butterflies feed on perennial bunch grasses (MacNeill, 1964) while the majority of naturalized exotic grasses are annuals; there are hardly any published records of butterflies utilizing

Table 2
Plant families with specialist butterflies in California but no naturalized host plants

Plant family	Butterfly species
Acanthaceae	*Dymasia chara imperialis*
Agavaceae	*Agathymus alliae*
Agavaceas	*Agathymus baueri*
Agavaceae	*Megathymus coloradensis*
Aristolochiaceae	*Battus philenor*
Cupressaceae	*Mitoura barryi*
Cupressaceae	*Mitoura loki*
Cupressaceae	*Mitoura muiri*
Cupressaceae	*Mitoura nelsoni*
Cupressaceae	*Mitoura siva*
Cupressaceae	*Mitoura thornei*
Fagaceae	*Adelpha bredowii*
Fagaceae	*Erynnis brizo*
Fagaceae	*Erynnis propertius*
Fagaceae	*Erynnis tristis*
Fagaceae	*Habrodais grunus*
Fagaceae	*Satyrium auretorum*
Fumariaceae	*Parnassius clodius*
Pinaceae	*Incisalia eryphon*
Pinaceae	*Neophasia menapia*
Rhamnaceae	*Erynnis pacuvius*
Rhamnaceae	*Tharsalea hermes*
Rhamnaceae	*Nymphalis californica*
Rhamnaceae	*Satyrium saepium*

the many annual grasses, and the few that do exist tend to be on summer–autumn, not spring, annuals.

Pierids that feed on plants in the Brassicaceae represent the other extreme; they tend to be well-studied and many of them are recorded from introduced taxa. *Pieris rapae*, the European cabbage butterfly, itself was introduced in Quebec around 1860 and from there, spread rapidly. Records of a butterfly thought to be *P. rapae* appear in California as early as 1867, suggesting that this butterfly may have been introduced there by the Spanish sometime before that date (Shapiro, 1975a). The use of crucifers introduced from Europe by *P. rapae* probably represents little more than recolonization of hosts from its native land. However, 9 out of 10 of California's native pierids are also recorded as feeding on one to many introduced crucifers (Table 1). This is not surprising given the chemical basis of this host specialization. Chemically unusual crucifers such as *Capsella* and *Lunaria* are typically eschewed by North American Pierids. The one species not recorded on introduced plant taxa is *Anthocaris cethura*, predominantly a desert species with an isolated subspecies found on Catalina Island. Of the 40 species that feed on natives in the Fabaceae, 22 (55%) are reported on exotics. However, the number of naturalized Malvaceae is relatively low (12 species), but virtually all of them are used, often heavily, by 5 of the 9 (55%) native mallow-feeding butterflies. Thus, the number of species of exotics

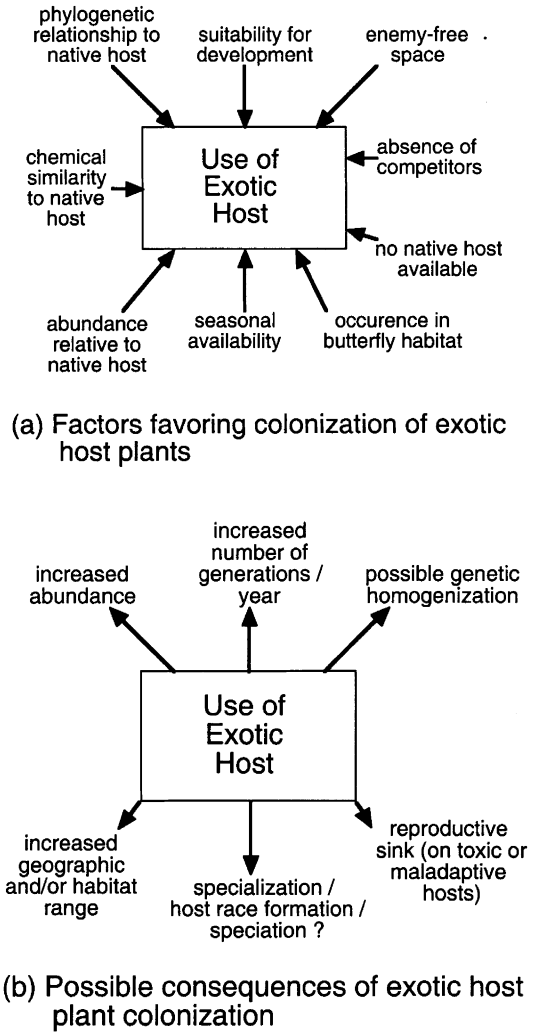

Fig. 5. Factors affecting and affected by colonization of exotic hosts.

in a family seems at best a crude predictor of butterfly exotic host use patterns.

Insects colonizing newly introduced exotics tend to be largely polyphagous (Strong et al., 1984) so we might expect oligophagous or polyphagous butterfly taxa, those that naturally feed on plants in multiple plant families, to utilize exotic hosts. Garth and Tilden's California Butterflies (1986) records 21 butterfly species as utilizing native California plants belonging to more than one family. Of these, fully 16 (76%) are also recorded on introduced taxa. In contrast, the remaining 67 taxa recorded as associated with exotics come from a pool of 200 species (34%) which, according to Garth and Tilden (1986) utilize only a single family of native plants (taxa whose host plants were unknown in California were omitted for this analysis). Two California species exemplify this pattern of taxa with broad native host associations easily colonizing exotic taxa: *S. melinus*, the common hairstreak, and *V. cardui*, the painted lady. *Strymon melinus* is broadly distributed across North America. *Vanessa cardui* is considered the most

widely distributed butterfly in the world and is well known in California for occasional migrations of millions of individuals northward from the deserts of southern California (Garth and Tilden, 1986). Both of these taxa are recorded as feeding on many different exotic plants, from a number of plant families in California (Table 1). *V. cardui* is particularly likely to be found utilizing unusual hosts—both native and naturalized—in years of outbreak.

Many of the records listed in Table 1 are undoubtedly invalid; such records often get repeated without confirmation in the secondary literature, thus multiple citations do not necessarily imply multiple records (Shields et al., 1969). Shapiro (1983) traced eight errors in the Mexican butterfly literature to two sources in the US literature; one was a 19th century error, endlessly repeated. Shields et al. (1969) report that Lincoln Brower traced another error; *Papilio rutulus* was incorrectly reported as feeding on *Humulus lupulus* (''hops'') due to a report by Comstock of *P. rutulus* on ''hop'', meaning Hop-Tree, *Ptelea baldwinii* (Rutaceae). Other records in Table 1 are no doubt valid in other states, but not in California. It is also true that seemingly unlikely records can be true, e.g. *Papilio eurymedon*, a butterfly that feeds on woody Rhamnaceae, ovipositing on *Melilotus alba*, white sweetclover (AMS, personal observation). Therefore, the subjective rankings assigned to the butterfly – plant combinations in Fig. 1 should be taken seriously, but not literally.

6. Conclusions

California butterflies now feed on a number of introduced plant taxa. Some of these reports of oviposition or feeding are no doubt rare compared to use of native host plants however, use of exotic hosts by a number of taxa has resulted in range expansion, increased population size, and/or extension of the breeding season. Feeding on exotic taxa has also allowed some butterfly species to remain in areas that have lost most native host plant species due to development and other human activities. The use of exotic taxa may sometimes bring previously isolated ecotypes into contact with one another, resulting in genetic homogenization within the species. Use of introduced hosts is also leading to homogenization of urban butterfly faunas (Blair, 2001; Shapiro, unpublished). In other cases, exotic, usually ornamental or cultivated plant species, have permitted butterflies from other areas to invade and breed in the state. There are three documented cases where a native California butterfly commonly lays on an introduced plant toxic to larvae; other cases may exist as well. A summary of these possible direct consequences is presented in Fig. 5. Indirect effects of introduced species on California's butterflies were not considered in this paper though they be important in individual cases. An example of such an effect is where exotic plant taxa have excluded native host plants from all or part of their natural range, thus reducing the range of the associated butterfly taxa.

The use of introduced hosts varies greatly across butterfly taxa. None of the high elevation (alpine) butterfly taxa and few of the desert taxa in California are recorded as using exotic hosts, a pattern that likely results from their restriction to habitats that have experienced few or no successful invasions by introduced plants. Butterfly species specialized on plant lineages that contain no exotic species in California were almost never associated with introduced hosts. In addition, taxa whose native host range encompassed multiple plant families were much more likely to utilize exotic taxa than those whose native host range was limited to a single family. Strong et al. (1984) predict that the initial rapid colonization of an exotic host by native species will result primarily from these two pools: polyphagous species and species whose native host affinities preadapt them to feed on the exotic taxa. Colonization by specialized feeders on other plant taxa, when it does occur, is expected to take longer and be less predictable. Thus, the probability a given butterfly taxon will use introduced plants increases if it is found in areas of the state with large numbers of exotic plants, if there are many exotic plant species in the plant family and genera on which it feeds, and if it is oligophagous or polyphagous rather than being more specialized (Fig. 5). Once oviposition occurs on a plant (a phenomenon that may be facilitated in disturbed habitats, especially when native hosts become rare) the probablility of true colonization of a plant will depend on suitability for larval development, presence or absence of competitors and natural enemies, and other factors (Fig. 5). Colonization is even possible in cases where females oviposit on exotics toxic to larvae. Given sufficient variation in tolerance, natural selection may result in improved performance on the plant instead of avoidance by ovipositing females. Such a scenario seems possible for *Papilio zelicaon* on *Ammi visnaga* in California in that tolerance varies greatly among populations in the state (Graves, 1997).

As the population of California grows and development of natural areas continues at a rapid pace, more and more introduced plant taxa will invade the habitats of California's butterflies (Bossard et al., 2000). Our ability to mitigate negative effects of interactions between exotic plants and native butterflies will depend on documenting and studying these interactions as they occur. We may also be able to predict potential pest situations before they occur or identify native butterfly species that might serve as biological control agents for invasive weeds. On the other hand, the extensive adoption of introduced host plants has clearly been beneficial for a significant segment of the California butterfly fauna, including most of the familiar species of urban,

suburban and agricultural environments. Some of these species are now almost completely dependent on exotics (Shapiro, 2002), and would disappear were weed control more effective than it currently is.

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References

Barbehenn, R.V., 1994. Host plants of *Poanes melane* (Hesperiidae). Journal of the Lepidopterists' Society 48, 386–388.

Bernays, E.A., Chapman, R.F., 1994. Host Selection by Phytophagous Insects. Chapman and Hall, New York.

Blair, R.B., 2001. Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna? In: Lockwood, J.L., McKinney, M.L. (Eds.), Biotic Homogenization. Kluwer Academic, New York, pp. 33–56.

Bossard, C.C., Randall, J.M., Hoshovsky, M.C. (Eds.), 2000. Invasive Plants of California's Wildlands. University of California Press, Berkeley & Los Angeles.

Bowden, S.R., 1971. American white butterflies (Pieridae) and English food-plants. Journal of the Lepidopterists' Society 25, 6–12.

Bowers, M.D., Stamp, N.E., Collinge, S.K., 1992. Early stage of host race expansion by a specialist herbivore, *Euphydryas phaeton* (Nymphalidae). Ecology 73, 526–536.

Brown, J.W., Real, H.G., Faulkner, D.K., 1992. Butterflies of Baja California: Faunal Survery, Natural History, Conservation Biology. Lepidoptera Research Foundation, Beverly Hills, California.

California Department of Food and Agriculture, 1996. California Agricultural Resource Directory. California Department of Food and Agriculture, Sacramento, California.

Camara, M.D., 1997. A recent host range expansion in *Junonia coenia* Hubner (Nymphalidae): oviposition preference, survival, growth, and chemical defense. Evolution 51 (3), 873–884.

Carroll, S.P., Klassen, S.T.P., Dingle, H., 1998. Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. Evolutionary Ecology 12, 955–968.

Chew, F.S., 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31, 568–579.

Comstock, J.A., 1927. Butterflies of California: A Popular Guide to a Knowledge of the Butterflies of California. Published by the author, Los Angeles, California.

Connor, E.F., Faeth, S.H., Simberloff, D., Opler, P.A., 1980. Taxonomic isolation and the accumlation of herbivorous insects: a comparison of introduced and native trees. Ecological Entomology 5, 205–211.

Copp, N.H., Davenport, D., 1978. *Agraulis* and *Passiflora* I. Control of specificity. Biological Bulletin 155, 98–112.

Cronk, Q.C.B., Fuller, J.L., 1995. Plant Invaders. Chapman and Hall, London, England.

Courant, A.V., Holbrook, A.E., Van Der Riejden, E.D., Chew, F.S., 1994. Native pierine butterfly (Pieridae) adapting to naturalized crucifer? Journal of the Lepidopterists' Society 48, 168–170.

Dimock, T.E., 1972. Type locality and habitat—*Cynthia annabella*. Journal of Research on the Lepidoptera 10, 265–266.

Dimock, T.E., 1978. Notes on the life cycle and natural history of *Vanessa annabella* (Nymphalidae). Journal of the Lepidopterists' Society 32, 88–96.

Dirig, R., Cryan, J.F., 1991. The status of silvery blue subspecies (*Glaucopsyche lygdamus*) in New York. Journal of the Lepidopterists' Society 45, 272–290.

Ehrlich, P.R., Raven, P.H., 1964. Butterflies and plants: a study in coevolution. Evolution 18, 586–608.

Emmel, J.F., Emmel, T.C., 1974. Ecological studies of Rhopalocera in a Sierra Nevadan community—Donner Pass, California. V. Faunal additions and foodplant records since 1962. Journal of the Lepidopterists' Society 28, 344–348.

Emmel, T.C., Emmel, J.F., 1973. The Butterflies of Southern California. Natural History Museum of Los Angeles County, Science Series 26, Los Angeles, California.

Emmel, T.C., Shields, O., 1978. Larval foodplant records for *Papilo Zelicaon* in the Western United States and further evidence for the conspecificity of *P. zelicaon* and *P. gothica*. Journal of Research on the Lepidoptera 17, 56–67.

Essig, E.O., 1915. Injurious and Beneficial Insects of California. California State Commission of Horticulture, Sacramento, California.

Feder, J.L., 1998. The apple maggot fly, *Rhagoletis pomonella*: flies in the face of conventional wisdom about speciation? In: Howard, D.J., Berlocher, S.H. (Eds.), Endless Forms: Species and Speciation. Oxford University Press, New York, pp. 130–144.

Fox, L.R., Eisenbach, J., 1992. Contrary choices—possible exploitation of enemy-free space by hervivorous insects in cultivated and wild crucifers. Oecologia 89, 574–579.

Frenkel, R.E., 1977. Ruderal Vegetation along some California Roadsides. University of California Press, Berkeley, California.

Garth, J.S., Tilden, J.W., 1986. California Butterflies. University of California Press, Berkeley, California.

Goeden, R.D., Ricker, D.W., 1982. Poison hemlock, *Conium maculatum*, in southern California—an alien weed attacked by few insects. Annals of the Entomological Society of America 75, 173–176.

Gratton, C., Welter, S.C., 1999. Does "enemy-free space" exist? Experimental host shifts of an herbivorous fly. Ecology 80, 773–785.

Graves, S.D., 1997. Evolutionary and Ecological Determinants of Host Plant Range in *Papilio zelicaon*, The Anise Swallowtail. Unpublished PhD dissertation, University of California, Davis.

Groman, J.D., Pellmyr, O., 2000. Rapid evolution and specialization following host colonization in a Yucca moth. Journal of Evolutionary Biology 13, 223–236.

Haeger, J.F., 1988. Notes on the biology of *Brephidium exilis* (Bousduval) (Lycaenidae). Journal of Research on the Lepidoptera 26, 254–255.

Heady, H.F., 1995. Valley grassland. In: Barbour, M.G., Major, J. (Eds.), Terrestrial Vegetation of California. California Native Plant Society Special Publication Number 9, Sacramento, California, pp. 491–514.

Hickman, J.C. (Ed.), 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley, California.

Hogan, E.L. (Ed.), 1988. Sunset Western Garden Book. Sunset Publishing Corporation, Menlo Park, California.

Jaenike, J., 1990. Host specialization in phytophagous insects. Annual Renew of Ecology and Systematics 21, 243–273.

James, L.F., Evans, J.O., Ralphs, M.H., Child, R.D., 1991. Noxious Range Weeds. Westview Press, Boulder, Colorado.

Karowe, D.N., 1990. Predicting host range evolution: colonization of *Coronilla varia* by *Colias philodice* (Lepidoptera: Pieridae). Evolution 44, 1637–1647.

Lane, J., 1993. Overwintering Monarch butterflies in California: past and present. In: Malcomb, S.B., Zlucki, M.P. (Eds.), Biology and Conservation of the Monarch Butterfly. Natural History Museum of Los Angeles County, Los Angeles, California.

Lorenz, R.J., Dewey, S.A., 1988. Noxious weeds that are poisonous. In: James, L.F., Ralphs, M.H., Nielsen, D.B. (Eds.), The Ecology and Economic Impact of Poisonous Plants on Livestock Production. Westview Press, Boulder, Colorado.

Loxdale, H.D., Lushai, G., 1999. Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. Philosophical Transactions of the Royal Society of London (B) 354, 1479–1495.

MacNeill, C.D., 1964. The skippers of the genus *Hesperia* in western North America with special reference to California. University of California Publications in Entomology 35, 1–230.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological applications 10, 689–710.

Munz, P., 1968. A California Flora. University of California Press, Berkeley, California.

Nagy, K.A., Henen, B.T., Vyas, D.B., 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32, 260–267.

Nice, C.C., Fordyce, J.A., Shapiro, A.M., Ffrnch-Constant, R., 2002. Lack of evidence for reproductive isolation among ecologically-specialised Lycaenid butterflies. Ecological Entomology 27, in press.

Opler, P.A., 1967. New host records for *Anthocharis* (Pieridae). Journal of the Lepidopterists' Society 21, 212.

Opler, P.A., Wright, A.B., 1999. Western Butterflies. Houghton Mifflin, Boston and New York.

Orsak, L.J., 1978. The Butterflies of Orange County, California. Museum of Systematic Biology Research Series no. 4. University of California, Irvine, California.

Porter, A., 1994. Implications of introduced garlic mustard (*Alliaria petiolata*) in the habitat of *Pieris virginiensis* (Pieridae). Journal of the Lepidopterists' Society 48, 171–172.

Powell, J.A., 1997. *Callophrys eryphon* (Lycaenidae) colonizes urban and suburban San Francisco Bay area, California, using planted Monterey pine. Journal of the Lepidopterists' Society 51, 176–179.

Randall, J.M., Rejmanek, M., Hunter, J.C., 1998. Characteristics of the exotic flora of California. Fremontia 26, 3–12.

Rejmanek, M., Randall, J.M., 1994. Invasive alien plants in California: 1993 summary and comparison with other areas in North America. Madroño 41, 161–177.

Rejmanek, M., Thomsen, C.D., Peters, I.D., 1991. Invasive vascular plants of California. In: Groves, R.H., Di Castri, F. (Eds.), Biogeography of Mediterranean Invasions. Cambridge University Press, Cambridge, England, pp. 81–101.

Remington, C.L., 1952. The biology of Nearctic Lepidoptera I. Foodplants and life-histories of Colorado Papilionidae. Psyche 59, 61–70.

Rhymer, J.M., Simberloff, D., 1996. Extraction by hybridization and introgression. Annual Review of Ecology and Systematics 27, 83–109.

Robbins, W.W., Bellue, M.K., Ball, W.S., 1951. Weeds of California. California Department of Agriculture, Sacramento, California.

Sakai, W.H., 1993. Notes on *Danaus gilippus strigosus* (Nymphalidae: Danainae) in southern California. Journal of the Lepidopterists' Society 47 (2), 160–161.

Schwartz, M.W., Porter, D.J., Randall, J.M., Lyons, K.E. 1996. Impact of nonindigenous plants. In: Sierra Nevada Ecosystem Project: Final Report to Congress, Vol. II. Center for Water and Wildland Resources, University of California, Davis, California, pp. 1203–1226.

Scott, J.A., 1979(80). Geographic variation in *Lycaena xanthoides*. Journal of Research on the Lepidoptera 18, 50–59.

Scott, J.A., 1986. The Butterflies of North America: A Natural History and Field Guide. Stanford University Press, Stanford, California.

Sevastopulo, D.G., 1964. Lepidoptera ovipositing on plants toxic to larvae. Journal of the Lepidopterists' Society 18, 104.

Shapiro, A.M., 1973. Host records for *Brephidium exilis* (Lycaenidae). Journal of the Lepidopterists' Society 27, 157–158.

Shapiro, A.M., 1974a. Butterflies of the Suisun Marsh, California. Journal of Research on the Lepidoptera 13, 191–206.

Shapiro, A.M., 1974b. The butterfly fauna of the Sacramento Valley, California. Journal of Research on the Lepidoptera 13, 73–82. 115–122, 137–148.

Shapiro, A.M., 1975a. The role of watercress, *Nasturtium officinale*, as a host of native and introduced butterflies in California. Journal of Research on the Lepidotera 14, 158–168.

Shapiro, A.M., 1975b. Supplementary records of butterflies in the Sacramento Valley and Suisun Marsh, lowland central California. Journal of Research on the Lepidoptera 14, 100–102.

Shapiro, A.M., 1976. The biological status of nearctic taxa in the *Pieris protodice-occidentalis* group (Pieridae). Journal of the Lepidopterists' Society 30, 289–300.

Shapiro, A.M., 1978. A new weedy host for the buckeye, *Precis coenia* (Nymphalidae). Journal of the Lepidopterists' Society 32, 224.

Shapiro, A.M., 1979. *Erynnis baptisiae* (Hesperiidae) on crown vetch (Leguminosae). Journal of the Lepidopterists' Society 33, 258.

Shapiro, A.M., 1980. Egg-load assessment and carryover diapause in *Anthocharis* (Pieridea). Journal of the Lepidopterists' Society 34, 307–315.

Shapiro, A.M., 1983. Errores en plantas huesped de mariposas mexicanas como una extrapolacion de la literatura estadounidense. Revista de la Sociedad Mexicana de Lepidopterologia 8, 47–48.

Shapiro, A.M., 1984. Geographical ecology of the Sacramento Valley riparian butterfly fauna. In: Warner, R.E., Hendricx, K.M. (Eds.), California Riparian systems: Ecology, Conservation and Productive Management. University of California Press, Berkeley, California, pp. 934–941.

Shapiro, A.M., 1995. From the mountains to the prairies to the ocean white with foam: *Papilio zelicaon* makes itself at home. In: Kruckberg, A.R., Walker, R.B., Leviton, A.E. (Eds.), Genecology and Ecogeographic Races. Pacific Division AAAS, San Francisco, California, pp. 67–99.

Shapiro, A.M., 1996. Status of butterflies. In: Sierra Nevada Ecosystem Project: Final Report to Congress. Vol. II. Center for Water and Wildland Resources, University of California, Davis, California, pp. 743–757.

Shapiro, A.M., 2002. The Californian urban butterfly fauna is dependent on alien plants. Diversity and Distributions 8, 31–40.

Shapiro, A.M., Masuda, K.K., 1980. The opportunistic origin of a new citrus pest. California Agriculture 34, 4–5.

Shields, O., Emmel, J.F., Breedlove, D.E., 1969. Butterfly larval foodplant records and a procedure for reporting foodplants. Journal of Research on the Lepidoptera 8, 21–36.

Singer, M.C., Thomas, C.D., Parmesan, C., 1993. Rapid human-induced evolution of insect-host associations. Nature 366, 681–683.

Stanford, R.E., Opler, P.A., 1993. Atlas of Western USA Butterflies. Published by the authors, Denver and Fort Collins, Colorado.

Straatman, R., 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. Journal of the Lepidopterists' Society 16, 99–103.

Strong, D.R., Lawton, J.H., Southwood, T.R.E., 1984. Insects on Plants. Blackwell Scientific, Oxford.

Tabashnik, B.E., 1983. Host range evolution: the shift from native legume hosts to alfalfa by the butterfly, *Colias philodice eriphyle*. Evolution 37, 150–162.

Thomas, C.D., Ng, D., Singer, M.C., Mallet, J.L.B., Parmesan, C., Billington, H.L., 1987. Incorporation of a European weed into the diet of a North American herbivore. Evolution 41, 892–901.

Tietz, H.M., 1972. An Index to the Described Life Histories, Early Stages, and Hosts of the Macrolepidoptera of the Continental United States and Canada. Allyn Museum of Entomology, Sarasota, Florida.

Tilden, J.W., 1976. *Urbanus simplicius* (Stoll), a new record for California. Journal of Research on the Lepidoptera 15, 40.

Westman, W.E., 1990. Managing for biodiversity: unresolved science and policy questions. BioScience 40, 26–33.

White, R.R., Singer, M.C., 1974. Geographical distribution of hostplant choice in *Euphydryas editha* (Nymphalidae). Journal of the Lepidopterists' Society 28, 103–107.

Whitson, T.D. (Ed.), 1996. Weeds of the West. University of Wyoming, Jackson, Wyoming.