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BIODIVERSITY VIEWPOINTS

The Californian urban butterfly fauna is dependent on alien plants

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Abstract. Using the unusually well-documented butterfly fauna of Davis, Yolo County, California, it is shown that the mainly native species commonly observed in gardens breed mostly or entirely on alien plants, especially naturalized weeds. Over 40% of the fauna has no known native hosts in the urban–suburban environment. Were certain alien weeds to be eradicated or their abundance greatly reduced, the urban-suburban butterfly fauna would disappear. This might be regarded as an unfortunate, and perhaps intolerable, side-effect of such programs.

Key words. Weeds, urban ecology, host plant switching, butterfly gardening, invasive plants, California Central Valley.

INTRODUCTION

Concern about the impacts of alien organisms on native biota and environments has risen dramatically in the past decade, accompanied by a spate of alarmist rhetoric and often dramatic metaphor. In a special section headed 'Biological Invaders Sweep In', the journal *Science* claimed that '... exotic species can devour or out-compete species that have called an ecosystem home for tens of thousands of years. Biological invasions are the second biggest cause of biodiversity loss in the United States, after habitat destruction ... they could soon become the first (Enserink, 1999).' In California, a state particularly heavily affected by naturalized aliens (Bossard *et al.*, 2000), agencies managing parks and wildlands have devoted increasing attention and resources to the management of introduced species. Such efforts sometimes appear driven more by ideology than ecology. Often the managers are unaware of benefits conferred by aliens and of potentially undesirable side-effects from their removal. Whitson (1996) reminded readers that 'the term "weed" does not always indicate that a plant is totally undesirable, or that it cannot be beneficial under certain situations.' As an ecologist working on butterflies in northern California for over 30 years, I am regularly consulted by garden clubs, park and planning commissions, civic organizations and members of the public as to methods of environmental enhancement for butterflies. The recent popularity of 'butterfly gardening' has increased the frequency of such contacts, but I have also been asked to advise on butterfly aspects in the restoration of degraded sites, augmentation of host plants and nectar sources in parks, and the like. I know of no systematic surveys of public attitudes on butterflies in the United States, but my own experience has convinced me that many people have positive feelings about butterflies and enthusiastically want them as part of the urban and suburban environment. Most adults who discuss the subject with me eventually claim that there are fewer butterflies today than in their childhood, and regret that 'fact.'

My interactions with garden clubs and private citizens demonstrate, however, that a clear gap exists between perception and reality in identifying resources for butterflies. The vast majority of my interlocutors believe, with no evidence, that butterfly gardening is grounded in the use of native plants. Most of them prefer to use natives on more or less ideological grounds, and it seems 'natural' to them that since native plants are

ecologically 'good', they must be better than aliens as resources for butterflies. I have been disabusing them of this previously harmless conceit these many years. More recently, however, an actual threat to the well-being of urban and suburban butterfly faunas has emerged in the form of eradication or control programs directed against essential butterfly resources which happen to be naturalized aliens. I now find myself arguing before government agencies to take into account the value of such species as butterfly resources. Some managers react with disbelief to the claim that 'native' butterflies could depend on 'weeds.'

This paper documents the degree of dependence of one urban–suburban butterfly fauna on alien plants and attempts to define the extent to which the results can be generalized.

THE FAUNA AND ITS SETTING

Davis, Yolo County, California sits in the Sacramento Valley, the northern half of the California Great Central Valley. Except for man-made structures it is essentially flat, with an official elevation of 15.85 m a.s.l. The population as of March 2001 was 60 308 and the area, including the campus of the University of California, was approximately 6100 ha. The climate is Mediterranean, with cloudy, wet but mild winters (with frost, but rarely hard frosts), and sunny, dry and hot summers, somewhat tempered by intermittent shallow intrusions of marine air through the nearby Sacramento-San Joaquin Delta. Davis is surrounded by agricultural land, producing a mixture of row and tree crops. Between Davis and Sacramento is the Yolo Bypass, a managed floodplain farmed in summer and used to divert excessive flows from the Sacramento River to the Delta in wet years to prevent urban flooding. The city is a patchwork of neighbourhoods of mostly single-family homes developed at different times between the late 19th Century and the present, now ringed by large peripheral subdivisions built on former agricultural land. Older neighbourhoods have relatively small single-family homes on small lots with mature landscaping, forming a nearly continuous canopy. Newer neighbourhoods have larger houses on larger lots and landscaping is correspondingly younger. There is a narrow fringe of disturbed riparian woodland along the south boundary of the city (Putah Creek). Most of the native plants in Davis occur here. Within the city there are two artificially constructed 'urban wetlands' (storm water ponds) which are planted with mostly native riparian plants and managed as wildlife habitat.

The urban vegetation is dominated by a relatively short list of (nearly all alien) woody species widely recommended and planted in inland Californian Mediterranean climates. The city has a street tree program which is also strongly dominated by aliens, though some species belong to genera with native members. Increasing numbers of individual gardeners are planting natives both woody and herbaceous; this has led to a conspicuous increase in the diversity of the urban flora since 1970. However, hardly any of these species are of any significance to butterflies, and the few that are remain too rare to affect urban butterfly numbers. There are several areas of community gardens or allotments, most of which are weedy, scattered in different parts of the city. Very few vacant lots remain within established neighbourhoods, and nearly all the drainage/irrigation ditches within the city have been culverted. There are significant corridors of ruderal vegetation bisecting the city north–south on the shoulders of Interstate Highway 80 and east–west on State Highway 113 and along the right-of-way of the California Northern Railroad. The highway embankments have been landscaped in places (with natives, in some cases) and are mowed in late spring for fire control. There is no comprehensive flora of Davis, and the list of cultivated species is so labile that one would be very difficult to maintain. I estimate — probably very conservatively — that at any given time aliens outnumber natives by at least 5 : 1. The vast majority of aliens are of no butterfly significance.

The butterfly fauna of Davis has been intensely monitored since winter 1971/72 and may be the best-documented such fauna in the United States. Given the domination of the urban flora and vegetation by aliens, the current fauna of 32 breeding butterfly species in the city appears rich. In addition, five species (*Satyrium californica*, *Erynnis persius*, *Epargyreus clarus*, *Ochlodes sylvanoides* and *Poanes melane*) have become extinct in Davis within the past 30 years. Of these, *E. clarus* fed only on aliens and *P. melane* (probably) in part on aliens.

The Appendix itemizes the extant fauna and its known host plants in the city. Two species which occur only in the 'urban wetlands' or in native riparian vegetation on Putah Creek (*Satyrium sylvinus* and *Limenitis lorquini*) and are not otherwise seen in the city are excluded. Approximately 15 other species have been seen at least once in the city; these include strays from the nearby Coast Range or Sierra Nevada foothills as well as long-distance migrants (e.g. from the deserts of south-eastern California). One species which has bred and been common in Davis (*Leptotes marina*) is excluded because it is a sporadic long-distance migrant apparently incapable of persisting. All the butterflies except *Pieris rapae* are presumed native, though there is some suggestion of range changes in the 20th century for several species.

Two riparian species, *Battus philenor* and *Atlides halesus*, are included because both are routinely seen in the city. The host plant of *B. philenor*, the native vine *Aristolochia californica*, occurs naturally in two sites but has been planted in part to encourage the butterfly, which does colonize it in gardens. The host of *A. halesus*, a mistletoe (*Phoradendron flavescens* var. *macrophyllum*), has spread to many cultivated trees and is abundant in older neighbourhoods.

DEPENDENCE ON ALIEN HOSTS

Twenty-nine of the 32 butterflies known to breed in Davis do so at least in part on alien plants; 13 have no known native host plants in Davis; three more (*Strymon melinus*, *Everes comyntas* and *Plebeius acmon*) have obligate seasonal host successions due to the ephemeral phenologies of some host species, and must use at least one alien during the year; and only three (*B. philenor*, A. *halesus* and *Phyciodes campestris*) have no known alien hosts in Davis, though the mistletoe host of A. *halesus* often parasitizes alien trees. Overall, the Davis butterfly fauna is thus markedly dependent on aliens. This is true even though a higher proportion of natives than aliens in the flora is utilized (the ratio of alien to native host records in the Appendix is 3.7 : 1, vs. at least 5 : 1 in the overall flora).

Relatively few of these alien hosts are deliberately cultivated. These include the woody hosts of *Nymphalis antiopa*, *Papilio rutulus* and *Erynnis tristis*. Some of these (*Ulmus*, *Celtis*) are hosts elsewhere in the butterfly's range and were present in California in the Tertiary. Others are phylogenetically and/or chemically closely related to native hosts (alien *Fraxinus*, *Platanus* and *Prunus* all have native congeners which are hosts of *Papilio rutulus* elsewhere; *Ligustrum* and *Syringa*, like *Fraxinus*, are in the Oleaceae). Butterflies that breed frequently on cultivated herbaceous aliens in gardens include *Vanessa cardui*, *Pieris rapae*, *Strymon melinus* and *Papilio zelicaon*. All of these also have weedy alien hosts, which are more common and more frequently used. The common garden hollyhock (*Alcea rosea*) is the only cultivated alien used by butterflies in three families, but its use is only occasional as compared to the ubiquitous weedy *Malva*. *Vanessa cardui* and *Strymon melinus* are both mallow feeders, but are also the most polyphagous butterflies in North America (Tietz, 1972). The skippers *Hylephila phyleus* and *Atalopedes campestris* breed primarily in mowed lawns, and *H. phyleus* is almost entirely an urban insect in California. These two skippers are the most abundant butterflies in Davis from August through October. The list of alien hosts continues to grow as new weeds are naturalized locally. *Kickxia* was colonized almost immediately by *Junonia coenia* (Shapiro, 1978). The prostrate mallow *Modiola caroliniana* is used by *Pyrgus communis* in nearby communities but was first reported in Davis in 2001 and has not yet been colonized.

Urban growth has altered the distribution and abundance of butterflies in Davis. When Shapiro (1982) described butterfly gardening in north-central Davis, it was still a productive activity. The culverting of nearby weedy drainage ditches drastically reduced butterfly numbers and diversity in the neighbourhood a few years later. The richest butterfly faunas in Davis are observed today in neighbourhoods near the community gardens, which are the major butterfly generators within the city. Two of the five species lost since 1970 were eradicated by habitat conversion at one site. The others are unexplained, though *Satyrium californica* was already extremely rare in the early 1970s and a subdivision was built around its host trees. One species, *Glaucopsyche lygdamus*, went extinct on its native host in the 1970s but resurfaced a few years later using introduced annual vetches, and has persisted to the present day. Two species (*Vanessa virginiensis*

and *Phyciodes campestris*) are not really permanent residents of Davis, but colonize often from nearby wildland populations. They rarely persist more than a couple of generations.

THE SITUATION IN CONTEXT

Any butterfly capable of breeding in urban or suburban environments obviously must have one or more host plants there. The prevalence of aliens in such places reflects deliberate introductions, accidental introductions, high degrees of disturbance, and in some cases ecophysiological discontinuities with the surrounding areas (e.g. those associated with irrigation). The last are especially telling in the California Central Valley.

The butterfly fauna of the Sacramento Valley was unstudied before the middle of the 20th Century; there are neither old records nor old specimens (Shapiro, 1974a). The composition of the pre-European fauna is thus unknowable. If we examine the extant fauna, it is strikingly different from the faunas of the nearby foothills (Shapiro, 1975). There were three types of vegetation in the pre-European Valley: riparian forest, 'tule marsh' (dominated by graminiforms but with a rich — mainly perennial — herbaceous flora), and bunchgrass and bunchgrass-oak savanna. Of these, only riparian forest has relatively intact, substantial remnants today; bunchgrass is nearly extirpated. The butterfly fauna of riparian forest, while less diverse than in the foothills, is continuous with that of the canyons that feed the major rivers. The riparian butterflies that feed on woody hosts are multivoltine in both the foothills and the Valley, except for the genus *Satyrium* which is always univoltine. The vast majority of nonriparian foothill butterflies are either univoltine or spring-bivoltine, which is a typical phenology in Mediterranean climates; reproduction occurs during the brief period in spring when weather conditions are favourable and soil moisture is still high. (A few undergo summer adult diapause, a strategy familiar in rainfall — seasonal tropics.) In summer most of the vegetation senesces or becomes dormant. In the Valley, however, nearly all of the butterflies feeding on herbaceous vegetation are multivoltine, producing a succession of broods from early spring to late fall. This is only possible in a Mediterranean climate if at least some host plants are dependent on summer irrigation. These, however, are overwhelmingly alien taxa.

Were these butterfly species previously uni- or spring-bivoltine — multivoltinism only evolving in the past two centuries of human disturbance? It is probably significant that the butterflies in question are geographically widespread and are mostly multivoltine throughout their ranges. While the number of generations in multivoltine species may vary greatly, relatively few species display uni- and multivoltine ecotypes, and univoltinism is strikingly conservative in entire butterfly lineages. Except for *Papilio zelicaon*, none of these species has a univoltine ecotype in the foothills today, and several of them do not occur there at all. Shapiro (1980) argued that many multivoltines must undergo constant dispersal to colonize host plants in new sites. However, one can observe most of them maintaining stable populations on native host plants in montane-meadow habitats in California, where they regularly produce 2–3 broods per year. These hosts — or very close relatives — formerly existed in the tule marshes, before they were drained and used for agriculture. They can still be found in small remnant marshes in the flood-control bypasses and in wildlife preserves and hunting clubs. Most of the extant urban-suburban multivoltine butterfly fauna probably has its roots in the marshes, which provided a unique opportunity for multivoltinism in a Mediterranean climate before irrigation. Many of these species occur in wetlands in the Great Basin as well, where summer rain favours multivoltinism.

The Malvaceous feeders, except *S. melinus*, can still be found feeding on native *Sidalcea* in meadows. This plant is nearly gone in the Central Valley. The thistle-feeder *Phyciodes mylitta*, now ubiquitous in waste ground, maintains apparently stable populations on montane meadows and bogs where it feeds on native *Cirsium*. Its lowland native marsh host, C. *hydrophilum*, is now reduced to a single population of a few hundred individuals in a protected marsh. The Anise Swallowtail, *Papilio zelicaon*, still breeds rarely on native Apiaceae (*Cicuta* and *Oenanthe*) in relict marshes, but otherwise is dependent on naturalized aliens: *Conium* is only usable from March to June and thereafter the only common host is *Foeniculum*, which becomes essential to the persistence of the species. (There is a low level of oviposition on cultivated Apiaceae, but

these are not common enough to sustain a population in Davis.) *Foeniculum* is regarded as invasive and undesirable and is often a target of eradication campaigns (Bossard *et al*., 2000). In its absence, *P. zelicaon* — if it could persist at all — would probably be restricted in the Valley to relict wetlands, much as the related *Papilio machaon britannicus* is endangered and restricted to relict fens in England (Dempster *et al.*, 1976). The complex mosaic of *P. zelicaon* ecotypes in California is described by Shapiro (1995); it is the one clear cut case of phenological ecotypes in close geographical proximity, but even here there is a strong hint that multivoltinism antedates European colonization in California.

In Mediterranean California, the urban–suburban butterfly fauna is sharply delimited from nearby faunas by its dependence on irrigation. In more humid climates this is not the case, nor have the autochthonous plant communities been so thoroughly devastated as in the Central Valley. Thus rural faunas are richer than urban ones, while in the Central Valley the reverse is true. This leads us to ask, is the Davis fauna exceptionally dependent on aliens? Fifteen of the 32 Davis butterflies are also urban species in the eastern United States (Shapiro, 1966, 1974b; Shapiro & Shapiro, 1973), and these make up about half the urban fauna there. They are apparently just as dependent on alien hosts in the Middle Atlantic states, even without the irrigation restriction. This is hardly surprising, though in the eastern United States two obscure, specialist skippers have 'exploded' on naturalized hosts, and in California the skipper *Poanes melane* has become an abundant urban insect near the coast, while remaining a riparian wildland specialist inland (Shapiro, 1979; Emmel & Emmel, 1973; Shapiro & Shapiro, 1973). Strikingly, Shapiro (1998) has shown that even in the southernmost butterfly fauna on earth, in far-southern Patagonia, native butterflies are breeding on aliens in urbanized settings.

CONCLUSIONS

For many native-plant ideologues, aliens are inherently 'bad.' For many people, butterflies are inherently 'good.' Leithauser (2001) writes:

> The appeal of butterflies is so immediate, and so universal, that any attempt to 'explain' it can seem a little fatuous. Any child understands; they're spectacularly beautiful.

Urban and suburban dwellers seem to cherish butterflies even more than those who live in the country. But we are not going to restore native plant communities in urban contexts, and our urban butterflies are now deeply committed to a naturalized and cultivated alien flora. We cannot rid ourselves of the plants and keep our urban butterflies too. The costs of alien control in urban settings would be better spent buying any remaining habitat fragments containing native vegetation, and managing those. This would have a variety of beneficial effects, which at this late date might not extend to butterflies — but certainly would not hurt them.

Papilio zelicaon vies with the Monarch, *Danaus plexippus*, as the butterfly most often reared for the education and edification of children in California. If its weedy host *Foeniculum* is eradicated from urban areas, as is contemplated for San Francisco, the butterfly will go away. Is this a price we are willing to pay?

It is time we built such considerations into the alien equation.

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Appendix The Davis, California, butterfly fauna and its recorded host plants 1971–2001. Butterfly taxonomy from Shapiro (1974a and 1996); plants from Munz & Keck (1973) and *§§Hickman (1993); cultivated plants from Sunset (1996).

Butterfly	Host*	Host Category:†				
		NN	NW	CN	CE	NE
Monarch, *Danaus plexippus*	*Asclepias fascicularis*	x				
	Asclepias speciosa	x				
	Asclepias curassavica				x	
Mourning Cloak, *Nymphalis antiopa*	*Celtis australis*				x	
	Celtis occidentalis				x	
	Celtis sinensis				x	
	Ulmus americana				x	
	Salix babylonica				x	
West Coast Lady, *Vanessa annabella*	*Malva nicaeensis*					x
	Malva parviflora					x
	Malva neglecta					x
	Malva mauritiana				x	
	Alcea rosea				x	
	Malvella leprosa (= *Sida hederacea*)		x			
Red Admiral, *Vanessa atalanta*	*Soleirolia soleirolii*				x	
	Pilea microphylla				x	
	Pilea involucrata				x	
	Pilea depressa				x	
Painted Lady, *Vanessa cardui*	*Malva nicaeensis*					x
	Malva parviflora					x
	Malva neglecta					x
	Alcea rosea				x	
	Malvella leprosa (= *Sida hederacea*)		x			
	Plantago lanceolata					x
	Helianthus annuus				x	x
	Xanthium strumarium‡		x			
	Carduus pycnocephalus					x
	Centaurea solstitialis					x
	Cirsium vulgare					x
	Silybum marianum					x
	Lupinus succulentus		x			
	Lippia (= *Phyla*) *nodiflora*‡		x	x		
	Symphytum officinale				x	
	Borago officinale				x	
	Amsinckia '*intermedia*'		x			
West Virginia Lady, *Vanessa virginiensis*	*Gnaphalium chilense*		x			
	Gazania uniflora				x	
Buckeye, *Junonia coenia*	*Lippia* (= *Phyla*) *nodiflora*‡		x	x		
	Plantago lanceolata					x
	Plantago major					x
	Kickxia spuria					x
	Kickxia elatine					x
Mylitta Crescent, *Phyciodes mylitta*	*Carduus pycnocephalus*					x
	Cirsium vulgare					x
	Silybum marianum					x
Field Crescent, *Phyciodes campestris*	*Aster chilensis*	x		x		
Gray Hairstreak, *Strymon melinus*	*Eremocarpus setigerus*		x			

Appendix *continued.*

Butterfly	Host*	Host Category:†				
		NN	NW	CN	CE	NE
	Medicago sativa				x	x
	Lotus purshianus		x			
	Lotus corniculatus				x	x
	Trifolium repens				x	
	Melilotus alba					x
	Malva nicaeensis					x
	Malva parviflora					x
	Malva neglecta					x
	Alcea rosea				x	
	Malvella leprosa (= *Sida hederacea*)		x			
	Callistemon sp. (0)				x	
Great Purple Hairstreak, *Atlides halesus*	*Phoradendron flavescens* var. *macrophyllum*		x			
Purplish Copper, *Lycaena helloides*	*Rumex crispus*					x
	Polygonum arenastrum/ aviculare complex					x
	Polygonum persicaria					x
Great Copper, *Lycaena xanthoides*	*Rumex crispus*					x
Acmon Blue, *Plebeius acmon*	*Lotus purshianus*		x			
	Melilotus alba					x
	Polygonum arenastrum/ aviculare complex					x
Eastern Tailed Blue, *Everes comyntas*	*Vicia benghalensis*					x
	Vicia villosa					x
	Lathyrus jepsonii ssp. *californicus*	x				
	Lotus purshianus		x			
	Lotus corniculatus				x	x
Pygmy Blue, *Brephidium exile*	*Atriplex semibaccata*					x
	Salsola iberica/tragus complex					x
Silvery Blue, *Glaucopsyche lygdamus*	*Vicia benghalensis*					x
	Vicia villosa					x
	Lathyrus jepsonii ssp. *californicus*	x				
Orange Sulphur, *Colias eurytheme*	*Medicago sativa*				x	x
	Melilotus alba					x
	Trifolium repens				x	
	Vicia benghalensis					x
	Vicia villosa					x
	Lathyrus jepsonii ssp. *californicus*	x				
	Lotus purshianus		x			
	Lotus corniculatus				x	x
	Lupinus succulentus		x			
Cabbage White, *Pieris rapae*	*Lepidium latifolium*					x
	Cardaria draba					x
	Alyssum species				x	
	Brassica nigra					x
	Brassica kaber (= *Sinapis arvensis*)					x
	Brassica rapa				x	x

Appendix *continued.*

Butterfly	Host*	Host Category:†				
		NN	NW	CN	CE	NE
	Brassica oleracea				x	
	Hirschfeldia incana (= *Brassica geniculata*)					x
	Sisymbrium officinale var. *leiocarpum*					x
	Raphanus sativus					x
	Tropaeolum majus				x	
	Isomeris arborea§			x		
Checkered White, *Pontia protodice*	*Lepidium latifolium*					x
	Cardaria draba					x
	Brassica nigra					x
	Hirschfeldia incana (= *Brassica geniculata*)					x
	Raphanus sativus					x
Large Marble, *Euchloe ausonides*	*Brassica nigra*					x
	Raphanus sativus					x
Western Tiger Swallowtail, *Papilio rutulus*	*Platanus orientalis*				x	
	Platanus occidentalis				x	
	Platanus racemosa			x		
	Fraxinus velutina				x	
	Ligustrum japonicum				x	
	Ligustrum lucidum				x	
	Syringa vulgaris				x	
	Prunus amygdalus				x	x
Anise Swallowtail, *Papilio zelicaon*	*Foeniculum vulgare*					x
	Conium maculatum					x
	Daucus carota				x	
	Apium graveolens				x	
	Anethum graveolens				x	
	Petroselinum crispum				x	
	Ammi majus (0)					x
	Ammi visnaga (0)					x
Pipevine Swallowtail, *Battus philenor*	*Aristolochia californica*	x		x		
Sad Duskywing, *Erynnis tristis*	*Quercus lobata*	x		x		
	Quercus suber				x	
Sooty Wing, *Pholisora catullus*	*Celosia cristata*				x	
	Celosia argentea				x	
	Amaranthus albus					x
	Amaranthus blitoides					x
	Amaranthus retroflexus					x
	Amaranthus powellii					x
	Amaranthus hybridus					x
Least Checkered Skipper, *Pyrgus scriptura*	*Malvella leprosa* (= *Sida hederacea*)		x			
Common Checkered Skipper, *Pyrgus communis*	*Malva nicaeensis*					x
	Malva parviflora					x
	Malva neglecta					x
	Alcea rosea				x	

Appendix *continued.*

Butterfly	Host*	Host Category:†				
		NN	NW	CN	CE	NE
	Malvella leprosa (= *Sida hederacea*)		x			
Fiery Skipper, *Hylephila phyleus*	*Cynodon dactylon*				x	x
Field Skipper, *Atalopedes campestris*	*Cynodon dactylon*				x	x
	Paspalum dilatatum					x
Sandhill Skipper, *Polites sabuleti*	*Cynodon dactylon*				x	x
	Distichlis spicata	x				
Eufala Skipper, *Lerodea eufala*	*Cynodon dactylon*				x	x
	Echinochloa crus-galii					x
	Sorghum halepense					x
Number of butterfly species: 32						
Number with no native hosts in Davis: 13						
Number with only native hosts in Davis: 3						
Number with seasonal successions of hosts requiring use of an alien: 3						
Number of host records in each plant category:		9	18	7	49	78
Number of host species in each plant category:		7	10	6	38	43

Notes:
* (0) = oviposition only observed; suitability of plant for feeding/development unknown.
† NN = native to California, non-weedy.
NW = native to California, weedy.
CN = cultivated, native to California.
CE = cultivated, alien.
NE = naturalized alien.
‡ Status (native or naturalized) uncertain.
§ Native to south-east California deserts, introduced in Central Valley.