Revisiting the pre-European butterfly fauna of the Sacramento Valley, California

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Abstract. The modern butterfly fauna of the Sacramento Valley, California appears poorly-adapted to the climate and native vegetation, instead reflecting drastic changes to the landscape since Europeans colonized the area ~200 years ago. This paper attempts to reconstruct the ecology of the pre-European butterfly fauna, based on current interpretations of the vegetation.

Key words: host plants, exotic weeds, vegetation history, butterflies.

Introduction

The butterfly fauna of most of lowland cismontane California (west of the Sierra Nevada-Cascade axis) is very peculiar in two respects: it appears grossly mismatched with the climate in which it occurs, and it is largely dependent on non-native larval host plants (Shapiro, 2002; Graves & Shapiro, 2003). Nearly all the species making up this fauna are multivoltine, despite the fact that no rain typically falls from April through October and no native host plants are available in most habitats during that time. The adjacent foothill faunas are overwhelmingly uni- or at most bivoltine (Shapiro, 1975; Shapiro *et al.,* 2003) thus matching the seasonal availability of their native hosts. But most of the Valley fauna today breeds on naturalized exotic plants, whose availability in summer depends on water supplied by human activity. Over 30 years ago I profiled the extant Sacramento Valley fauna as then understood and attempted to place it in an historical and geographical context (Shapiro, 1974a). Our understanding of pre-American ecology in the Sacramento Valley has improved substantially since then. This paper attempts to review the probable history and sources of this fauna in that updated context.

History of Sacramento Valley vegetation reconstructions

Plant ecologist Michael Barbour has said that coastal and interior [lowland] California "within 200 years experienced one of the most complete human-caused landscape transformations in the world." While this is certainly true, there is no unanimity as to the nature of the Sacramento Valley landscape or its vegetation before European colonization. Shapiro (1974) relied heavily on the characterizations provided by Thompson (1971), Sculley (1973) and Bakker (1971). All of these authors in turn accepted the then-conventional wisdom that much of the Valley had been a bunchgrass grassland dominated by *Nassella* (then put in *Stipa*) *pulchra*. This was the area identified as "alluvial plains—formerly savanna" on Shapiro's Fig. 2. Following the conventional wisdom, the accompanying text states that "Most of the bunchgrass prairie was put into pasture or under the plow; either way, the native bunchgrasses were competed out of existence by introduced annual grasses, mostly from Europe. With the bunchgrasses most of the native flora, both annual and perennial, also succumbed, to be replaced by weedy… aliens." But was there ever such a bunchgrass prairie and if not, why was it thought to have existed?

As late as 1977, Heady was promoting the bunchgrass prairie concept, but by 1981 serious questions had emerged. Bartolome and Gemmill (1981) argued that the ecological characteristics of *N. pulchra* made it an improbable dominant species. Wester (1981) could find no contemporary documentation to support the concept in the San Joaquin Valley. Holland and Keil (1989, 1995) questioned its validity. Hamilton (1997) examined the issue and concluded that – like many erroneous notions in North American plant ecology – the bunchgrass prairie concept grew out of Clementsian dogma rather than direct observation or even indirect inference. Clements himself (1920, 1934) had interpreted persistent stands of *N. pulchra* along railroad rights-of-way as relicts of a previously dominant condition, much as relicts of tall-grass prairie persist along (unsprayed) railroad corridors in the Midwest where much of the nearby landscape was agriculturalized in the 19th Century. In addition to

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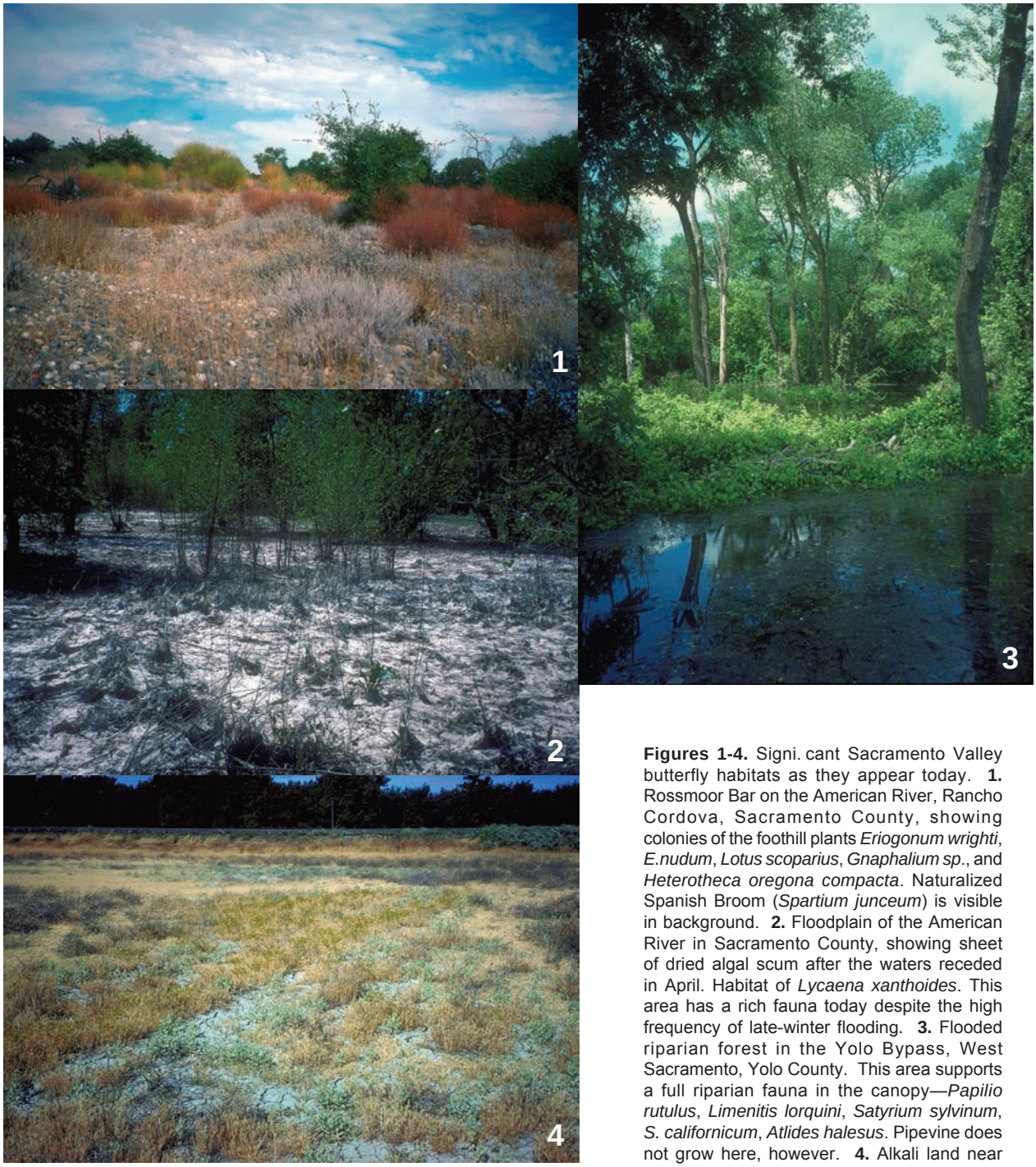

Figures 1-4. Signi. cant Sacramento Valley butterfly habitats as they appear today. **1.** Rossmoor Bar on the American River, Rancho Cordova, Sacramento County, showing colonies of the foothill plants *Eriogonum wrighti*, *E.nudum*, *Lotus scoparius*, *Gnaphalium sp*., and *Heterotheca oregona compacta*. Naturalized Spanish Broom (*Spartium junceum*) is visible in background. **2.** Floodplain of the American River in Sacramento County, showing sheet of dried algal scum after the waters receded in April. Habitat of *Lycaena xanthoides*. This area has a rich fauna today despite the high frequency of late-winter flooding. **3.** Flooded riparian forest in the Yolo Bypass, West Sacramento, Yolo County. This area supports a full riparian fauna in the canopy—*Papilio rutulus*, *Limenitis lorquini*, *Satyrium sylvinum*, *S. californicum*, *Atlides halesus*. Pipevine does not grow here, however. **4.** Alkali land near Woodland, Yolo County: home of *Brephidium exile*, *Pyrgus scriptura*, *Polites sabuleti*.

the railroad corridors, the most important supposed bunchgrass relict is located at Maine Prairie Road near Dixon, Solano County, at the northern edge of the Montezuma Hills– a site which has never been plowed. Wester (1981) noted that this site is unusual in being strongly influenced by the “sea breeze” coming through the Carquinez Strait gap in the Coast Range to the west, and thus cooler and moister than most

of the Valley, an argument reinforced by Dremann (1987) who noted that many species are "anomalously" distributed in agreement with this maritime influence. Holstein (2001) argues that the character of the soil (light sandy loam) at Maine Prairie Road may be the principal factor favoring dominance by *N. pulchra*, or interact with the sea breeze to do so. In any case, one's ability to generalize to vast areas of the Sacramento (and San Joaquin) Valleys where there is no corroborative evidence, either historical or contemporary, from these tiny putative relicts is called seriously into question.

From the standpoint of butterfly biology, the validity of the bunchgrass prairie concept is a serious issue. Echoing the Clementsian view, Shapiro (1984) raised the following question: "The most striking, and rather surprising, absence in the Valley grassland fauna is that of a set of specialist Satyrinae or Hesperiidae associated with the native bunchgrasses. The near-extermination of these grasses leaves little hope of finding relicts of a (totally hypothetical) pre-American fauna." Most of the temperate grasslands of both the Northern and Southern Hemispheres have distinctive faunas of grass-feeding butterflies belonging to the two families cited above (usually one or the other is clearly dominant). Shapiro (1984) observes of Patagonia: "The large rivers coming down from the Andes and crossing the vast treeless plateaus of Patagonia are fringed with a narrow band of riparian forest, but there is essentially no butterfly fauna there… The great majority of species are Satyrids that live not in the moist river bottoms but on the steppe proper, feeding on the bunchgrasses." There is no hint that either Satyrids or Hesperiids evolved to exploit the supposed bunchgrass prairie of the California Central Valley. This could reflect it being too recent as a community, a question best addressed by examining what little palynological record exists (although many Gramineae are not distinguishable at the generic level). But it could also reflect its not having been widespread or abundant at all.

The bunchgrass-feeding skippers *Hesperia lindseyi* Holl. and *H. columbia* Scud. occur in both the Coast Range and Sierra Nevada foothills but not on the Valley floor, nor has either been found in the Sutter Buttes. Different subspecies of a third *Hesperia, H. colorado* Scud. (formerly put in *H.comma* L.), occur on opposite sides of the Valley. In the absence of any relicts, the hypothesis of former cross-Valley contacts, as against dispersal along the respective mountains without crossing the Valley, might be testable using molecular phylogeography.

If bunchgrass prairie was not the dominant vegetation in this region, what might have been? The most penetrating and thoughtful treatment of this question, based on both contemporary and historical evidence, is by Holstein (2001). His analysis has been bolstered by the publication of the book *California's Fading Wildflowers* by Richard Minnich (2008) which, however, does not cite Holstein or Dremann though it cites the other sources cited above and many others. Minnich's focus is primarily farther south than the Sacramento Valley, however. Summing the contemporary vegetation literature, we are led to a somewhat different picture of what the butterfly fauna of the pre-European Sacramento (and especially San Joaquin) Valley might have been.

A new interpretation of the vegetation

Enormous masses of colorful wildflowers are bound to attract attention. They are the aspect of Californian native vegetation most often noted by both early Spanish and later American explorers and colonists, but they are not the only ones. These people were intensely interested in the potential uses of the landscapes through which they passed, and routinely made note of their value as grazing land ("*pasto*" or "*zacate*"). If there were extensive tracts of bunchgrass prairie, one would expect these to be noted. Unlike the hard, coarse Patagonian bunchgrasses ("*coirones*"), Californian bunchgrasses were soft and palatable to European livestock—a fact often adduced to account for their elimination and replacement by the coarse and early-desiccating Mediterranean annuals.

In fact, as demonstrated exhaustively by Minnich (2008), bunchgrass prairie is undocumented in the Central Valley. Depending on the season, the early chroniclers report either immense blooms of [annual] wildflowers – which Minnich refers to as "forbfields" – or, after late April or May, no living vegetation at all, or "summer desert" or "summer barrens." The pattern near the coast was quite different, with green vegetation and good pasture persisting essentially year-round. The *diseño* (map) of Rancho Tolenas in Solano County describes the slopes above the Sacramento River floodplain as *lomas muertas* (dead, i.e. barren, hills). The *diseño* for Rancho de los Molinos likewise describes the uplands as *tierra estéril* (sterile land), and so on. The introduction and naturalization of exotic annuals made relatively little difference to this pattern in the absence of irrigation. In 1844 Charles Wilkes described the Sacramento Valley as "barren and unproductive…affording but little good pasture." John Muir wrote of the Central Valley in 1904 that "The shrunken mass of leaves and stalks of the dead vegetation crinkle and turn to dust beneath the foot, as if it had been literally cast into the oven." Clarence

King (1915) described the Valley as "a plain slightly browned with the traces of dried herbaceous plants." These sorts of descriptions apply to precisely the areas treated by Clementsians as bunchgrass prairie and so mapped in my 1974 Fig.2. Actual bunchgrass grasslands are documented in the foothills (where they still occur) (Fremont, 1848; Beetle, 1947). The annual forb flora that made up these ephemeral blooms broadly overlaps the surviving flora of vernal pools in the Central Valley. The vernal pool biotope, even when nearly intact and extensive as at Jepson Prairie, Solano County, at Vina, Butte County, or various locations in eastern Sacramento County, has no butterfly fauna at all, a fact documented by Shapiro and his graduate student Carrie Shaw in field surveys and remarked upon in Shapiro (1984): "The surviving vernal-pool communities in the Sacramento Valley have their specialist bees, but no butterflies." I speculated elsewhere (Shapiro, 1975) that this was due to the year-to-year variability in the timing of a very short window of resource availability. (There are a few moths, especially Heliothentine Noctuidae feeding on either tarweeds (Asteraceae) or Scrophulariaceae *sensu lato*, successfully adapted to this very rigorous regime). There is no reason to believe the forbfields of the pre-irrigation Valley had a butterfly fauna, either. We are thus presented with the paradox of a landscape covered with brightly colored flowers, and no or very few butterflies among their visitors. Tarweeds (Asteraceae: *Holocarpha virgata* and species of *Hemizonia*), which are summer –blooming annuals, are today codominant with Mediterranean grasses over large areas that have never been plowed due to poor soils or hardpan. They are remarkably absent from the antique descriptions of the summer uplands, yet they must have been there. Unpublished observations by Shapiro in the 1970s in what is now the Stone Lakes National Wildlife Refuge near Elk Grove, Sacramento County, and in other areas with summer-dry tarweed-annual communities near Sacramento, consistently demonstrated a dry-season fauna of three butterfly species: *Junonia coenia* Hubner, *O. sylvanoides* (remarkably consistently associated with the summer-blooming forb *Trichostema lanceolatum*, Lamiaceae, to which it uniquely among our butterflies is adapted as a pollinator), and, when present regionally (as it often is not), *Pontia protodice* Bdv. & Le C. Of these, as discussed below, only *O. sylvanoides* was certainly an historic presence. One additional surviving member of the dry-summer upland flora is the Turkey Mullein, *Eremocarpus* (or *Croton*) *setigerus* (Euphorbiaceae), used as a nectar source by various butterflies and as a (strongly seasonal) larval host by the weedy multivoltine *Strymon melinus pudica* H. Edwards, which might have had alternate, early-season hosts in the late winter-early spring forbfields.

Alternatively, one can envision highly-mobile butterfly species moving into the seasonal forbfields to exploit the abundant hostplant resources there, and then moving on. The one species that unambiguously employed, and still employs, this strategy is *Vanessa cardui* L. Shapiro (1973, 1974b, 1980) posited a regular rhythm of up- and downslope colonization by multivoltine species in pursuit of host plants in good condition. The biggest problem with such a scenario for the forbfields is getting colonists in place in late winter-early spring (since there had been no previous fall generation there). *V. cardui* is a mass migrant, but the vast majority of weedy butterflies disperse as singletons.

Holstein (2001) makes what for me is a compelling case that the dominant graminiforms of uplands in the pre-European Valley were not bunchgrasses but rhizomatous clonal species which dominated the understory of oak savanna and ecotones between the summer-dry uplands and wetlands and riparian forest. Of these the grass *Leymus* (formerly *Elymus*) *triticoides* and the sedges *Carex barbarae* and *C. praegracilis* were probably most important. Relict stands of these plants are still fairly common and able to hold their own against naturalized exotics even in my own study sites (North Sacramento, West Sacramento, Rancho Cordova and Willow Slough). *Leymus* and *Phalaris* are both used as hosts today by at least two native Valley butterflies, *Coenonympha tullia california* Westwood & Hewitson and *Ochlodes sylvanoides* Bdv., both of which are in decline in synchrony with habitat conversion and urbanization in the Valley.

Out of the tules?

In Shapiro (2002, 2003) and Graves and Shapiro (2003) as well as in *Field Guide to Butterflies of the San Francisco Bay and Sacramento Valley Regions* (2007), I consistently argue that the weedy, multivoltine butterfly fauna of the modern Sacramento Valley must be derived from that of the tule marshes that previously occupied extensive parts of the Valley, mainly to the east. The basic argument is that these butterflies (a) are multivoltine elsewhere and are thus unlikely to have evolved multivoltinism in the 200 years since the Valley was colonized by Europeans and (b) today feed on plants naturalized from abroad but closely related to autochthonous plants of the tule marshes, many of which are still used occasionally today in remnant wetland habitats. A few additional remarks on the marshes and the historic flooding regimes of the Valley seem useful in evaluating this scenario.

Flooding was a recurrent phenomenon in the 19th-Century Sacramento Valley. In autumn of 1837 – 12 years before the Gold Rush–Sir Edward Belcher explored the Sacramento River drainage before the onset of the rains. He wrote: "All the trees and roots on the banks afford unequivocal proofs of the power of the flood-streams, the mud-line on a tree we measured exhibiting a rise of ten feet above the present level, and that of recent date… During the rainy season, which commences about the middle of November and terminates about the end of February, the river is said to overflow its banks, when its impetuosity is such that navigation is then impossible. The annual rains do not, however, of necessity inundate these low lands, but in severe seasons, after heavy falls of snow [in the Sierra Nevada], they produce one immense sea, leaving only a few scattered eminences…as so many islets or spots of refuge."

Charles Wilkes (1849) commented that "a large part of [the Sacramento Valley] is undoubtedly barren and unproductive, and must forever remain so. The part that is deemed good soil is inundated annually, not for any great length of time, yet sufficiently long to make it unfit for advantageous settlement." And George Derby, who famously surveyed and mapped the region in 1849, said of the Valley between Cache and Putah Creeks (i.e. in the vicinity of modern Woodland and Davis, Yolo County): "The whole country between the creeks is liable to overflow, and is very dangerous to attempt travelling after a heavy rain. The 'tule' swamp, upon the western bank of the Sacramento, extending to the vicinity of Butte Creek, and occurring occasionally above, is from three to six miles in width, and impassable for six months out of the year." It is important to note that there are abundant historical records of Sacramento Valley flooding well before the practice of hydraulic mining led to downstream siltation of the riverbeds and thus exacerbated the problem (Kelley, 1959, Thompson, 1960).

The location of the tule marshes was dictated by the unusual topography of the Valley, well described by Thompson (1960). During their overflows the rivers laid down "natural levees" raised several (5-20) feet above the surrounding plain. Tributary creeks were dammed by them and unable to reach the river directly. Their waters thus ponded up behind the natural levees, creating extensive wetlands which in the wettest years would not dry out at all. These were the tulares, named from the Spanish word for "reeds." In very wet years the tributary streams might breach the natural levees, or the flows coming down the Sacramento River might overwhelm them. The entire system was clearly very dynamic from year to year. As early as 1848, radical reclamation projects were proposed for the flood basins. In 1850 T. Butler King advanced specific proposals to that end. The history of implementation is complex and involves political rivalries, feuds, and violence (Kelley, 1989). Ultimately most of the marshes were drained and a system of levees and fixed weirs created which enabled the former flood basins to be used as diversion channels during periods of heavy flow, thereby sparing urban and agricultural land from flooding; during the dry season their rich alluvial soils could be farmed. This is the system in place today, and from its dynamics we can draw inferences about the biology of butterflies in the tule marshes of yore.

Half of my West Sacramento study site (see http://butterfly.ucdavis.edu for maps and description) lies in the Yolo Bypass, one of the diversion channel successors to the tules. During the period of my studies there, the Bypass portion has been unflooded in very dry years and flooded continuously for as long as six months in very wet ones. The non-agricultural plant communities in the floodplain include substantial amounts of native riparian vegetation, as well as many naturalized exotics. The composition of the annual vegetation is extremely labile and related to the timing of flooding and drying. Although flooding has occurred to a depth of 19 feet (5.7+ m), there are potential refuges for overwintering individuals of at least some species, in taller trees and on elevated roadway and railway supports. Flooding to a depth of 2 m or more which persists more than a few weeks appears to cause widespread mortality but only very local extinctions, while the most extreme flooding events (as in the winter of 2005-06) appear to eradicate the entire butterfly fauna over a larger area. The site is then rapidly reinvaded from adjacent upland habitats and typically experiences very rapid population growth and a multivoltine-butterfly "bloom" by late in the same season, perhaps favored by the temporary local eradication of parasitoids with poorer colonizing ability than the butterflies themselves. In the Suisun Marsh, Solano County, flooding, while frequent, is less extreme and very few (even local) extinctions have been observed in 37 years. The persistence of specialized wetland butterfly faunas elsewhere (in the humid Northeast, for example, or in the British and Low Countries fenlands) demonstrates that such faunas are well-adapted to ordinary seasonal inundation cycles. The most extreme events must have adverselyimpacted the pre-American butterfly fauna of the tule marshes, without however being catastrophic to them. It should be noted parenthetically that we know next to nothing about how most wetland butterflies survive inundation.

The importance of river bars

Sand and gravel bars on the accreting sides of rivers and streams probably have had an important role as butterfly habitats in the Valley, providing a combination of strong sunshine and ready availability of near-surface water. In the contemporary Valley such bars routinely provide habitat for foothill plants otherwise not seen in the Valley today, including *Eriogonum umbellatum*, *E. wrightii*, *Penstemon heterophyllus*, *Keckiella breviflora*, *Mimulus aurantiacus*, *Mentzelia laevicaulis*, *Heterotheca oregona compacta*, *Baccharis viminea*, *Brickellia californica*, and even good-sized shrubs such as *Philadelphus lewisii*. These are mostly plants demanding a rocky or gravelly substrate, otherwise unavailable in the Valley where bedrock lies buried under thousands of feet of alluvium. Such species as *Callophrys dumetorum*, *Plebejus acmon*, *Strymon melinus* and *Erynnis persius* breed in such habitats today and may have been almost completely dependent on them in the past. This is true despite their inherent instability and vulnerability to inundation; river bar species must be good colonizers. River bars also may have provided corridors for foothill species to come down to the Valley floor: *Papilio eurymedon*, *Anthocharis sara*, *Euphydryas chalcedona*, *Chlosyne palla*, and *Ochlodes agricola* still do so without, however, being breeding residents below the lowest foothills. *E. chalcedona* breeds down to Folsom and Fair Oaks, Sacramento County, and strays from the west have been taken along the Putah Creek channel at Davis, Yolo County, but the Sierra and Coast Range foothill populations differ in a variety of ways including larval coloration, suggesting that despite their close proximity they were not in contact across the Valley floor: perhaps the tule marshes were an impenetrable barrier to them. Host plants of *Satyrium saepium* Bdv. (*Ceanothus*) and *S. tetra* Edw. (*Cercocarpus betuloides*) and of *Philotes sonorensis* Feld. & Feld. (*Dudleya*), *Mitoura johnsoni* Skin. and *M. spinetorum* Hew. (*Arceuthobium*) all occur on the lowest foothills but there is no evidence they, or the butterflies, ever existed on the Valley floor. Molecular phylogeography, as earlier noted, offers promise of testing hypotheses of prior connectivity across the Valley by what are today foothill species.

What was where, and doing what?

Based on the reinterpretation of the Sacramento Valley vegetation, here are scenarios for the pre-European ecologies of the resident butterfly species. Like much of "environmental history" or "Historical ecology" (Egan & Howell, 2001), these are at best informed guesses—but perhaps better than taking the existing fauna as an ahistorical "given." When necessary, the taxonomy has been modified from Shapiro (1974).

Danaus plexippus L. May have bred seasonally in the tules or along streams on *Asclepias fascicularis*. Other species of Milkweeds were certainly present in the foothills and coastwise. *A. speciosa* occurs today in riparian areas and may have in pre-American time.

Coenonympha tullia california Westw. & Hew. In rapid decline today, but probably previously widespread in rhizomatous-grass riparian ecotones in the past.

Cercyonis pegala boopis Behr. Not recorded in the Valley today, but very likely to have occurred along streams and ecotones historically.

Speyeria callippe Bdv. Probably widespread where Johnny Jump-Up, *Viola pedunculata*, occurred, in vernal pool and forbfield areas. Possibly now extinct in the Valley.

Speyeria coronis Behr. Given its demonstrated capacity to reach the Valley, may also have been present in pre-American time, presumably also on Johnny Jump-Up.

Phyciodes campestris Behr. Probably common in the Delta and in the tules, with *Aster chilensis*.

Phyciodes mylitta Edw. Probably mostly (or entirely) a wetland species on native thistles (*Cirsium*). Until the introduction of weedy thistles this species would have had no upland summer hosts available.

Polygonia satyrus Edw. Essentially unchanged: tule marsh and riparian forest with its host the native nettle *Urtica holosericea*.

Nymphalis antiopa L. Riparian, river bars, and marshlands, on Willow (*Salix*).

Nymphalis milberti Latr. Riparian and marshlands, on *Urtica holosericea*.

Vanessa atalanta L. Riparian and marshlands, on *Urtica holosericea*.

Vanessa virginiensis Dru. Riparian and marshlands, river bars, on native everlastings, mainly *Gnaphalium*.

Vanessa annabella Field. Riparian and marshland, on *Urtica* and the native mallow *Sidalcea*. Possibly in alkali

lands on *Malvella leprosa*.

Vanessa cardui L. Everywhere, breeding unimpeded on native hosts (Asteraceae, Malvaceae, Boraginaceae) in spring forbfields and then moving on. This seasonal rhythm is completely consistent with its migratory pattern, and helps to explain why summer breeding is so rare and spotty in the Valley today.

Junonia coenia Hbn. It is not certain that this species was present in the Valley, but if so it was probably as a migrant or sporadic breeder. If *Lippia* (*Phyla*) *nodiflora* (Verbenaceae) is native—the matter remains in dispute—it could have provided a year-round resource in riparian habitats. Otherwise, all its potential native hosts (Scrophulariaceae in the broad sense) are highly seasonal. Other than *Lippia*, all its dry-season hosts today are naturalized exotics.

Limenitis lorquini Bdv. Riparian and marshlands, probably river bars, on *Salix*.

Adelpha bredowii californica Butl. Oak woodland along the margins of the Valley, and in riparian forest.

Atlides halesus Hbn. Riparian and oak woodland, on *Phoradendron*.

Strymon melinus pudica H. Edw. This weedy species might have been able to utilize a seasonal succession of hosts to be multivoltine in forbland and perhaps on river bars, though necessarily highly mobile. Candidate hosts include *Lotus purshianus*, *Eremocarpus setigerus*, and in alkali lands, *Malvella leprosa*.

Satyrium californica Edw. Restricted to oak woodland and riparian forest.

Satyrium sylvinum Bdv. Riparian, river bars and marshland, with *Salix*.

Satyrium auretorum Bdv. Oak woodland and oak-rich riparian forest.

Incisalia iroides Bdv. Possibly in riparian and tule marsh on Dodder (*Cuscuta*) and/or on uplands on Soap Plant (*Chlorogalum pomeridianum*). Both are used regionally today.

Callophrys dumetorum Bdv. Possibly in uplands and river bars or even forblands on either *Lotus scoparius* or *Eriogonum nudum*.

Lycaena xanthoides Bdv. Much of the distribution of this species today depends on the presence of the introduced weed *Rumex crispus*, which is tolerant of drier conditions than the native *Rumex*. Its historic distribution was probably restricted to the tule marshes where native hosts would have occurred.

Lycaena helloides Bdv. The same restriction applies to this species; its native hosts (*Rumex, Polygonum*) are wetland species, while its weedy exotic hosts today allow it to occupy drier habitats.

Brephidium exile Bdv. Presumably restricted to alkaline and saline moist habitats where native hosts (*Suaeda, Salicornia, Sesuvium*) occur. It would be so restricted today in the absence of the roadside weed *Salsola*.

Everes comyntas Godt. Although it has been suggested that this species is an introduction, there is no solid evidence to support that claim. If it was present in pre-European times it could have existed in riparian habitat, using either native perennial *Lathyrus* or annual *Lotus* (e.g., *purshianus*) as hosts in various generations. *Lathyrus jepsonii* var. *jepsonii* is a marsh plant.

Plebejus acmon Westw. & Hew. As with *Callophrys dumetorum*, possibly in uplands, river bars and forblands with *Eriogonum nudum* and/or *Lotus* species. Also possibly with *Lotus scoparius* and/or *Eriogonum wrightii* on river bars.

Plebejus icarioides Bdv. I collected one specimen in West Sacramento in 1973. At that time the perennial lupine *Lupinus formosus* was still fairly common on the Valley floor, mostly along railroad rights-of-way. It is now nearly extinct regionally. This is a host plant of *P. icarioides* in the hills in Solano County and I consider it likely that it supported this butterfly until fairly recently in grassland and forbland on the Valley floor.

Holstein (2001) says: "In valley and foothill prairie remnants with soils similar to those most suitable for bunchgrasses another forb, *Lupinus formosus*…is frequent… It occurs at Stone Lakes refuge away from *Leymus triticoides* on somewhat sandier sites, is frequent on Delhi sands in Merced County, and also occurs on steep Coast Range foothills north of Fairfield in Solano County." I did not find *P. icarioides* at Stone Lakes in the 1970s, nor in the early 2000s.

Glaucopsyche lygdamus Dbl. Possibly occurred in tule marsh or riparian forest with native perennial *Lathyrus*, or with *Lupinus formosus* on sandy soils, or perhaps with annual lupines such as *L. succulentus* in forbfields. In

southern California this species sometimes breeds on *Lotus scoparius*. It does not use this plant here today, but if it did previously it could have occurred with it on river bars.

Celastrina ladon echo Edw. Status on Valley floor very uncertain, but if it did occur it would have had to have been in riparian forest, perhaps on shrubby dogwood (*Cornus*) and/or California Buckeye (*Aesculus californica*). It is not clear how deeply Buckeye penetrated the Valley floor in riparian corridors. Another host, *Ceanothus cuneatus*, occurs in riparian forest to the lowest foothills, but not on the Valley floor today.

Apodemia mormo Feld. & Feld. It is not inconceivable that the Mormon Metalmark occurred on sandy soils and/or river bars with *Eriogonum nudum* and/or *E. wrightii*—perhaps even in forbfields where these plants provided a second wave of bloom in late summer or autumn.

Battus philenor L. Riparian forest with *Aristolochia californica*, as today.

Papilio zelicaon Luc. Almost certainly a tule marsh species, where hosts capable of supporting more than one generation occurred – *Cicuta, Oenanthe*.

Papilio rutulus Luc. Riparian forest, where preferred hosts *Platanus, Fraxinus* and *Salix* occur, along with preferred nectar source *Cephalanthus*.

Papilio multicaudatus Kirby. Riparian forest, probably with *P. rutulus*.

Pontia protodice Bdv. & Le C. Although a dryland-adapted species, the occurrence of the Checkered White in the Central Valley today is dependent on naturalized hosts (*Hirschfeldia incana*, *Lepidium latifolium*). There are no summer hosts in the native flora, so it is likely this species was not a breeding resident in pre-European time.

Euchloe ausonides Bdv. The only native Crucifer with suitable characteristics (growth form, stature) to be a pre-European host is *Guillenia lasiophylla*, now a rare plant mostly confined to railway rights-of-way, but probably a fairly common component of forbfields and, given its soil preferences, of any bunchgrass prairie that did exist. As strictly a spring species, this Pierid was well-adapted to the Valley climate.

Colias eurytheme Bdv. Status uncertain. The Orange Sulphur could have been resident in the Valley by changing its host plant with almost every generation, and being highly mobile. It also could have undergone a regular seasonal altitudinal migration, of which hints persist today.

Zerene eurydice Bdv. Riparian forest, with its host *Amorpha californica*, now nearly extinct on the Valley floor.

Epargyreus clarus Cramer. Riparian forest with *Amorpha californica* and possibly *Lathyrus* and/or *Lotus crassifolius*.

Pyrgus scriptura Bdv. Despite the recency of the oldest museum records, I am treating this as native, in alkali lands with its sole host *Malvella leprosa*.

Pyrgus communis Grote. The ubiquity of this species today is an artifact of naturalized weedy hosts. In pre-European times it would have been restricted to *Malvella leprosa* in alkali lands and *Sidalcea* in the tule marshes; it could not have been multivoltine on ephemeral forbland mallows.

Pholisora catullus Fabr. Status uncertain; it is not clear which, if any, *Amaranthus* species occurred in the pre-European Valley, and in what habitats.

Erynnis persius Scud. In sandy areas and on river bars, with *Lotus purshianus*, and in riparian habitat with perennial *Lathyrus*.

Erynnis propertius Scud. & Burg. Riparian forest with oaks.

Erynnis tristis Bdv. Riparian forest with oaks.

Atalopedes campestris Bdv. Status uncertain; may not be native in Central Valley. Now too human-associated to infer original habitat associations.

Ochlodes sylvanoides Bdv. Riparian forest, tule marsh, and ecotones; bunchgrass areas; relationship to summer forbs today indicates a long association.

Ochlodes yuma Edw. Despite claims that this is an introduction in cismontane California, this species is treated here as native in the Delta and Suisun Marsh and perhaps more widely in the pre-European Valley, with *Phragmites*.

Polites sabuleti Bdv. Alkali and saline areas and possibly sandy soils and river bars, with the native perennial

turfgrass *Distichlis spicata.*

Poanes melane Edw. Riparian forest; native hosts unidentified.

The following species are omitted from this treatment as presumptive introductions since European colonization: *Agraulis vanillae* L., *Pieris rapae* L., *Hylephila phyleus* Dru., *Lerodea eufala* Edw.

This is a postulated fauna of 53 species. Of these four (*C. p. boopis, S. coronis, P. icarioides, A. mormo*) are hypothetical; three (*E. comyntas ,P. scriptura, O. yuma*) have been claimed by some authors to be non-native but are assumed here to be native; and five (*J. coenia, P. protodice, C. eurytheme, P. catullus, A. campestris*) do not have well-defined pre-American host relationships, and may not have been resident. This leaves 41 species believed to be unambiguously autochthonous in the Valley. When these are broken down by inferred pre-European habitats (a species may have several), they cluster as follows: Riparian 29 (of which 6 require Oak), Tule marsh 19, River bars 10, Forbfields 7 (some with reservations), Alkali lands 6, Bunchgrass prairie/sandy soils 3. The role of summer water availability in shaping this fauna is obvious. Equally obvious is that the existence of bunchgrass prairie was never necessary to explain the characteristics of the Sacramento Valley fauna. It was, in fact, irrelevant.

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