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Mediterranean Climate and Butterfly Migration: An Overview of the California Fauna

by
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„I find," said 'e, „things very much
as 'ow I've always found,
„For mostly they goes up and down or else
goes round and round."

– PATRICK REGINALD CHALMERS,
Roundabouts and Swings

California has been getting drier for several million years. The general floristic consequences of the evolution of a Mediterranean climate on the Pacific Coast since the Miocene are well known. AXELROD (1977) wrote: „... many taxa disappeared from the region as summer rainfall gradually decreased adaptation to the emerging Mediterranean climate was chiefly physiological. This probably was accomplished by shifting germination and growth into the moister and cooler part of the year." Some woody genera, such as *Arctostaphylos* (Ericaceae) and *Ceanothus* (Rhamnaceae), underwent bursts of speciation, but most of the adaptive radiation accompanying Mediterraneanization of the California climate took place in herbaceous groups. The directional climatic change that so profoundly altered the California flora and vegetation inevitably had pervasive impacts on the fauna as well, but these have been for the most part ignored by zoologists.

What are the climate-related problems faced by a butterfly in contemporary California? They are at two levels: the direct animal – environment interface, and mediated through plants. Consider a mordant summary of the climate by MAJOR (1977): „The typical Californian climate combines the very worst features of arid and humid climates. It is extremely hot and arid in summer cool and humid in winter. The supply of water and the need for water are exactly out of phase The growing season is limited by the cool temperatures of winter as well as the summer drought. Native vegetation is lush in the spring, when higher temperatures occur temporarily with adequate water supplies; it is desiccated or fails to grow in summer no anomalies, no compensatory features, a desert in summer, a sodden, dripping landscape in winter, a glory of wildflowers in spring."

In brief, a butterfly in lowland California can escape the summer drought either in time, by diapause, or in space, by migration. Both phenomena occur; between

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them, they circumscribe the options available to all but a small fraction of the fauna.

Univoltinism and Diapause

Lowland California is one of RAUNKIAERs therophyte climates: annuals make up a high percentage of the native flora. Most are winter-spring annuals, though a few flower in late summer (some Chenopods and tarweeds, for example). Spring annuals escape the seasonal drought by rushing through their life cycle in a few weeks, producing seeds with a high dormancy potential and shutting down „for the duration." The spring-annual life cycle is very common among California herbs, especially Cruciferae, Leguminosae, and Compositae, but only a handful of butterflies specializes on them. In the foothills, *Pieris sisymbrii* and *Euchloe hyantis* use endemic annual *Streptanthus* (Cruciferae), mostly on ultrabasic soils. In the valleys, *Euchloe ausonides* – which has now accommodated itself to weedy European Crucifers – probably used to feed on the native *Thelypodium lasiophyllum*. That's it. There are no special butterflies in the distinctive vernal pool habitats of the Sacramento Valley. Often there are no butterflies at all.

The herbaceous perennial flora is also primarily vernal and ephemeral. A much larger segment of the lowland butterfly fauna uses such plants, whose occurence is considerably more predictable in both space and time than is true for the annuals. The greater part of the lowland California fauna derived from moist-temperate Holarctic sources (Arcto-Tertiary) falls here: *Thorybes pylades* and *Glaucopsyche lygdamus* (on *Lathyrus*), *Pieris napi* and *Anthocharis sara* (on *Dentaria*), *Papilio indra* and *P. zelicaon* (in its pre-*Foeniculum avatar*, SIMS, 1980) (on *Lomatium*), etc. All are vernal-univoltine or (*napi, sara*) partially bivoltine, synchronized with their hosts; all grow extremely rapidly as larvae, only to spend 10 or 11 months in diapause (generally as a pupa). For such species, survival in a Mediterranean climate entailed ad shift from physiological tolerance of cold and desiccation to tolerance of heat and desiccation. The reserve seems to have happened readily in the colonization of the Sierran alpine zone by plants (CHABOT and BILLINGS, 1972). In Californian *P. napi*, SHAPIRO (1975a, 1977) has found that the genetic basis for both multivoltinism and polyphenism remains intact even in univoltine-monophenic populations, but thresholds for diapause induction have been shifted to assure virtually 100 % pupal dormancy.

The woody flora is strongly seasonal too: „There is generally a strong synchronization of vegetative growth, although reproductive activity may be asynchronous. This generalization is particularly valid for the Californian evergreen shrubs, all of which have a strong spring-growth period" (MOONEY et al., 1977). *Satyrium saepium* and *tetra, Erynnis pacuvius*, and *Papilio eurymedon* and the moth *Saturnia mendocino* are all chaparral univoltines showing this phenology.

Multivoltinism and Horizontal Dispersal/Migration

There are few California butterflies which are multivoltine and can stay in one place all year. All are found in riparian forest: *Papilio rutulus* and *P. multicaudatus* (on Salicaceae, Oleaceae, Platanaceae, and Rosaceae); *Atlides halesus* (on mistletoe on various trees); *Adelpha bredowii* and *Erynnis tristis* (on oaks, the latter only using the sporadic tender shoots); and *Limenitis lorquini* (on willows). Other willow feeders, including *Satyrium sylvinus* and *dryope, Nymphalis antiopa* (from Fairfield inland), and the Saturniid *Pseudohazis eglanterina*, are univoltine. So are oak feeders such as *Satyrium californica, Habrodais grunus*, and *Erynnis propertius* (locally partially bivoltine).

DINGLE (1978) explicitly recognizes diapause and migration as alternative escapes from seasonal stress. A very large proportion of the present lowland California butterfly fauna is multivoltine. With the exception of *Papilio zelicaon* on the introduced weed *Foeniculum* (SIMS, 1980) it seems unlikely that this phenology arose recently as a consequence of human perturbation of the ecosystem. **Virtually the entire multivoltine fauna depends on constant dispersal and colonization of hosts to maintain itself through the season.** I believe these species have done something of the sort throughout their histories, dispersing in search of alternate species of hosts or hosts in more suitable phenophases. Except where irrigation has created reasonably stable year-round host populations, it is doubtful whether such butterflies have ongoing populations at all. Even if they are recorded year after year in a given location, close inspection reveals they are not present brood after brood – each year sees a new colonization, and this year's butterflies need not be genetically descended from last year's. *Plebeius acmon* is a good example. It is „always" present in the Sacramento Valley but it overwinters only very sporadically; most „populations" last no more than three generations; most colonizations are probably by single gravid females. I have seen it come and go in urban vacant lots in a month.

Vanessa annabella and *Pyrgus communis* can maintain themselves year-round in urban situations on the weedy European *Malvas*. In pre-European California the only herbaceous mallows available to support summer breeding were *Sidalcea* species in tule marshes. (The shrubby *Malacothamnus* is apparently dominated by *Heliopetes ericetorum*, which is itself migratory; *Hibiscus californicus*, now rare, is not used at all as far as I know.) We know so little of this habitat that it is impossible to say whether either butterfly could have persisted in summer there; certainly neither does in noticeable numbers now.

Everes comyntas is able to persist in riparian habitat by switching among several species of (mostly annual) Leguminosae which form a seasonal succession. Since an especially prominent component in this succession is introduced annual *Vicia*, it is not clear how *E. comyntas* functioned before the white man came. I know, however, of one localized grassland population without access to *Vicia* that has persisted for at least nine years. *Plebeius acmon* shifts among Legumes and Polygonaceae, and *Lycaena helloides* among Polygonaceous hosts. *Strymon*

melinus uses a variety of hosts; it can now breed all summer on European *Malva* and on the weedy perennial *Sida hederacea* probably introduced into northern California from the desert, but 200 years ago it may have been limited in summer to the odd borage *Eremocarpus setigerus*.

Multivoltinism and Vertical Dispersal/Migration

Most of the weedy lowland butterflies turn up regularly at moderate to high elevations in the Sierra Nevada of California (SHAPIRO, 1973, 1974) and the Trinity Alps (SHAPIRO, PALM and WCISLO, 1980). Many breed there but do not overwinter in normal years. The following species appear to colonize temporarily above 5000 feet (1500 m) nearly every year: *Strymon melinus, Plebeius acmon, Lycaena helloides, Pieris protodice* and *Precis coenia*. Rarer, but never unexpected, altitudinal vagrants include *Brephidium exilis* (the smallest butterfly in North America!), *Lerodea eufala, Atalopedes campestris, Hylephila phyleus* and *Pholisora catullus*. Several species which do overwinter in the mountains also disperse upslope into them in numbers, and can be detected by condition and seasonal phenotypes: these include *Pieris rapae, Colias eurytheme* and *Pyrgus communis*. All of these species, I believe, can be placed along a continuum from regular seasonal migrants to occasional, essentially random, long-distance dispersers. The best known are the mass migrants, which despite their immense literature remain poorly understood both ecologically and physiologically.

The mass migrants are the Monarch, *Danaus plexippus*, of which no more will be said (because so much has already been said); the California Tortoiseshell, *Nymphalis californica*; and the Painted Lady, *Vanessa cardui*.

In 1975 (b) I proposed that *Nymphalis californica*, which had been viewed as a cyclic species migrating erratically in response to high density, in reality migrated seasonally independently of density. I have seen nothing in the past five years to change my mind. *N. californica* oviposits only on the genus *Ceanothus* (though the larvae will eat other things, such as *Ulmus*, a genus lost in the drying-out of California); its larvae must start on tender young growth, but mature larvae will eat mature, tough foliage. Since tender growth is only seasonally available, the only way *N. californica* can rear several successive broods is by following *Ceanothus* upslope and northward with the spring. This is what it seems to do.

Nymphalis milberti is another tortoiseshell that feeds on stinging nettle (*Urtica*). In its eastern range it seems normally non-migratory, rearing three broods in central New York. In California it, like *N. californica*, seems to overwinter in the foothills, rear a brood there in very early spring, then disperse to the high country for summer breeding (SHAPIRO, 1974, 1979). Presumably there is an inconspicuous return flight in autumn. This pattern obviously extends the breeding season, but the phenology of *Urtica* hardly requires it. It is worth noting that the Red Admiral, *Vanessa atalanta*, which also feeds on *Urtica*, is migra-

tory in the eastern United States and in Europe. It is too uncommon in California to make out a pattern. *Nymphalis vau-album* in upstate New York feeds on birch and is strictly univoltine, but disperses downslope in autumn and hibernates in the lowlands, often far from breeding habitat. A tendency to seasonal migration, perhaps initially in search of hibernation sites, is clearly present in this genus and perhaps has been elaborated in more than one selective context.

Vanessa cardui, the most nearly cosmopolitan butterfly on earth, migrates in both the Old World and the New. Nearly all of its hosts are empheral annual Compositae, Boraginaceae, or Malvaceae. Its longrange migrations – from Mexico to the northern United States and from North Africa to northern Europe – seem to track the northward progress of spring. There may be no such thing as a „permanent" population of *V. cardui* anywhere in the world. It can neither overwinter in the north nor oversummer in the south. I have in press (SHAPIRO, 1980b) an account of its 1979 outbreak in northern California. This culminated in a very large but very late southward migration in fall. Most of the females were forced to dump their eggs too far north to survive; winter populations in the desert were poor, and a cool, wet, late spring impeded breeding. There were thus almost no northward migrants in spring, 1980, and the species failed to breed in the Sacramento Valley despite a bumper crop of hosts.

Of the other species which colonize montane habitats from the lowlands, only *Precis coenia* has anything remotely resembling an organized seasonal migration, and not in all years. I had not seen *coenia* migrating in California until 1978. On 28 April of that year a well-defined migratory front passed Davis from SW to NE. By 3. May it had reached 5000 feet (1500 m) on the Sierran west slope (Lang Crossing, Nevada County); on 14. June *P. coenia* was common at Donner Pass (7000 feet, 2100 m) with snow still covering the ground; on 25. July, with up to 8 feet of snow on the ground, it was flying above timberline on Castle Peak (9000 feet, 2700 m) – and it was still there on 5. November! In most years *P. coenia* first reaches Donner Pass in August or September, if then. In 1979 it migrated through Davis again from SW to NE on 29. April – 1. May and was at 5000 feet on 23. May and at 9000 feet on 14. July. In 1980 no migration at all was observed. It should be noted that shorterramge dispersal occurs predictably in this species every year. It does not overwinter normally on the floor of the Sacramento Valley; though it may be common in February in warm foothill canyons, it is rarely seen on the valley floor before mid-March to early April. Its hosts are mostly perennials (*Lippia=Phyla*, Verbenaceae; cultivated and wild Scrophulariaceae, both herbaceous and woody; both native annual and introduced perennial *Plantago*).

The Movements of Weedy Pierids

Pieris rapae, which was introduced from Europe before 1860, and *Colias eurytheme* undergo vertical dispersal in spring which carries second brood animals

(recognizable by phenotype) up to snow line as early as April or May every year. Gravid second brood females of both can be found in Donner Pass with snow on the ground, weeks before the emergence of locally-overwintered individuals. For example, on 3 May 1980 none of the indigenous butterflies was yet flying near Truckee, Nevada County, but a large second brood male of *C. eurytheme* (which must have come up from the desert) was encountered far out on the sagebrush flats near Martis Creek.

In Europe *P. rapae* and *P. brassicae* are able to winter far to the north, just as *P. rapae* and *C. eurytheme* can do so at Donner Pass. (I have personal experience with *rapae* survival north to Scrabster, Caithness, Scotland and *brassicae* to Hoy, Orkney; SHAPIRO, 1970). Still, northern populations are regularly inundated by more or less massive immigration from the south-apparently dispersing as the Crucifers dry up in late spring around the Mediterranean. Although mass migration by *rapae* is unknown in the United States, the easily observed upslope dispersal in spring also constitutes an escape from a Mediterranean climate. The resource base of *P. rapae* in lowland California is seasonally labile. From vast blooms of weedy species in spring, it contracts to local pockets of *Brassica geniculata* and *Lepidium latifolium* on special soils in summer.

The movements of American *C. eurytheme* are mirrored by *C. croceus* in Europe (as chronicled by the indefatigable VERA MOLESWORTH MUSPRATT) and *C. lesbia* in Argentina. In California, for reasons not at all clear, *C. eurytheme* overwinters very poorly in alfalfa (*Medicago sativa*) fields. Late winter – early spring breeding is mostly on weedy European *Vicia* in ruderal habitats. Only when these dry up in May and June is cultivated alfalfa heavily colonized. Upslope dispersal occurs at the same time. Thus, both *P. rapae* and *C. eurytheme* exhibit simultaneous horizontal and vertical dispersal correlated with deterioration of the first-brood larval hosts.

Pieris protodice is probably not native west of the Sierran crest, and can persist there now only because *Brassica geniculata* supports summer breeding. It routinely colonizes up – and downslope in the southern Rockies and Great Basin, and apparently brought these habits with it into California (SHAPIRO, 1980a). Its precise Old World ecological equivalent is *Pontia daplidice*.

Coda

I could go on, but the point is clear: without constant dispersal and colonization most of the multivoltine butterflies of lowland California would become extinct. This seasonal rhythm has obvious implications for gene flow: if there are no populations, there can be no differentiation of populations. Local inbreeding is a fleeting phenomenon, lasting only as long as a patch of host plant does.

But a warning is in order. Neither diapause nor dispersal can be assumed to be an adaptive response to the Mediterraneanization of the California climate. It is not enough that each is a prerequisite for the survival of certain species

there. Many of the vagile Californians disperse a great deal elsewhere, too. *Precis coenia, Pyrgus communis* and *Hylephila phyleus* (to name three) all disperse northward along the Atlantic Coastal Plain too, where it hardly seems „necessary." Much of the southwestern desert fauna is extremely dispersive: *Euptoieta claudia, Eurema nicippe, E. mexicana, Nathalis iole* and *Hemiargus isola* come to mind. Perhaps the drying out of California merely selected from the available species pool a preadapted fauna capable of escaping in space or time. Though I think I can see the fruits of directional selection in the physiology of interior Californian *Pieris napi*, I am not yet willing to generalize to an entire fauna. How many summer univoltines not found in California could shift to a spring mode successfully with a minimum of genetic reshuffling? Until someone finds out, I will merely note that if „life is motion," motion means life for a butterfly trying to breed in summer in California, and leave it at that.

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Nordwärts gerichtete Frühjahrswanderungen palaearktischer Schmetterlinge, Fliegen und Hummeln im Himalaya- und Transhimalayagebiet Nepals

von

WULF GATTER

1. Einleitung

Durch die zusammenfassende Übersicht von WILLIAMS (1935) sind wir über Insektenwanderungen auf dem indischen Subkontinent und am Südrand des Himalaya einigermaßen orientiert. Aus den Hochlagen des Himalaya liegen Einzelhinweise vor (CHAPMAN, 1940; WESTMACOTT & WILLIAMS, 1954). Über erfolgreiche Migrationen von Wanderfaltern zwischen der Himalayasüdabdachung und der Transhimalayaregion ist mir nichts bekannt geworden. Während einer 23-tägigen Wanderung um das Annapurnamassiv konnten meine Frau und ich im Mai 1979 keine gewaltigen Insektenmigrationen registrieren. Trotzdem beobachteten wir fast täglich zwischen 600 – 5400 m NN gerichtete Migrationen meist einzelner Tiere als Zeichen eines sich auf breiter Front abspielenden Zuggeschehens.

Unsere Wanderung ging von dem im subtropischen Hügelland gelegenen Pokhara