Life history and ecology of the San Emigdio blue butterfly (Lepidoptera: Lycaenidae)

Gregory R. Ballmer
5894 Grand Av., Riverside, CA 92504
gballmer@gmail.com

ABSTRACT. The San Emigdio blue butterfly, *Plebulina emigdionis* (Grinnell, 1905), occurs in small, scattered colonies in and near the southwestern Mojave Desert of California. Colonies depend on a symbiotic relationship with the ant *Formica francoeuri* (Bolton), and occur only where the ant's range (primarily in more mesic cis-montane habitats) narrowly overlaps that of the butterfly's more widely distributed *Atriplex* larval hosts in more xeric habitats. Colonies of *P. emigdionis* are often localized around a few host plants and, therefore, sensitive to habitat changes due to anthropocentric causes and environmental stochasticity. The biology, ecology, and status of known colonies of *P emigdionis* are presented with intent to offer insights into the species' conservation. The status of all *P. emigdionis* colony sites known from museum records, published accounts, and the personal records of other lepidopterists is assessed.

KEY WORDS: myrmecophily, extinction.

TAXONOMY

The San Emigdio blue, *Plebulina emigdionis* (Grinnell, 1905) (Lepidoptera: Lycaenidae: Polyommatinae), is a small butterfly (Figs. 1, 2) whose restricted range includes scattered colonies in and around the western Mojave Desert of California (Comstock, 1927, Emmel & Emmel, 1975). Although some recent authors place this taxon in the Holarctic genus *Plebejus* (*e.g.* Balint & Johnson, 1995; Pelham, 2008), it is nevertheless distinguished by a unique suite of morphological, ecological, and biochemical traits (*e.g.* Nabokov, 1945; Ballmer & Pratt, 1991a, b; Pratt *et al*, 2006, Talavera *et al,* 2012) within the subtribe Polyommatina [= informal Polyommatus Section (*sensu* Eliot, 1973)]. Talavera *et al* (*ibid*), used DNA markers to justify reinstating the monotypic genus *Plebulina* Nabokov, 1945; they further indicated its phylogenetic position as sister to the wholly Nearctic *Icaricia* Nabokov, 1945, and together with the latter group of species, as sister to the remainder of Holarctic Polyommatina.

BIOLOGY/ECOLOGY

One remarkable feature of the distribution of *P. emigdionis* is its occurrence in small, dense, discrete colonies, where adults and larvae are typically associated with just a few individual

larval host plants, often among or near many other apparently suitable host plants. Fordyce Grinnell (1905) described the colony at the type locality in San Emigdio Canyon, southern Kern County, CA, as "… extremely local, being found in only one place, and extending along the canon for about a hundred yards." Most, and perhaps all, extant and recently extirpated colonies of *P. emigdionis* are/were similarly restricted in geographic extent.

The first reported host for *P. emigdionis* (as *Lycaena Melimona*) is that by W. G. Wright (1905), who asserted that larvae fed on *Acmispon americanus* (Nutt.) Rybd. (Fabaceae) (as *Hosakia purshianus*). Wright (*ibid*) considered *L. Melimona* to be a hybrid of *Icaricia acmon* (Westwood) and *Lycaeides melissa* (W. H. Edwards), both of which he reported to use *A. americanus* as a larval host. Although Pratt & Ballmer (1991) reported that larvae of *P. emigdionis* fed on foliage (but not flowers or fruit) of *Acmispon glaber* (Vogel) Brouillet (as *Lotus scoparius* (Nutt.) Ottley) under laboratory conditions, there are no recent reports of any fabaceous host being used by *P. emigdionis* in the field.

Comstock & Dammers (1932) described the life history of *P. emigdionis* for a colony near Victorville, CA, and reported the larval host as *Atriplex canescens* (Pursh.) Nutt (Amaranthaceae), which is present at nearly all known *P. emigdionis* colony sites. In May 1989, the author (with G. F. Pratt), conducted a line transect survey across a colony of *P. emigdionis* dominated by two *Atriplex* species near Victorville, CA. Larvae of *P. emigdionis* were found on two of 21 *At. canescens* and 23 of 97 *At. torreyi* (S. Watson) S. Watson shrubs. In a subsequent survey (same month and same observers) of all *Atriplex* plants within a central 400 sq-ft portion of the same colony, a total of 26 larvae and pupae were found on six of ten *At. canescens* and 105 larvae and pupae were found on ten of 11 *At. torreyi* plants. Adults and larvae of *P. emigdionis* have also been associated with *At. polycarpa* (Torrey) S. Watson at three colony sites: Helendale, San Bernardino Co. and Alabama Hills and Cartago Creek, Inyo Co., CA. In captivity, larvae of *P. emigdionis* have also been reared on foliage of *Atriplex lentiformis* (Torrey) S. Watson, a close relative of *At. torreyi*.

Larvae of *P. emigdionis* are primarily nocturnally active, although they have been observed to forage diurnally on cloudy days in the field (G. F. Pratt, personal communication) and while in captivity under subdued lighting conditions. During daylight hours, larvae of *P. emigdionis* have been found resting on the crowns and undersides of prostrate branches of host plants (figs. 5, 6), beneath leaf litter, and always in association with colonies of *Formica francoueri* (Bolton) (Hymenoptera: Formicidae). This ant association was reported earlier (as *F. pilicornis*) for the Victorville colony (Ballmer & Pratt, 1991b); now it is confirmed for all extant colonies recently visited.

It is notable that *Atriplex* shrubs on which *P. emigdionis* larvae occur often also harbor homopterous insects (various aphid and scale species), which produce fluid secretions on which *F. francoueri* workers may forage. Scale insects found in association with shrubs utilized by *P. emigdionis* larvae include *Ceroplastes irregularis* Cockerell (Cerococcidae), *Lecanodiaspis rufescens* (Cockerell) (Lecanodiaspididae), and *Orthezia annae* Cockerell (Ortheziidae). Various aphids have been found on plants occupied by *P. emigdionis*, primarily during the spring season on young foliage, but only *Pemphigus cf betae* Doane has been found in close association with *P.*

emigdionis larvae and *F. francoueri* on the roots and crowns of host plants, notably near its alternate host *Populus fremontii* S. Watson (Salicaceae).

The occurrence of *P. emigdionis* with *F. francoueri* colonies may indicate an obligate relationship, although the mechanism for this symbiosis remains speculative. Ant presence is not necessary for *P. emigdionis* larvae to grow and complete their development in captivity. However, ant presence may be a necessary cue for oviposition, and may be important for inhibiting larval predation and parasitization.

Ant symbioses with lycaenid larvae are frequently attributed to the ants providing protection from insect predators and parasitoids in return for nutritive secretions from the larva's dorsal nectary organ (DNO) (see Malicky, 1970; Fiedler, 1995). Although the imbibing by ants of DNO secretions has not been observed with captive *P. emigdionis* larvae, the possibility exists that it may occur under field conditions.

Other ant organs associated with myrmecophily in *P. emigdionis* and other polyommatine lycaenids include lenticles, eversible tentacular organs (TOs), and dendritic setae. Lenticles are small, low cuticular structures (often resembling setal chalazae) with perforations which may emit substances which affect ant behavior (Malicky, 1970). Paired TOs on the seventh abdominal segment of most polyommatine species have been associated, when everted, with excited ant behavior, presumably by releasing a semiochemical mimicking an ant alarm pheromone. Ants in proximity to larvae of *P. emigdionis* which have everted their TOs usually become agitated and/or are attracted to the larvae.

The function of dendritic setae in myrmecophily is not as well recognized as other so-called ant organs, but seems to be a major contributor to myrmecophily in some species, especially copper larvae (*eg. Lycaena xanthoides* (Boisduval)) which lack most other "ant organs" (Ballmer and Pratt, 1991). Dendritic setae are not prominent on *P. emigdionis* larvae and may not contribute to myrmecophily in this species (Ballmer and Pratt, *ibid*).

Plebulina emigdionis larvae often display their tentacle organs (TOs) on the eighth abdominal segment when disturbed or while foraging. The TOs on foraging larvae appear to attract nearby *F. francoueri* workers, which may serve to deter predators or parasites. Quiescent larvae on the host plant crown also display their TOs when disturbed worker ants swarm out of their subterranean nests, presumably in response to an alarm pheromone, to defend against the invader. Such "alarmed" ants run around rapidly and often come in contact with any *P. emigdionis* larvae which are present. Some such larvae often evert their TOs, either when contacted by ants, or perhaps in response to the same disturbance which excited the ants. In addition to chemical response, larvae may also evert their TOs in response to substrate-borne vibrations, by which ants and many lycaenid larvae communicate (DeVries, 1991). Although such agitated worker ants frequently contact *P. emigdionis* larvae, they do not usually remain in protracted contact.

The display of TOs by *P. emigdionis* larvae varies according to the context. Foraging *P. emigdionis* larvae, accompanied by *F. francoueri* workers, exhibit prolonged display of their TOs, while quiescent *P. emigdionis* larvae on host plant crowns usually evert their TOs more

briefly, but repeatedly when disturbed. This could be interpreted as a prolonged release of an aggregation pheromone in foraging larvae and a briefer, but more concentrated, release of an alarm pheromone in quiescent larvae. This comports with observations that the same pheromone may function as an ant alarm pheromone at high concentration and an aggregation pheromone at lower concentrations (Henning, 1983).

Female *P. emigdionis* often deposit eggs on peripheral foliage of host plants (Figs. 2, 3), although eggs may also be found on mature branches near the host plant crown (Fig. 4). In all cases where eggs have been found, *F. francoueri* workers were also present on the plants. Comstock & Dammers (1932) reported that the *P. emigdionis* egg stage (from oviposition in May) lasted 8-10 days; the incubation temperature was not reported. In recent laboratory observations, a captive female from Victorville, produced 28 ova within four days of capture; 10 eggs eclosed within four days, while the remainder eclosed within six days, of her capture. Thus, the egg stage lasted a minimum four days and maximum six days; all ova were maintained at 80° F (26.6° C). The differences in egg eclosion times reported here and by Comstock & Dammers could be due to different incubation temperatures.

Several efforts to induce oviposition by captive females have been only modestly successful. While occasional captive females produced up to a few dozen ova, more often they produced only 1-2 or none. Anecdotal observations suggest that oviposition by captive females may be increased when offered sprigs of host plants on which *F. francoueri* were present or had recently been present; suggesting that, ant trail pheromones may serve to stimulate oviposition. This also comports with field observations that host plants, with which adult female *P. emigdionis* are closely associated, invariably also have foraging *F. francoueri*. Nevertheless, ovipositing female *P. emigdionis* are not immune from attack by foraging *F. francoueri* and take flight if approached closely by the ants.

Larvae of *P. emigdionis* (Fig. 7) are relatively glabrous; the ground color is matte pale green-to-grayish green, or beige, which matches the foliage and/or woody branches and fallen leaves of the host plants. Young larvae typically feed by scraping the leaf surface tissues but, as they mature, may also feed at leaf margins (Fig. 8). Larvae may also mine the interior of leaves (especially *At. canescens*), leaving the dry papery epidermis to resemble an empty paper bag. Although the larva may be too large to entirely enter the leaf interior, its extensible neck allows the head to do so while feeding.

During daylight hours, larvae remain concealed on the underside of prostrate branches and below ground or leaf litter on the crown within a few inches of the soil surface. Such larvae often occur in clusters (Figs. 5, 6) and are always associated with ant galleries around the plant crown and roots.

Larvae have a few anatomical and behavioral traits which distinguish them from other polyommatine lycaenids and which may serve to facilitate escape from predation. Specifically, while many foliage-feeding lepidopterous larvae spin a silken lattice on the surface of foliage, which enables firm attachment by their proleg crochets (similar to Velcro), *P. emigdionis* larvae do not. Also, unlike typical lycaenid larvae, *P. emigdionis* larvae lack a fleshy median lobe on

the planta of the prolegs. These factors may increase larval survival by facilitating rapid dropping to the ground at the approach of would-be predators and parasites. Such fallen larvae initially remain motionless and are cryptic among leaf litter where they may gain protection from foraging *F. francoueri*.

Pupae of *P. emigdionis* are pale tan and macroscopically glabrous (Figs. 9, 10). Pupation occurs on the underside of prostrate branches and on root crowns in proximity to the soil surface or beneath leaf litter. Pupae are loosely attached, as they lack a silken girdle and silken pad for attachment, which are commonplace features among other polyommatine lycaenids.

Comstock & Dammers (*ibid*) reported that two larvae completed growth, pupated, and eclosed in late July, while others from the same cohort of ova fed intermittently until entering diapause in October. Similar results were obtained by the author from larvae reared in captivity representing multiple wild colony sources. This comports with observations of a major spring flight and partial subsequent flights, as indicated by occasional adults observed in the field throughout the summer and early fall seasons. Larvae prefer to feed on fresh foliage, which is most reliably available following late-fall and winter precipitation events, coincident with the end of larval diapause. However, minimal vegetative growth may also occur on otherwise dormant host plants during the normally dry summer and early fall seasons, especially following sporadic summer monsoon rains.

Ballmer & Pratt (1991a) reported that *P. emigdionis* larvae pass through five instars prior to pupation, based on larvae which matured and pupated without undergoing a semi-dormant summer estivation. Those larvae were reared from ova from a female captured in April 1988 at the Cuyama River Wash, San Luis Obispo Co., CA. The capture date suggests a female from an overwintering larva; all larvae pupated and all but one pupa eclosed without entering diapause (the single non-eclosing pupa died). A second cohort of larvae, the progeny of a female captured in May 1989, at Victorville, CA, was reared under controlled conditions (12 hrs light: 12 hrs dark) at a constant 80° F (26.6° C), until the temperature regulator failed and caused all larvae to perish from hyperthermia in the early 5th instar. The mean duration in days was 5.0, 4.9, 5.1, and 6.8, respectively, for 1st, 2nd, 3rd, and 4th instar larvae; as noted, all larvae died before completing the 5th instar.

Recent observations with captive larvae reinforce the observed phenology of *P. emigdionis* which entails a primary flight of adults in late winter to spring from overwintering larvae. Eggs from the spring flight of adults produce larvae which largely (not entirely) enter a semidormant quiescent stage in the penultimate larval instar. Those larvae remain more-or-less dormant during the summer and fall seasons, but molt to the final larval instar and resume active feeding and maturation in the subsequent winter season. The likely trigger for termination of larval diapause may be seasonal changes in day length, daily temperature fluctuations, or both.

A cohort of captive *P. emigdionis* larvae, with *F. francoueri* workers, monitored daily from May until the following January remained stationary (dormant) for several-to-many days at a time. Occasionally, 1-2 larvae broke dormancy by molting and feeding for a brief period before becoming quiescent again. All larval exuviae recovered between May and January had mean width of associated cranial exuviae of 0.9 mm, which corresponds to that of 4th instar larvae.

This suggests that observed sporadic feeding activity of such otherwise dormant larvae is not accompanied by growth and maturation to the final larval instar until January. Post-diapause larvae did not molt again prior to pupation.

Larvae of *P. emigdionis* are resistant to the annual summer drought, typical of their environment, by virtue of a facultative semi-dormant state prior to the final larval instar. However, they may not be able to endure prolonged drought resulting in extended absence (beyond one season) of sufficient suitable host plant foliage. Thus, of 22 captive larvae which broke diapause, molted to the final (prepupal) instar, and resumed active feeding in early winter, only four pupated when fresh host plant foliage was withheld; and these pupae produced abnormally small adults. The 18 less well-fed post-diapause larvae failed to pupate and died without re-entering a dormant physiological state. This is unlike some other polyommatine lycaenids, such as *Euphilotes* spp., which are capable of multiyear pupal diapause (Ballmer, personal observations), or of multiyear larval diapause, as in the nymphalid *Euphydryas editha quino* (Wright) (Pratt & Emmel, 2010). It remains unknown whether larvae may remain in extended diapause under field conditions.

Natural enemies

As with other myrmecophilous lycaenids, ant attendance or proximity of ants to *P. emigdionis* larvae may help to prevent predation or parasitization. While various hymenopterous parasitoids, chiefly Braconidae, Chalcididae, Eulophidae, and Ichneumonidae (Hymenoptera), have been reared from the immature stages of many other lycaenid species which have variable degrees of ant associations, such parasitism of *P. emigdionis* larvae has not been observed. This may be due to the larva's normally nocturnal foraging behavior and/or close association with *F. francoueri*. However, parasitoid tachinid flies (Diptera: Tachinidae) have been reared from *P. emigdionis* pupae, collected as larvae in the field.

At least two eryciine tachinid species have been reared from *P. emigdionis* pupae, one of which appears to be in or near the genus *Siphosturmia*, while the other has yet to be determined (Fig.11). Based on voucher specimens in the Entomology Research Museum at the University of California at Riverside, the tachinid species most frequently reared from various lycaenid species, other than *P. emigdionis,* in Southern California is *Aplomya theclarum* (Scudder) (Tachinidae, Eryciinae; see also Arnaud 1978). The tachinid species reared from *P. emigdionis* may be specialized to parasitize *P. emigdionis* larvae.

Fig. 1. Adult *P. emigdionis*. **Fig. 2**. *P. emigdionis* ovipositing. **Fig. 3**. *P. emigdionis* egg on *A. canescens* leaf. **Fig. 4**. *P. emigdionis* egg on *A. canescens* crown. **Fig. 5.** *P. emigdionis* larval cluster on underside of prostrate branch. **Fig. 6**. *F. francoueri* with 2nd instar *P. emigdionis* larvae. All figures are on *A. canescens*.
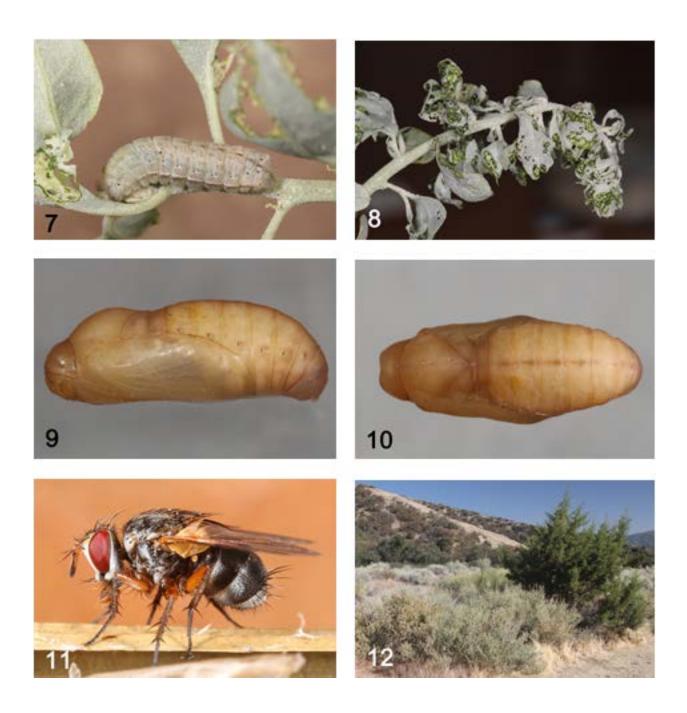
Fig. 7. *P. emigdionis* mature larva on *At. canescens*. **Fig. 8.** *P. emigdionis* larval feeding damage on *At. canescens*. **Fig. 9.** *P. emigdionis* pupa, lateral view. **Fig. 10.** *P. emigdioni*s pupa, lateral view. **Fig. 11.** Tachinid fly ex *P. emigdionis* pupa. **Fig. 12.** *P. emigdionis* colony site near Gorman, Los Angeles Co.

Fig. 13. *P. emigdionis* colony site near Dome Spring, Ventura Co. **Fig. 14.** *P. emigdionis* colony site at Conejo Gate, Coso Mts., Inyo Co. **Fig. 15.** burned colony site of *P. emigdionis* near Cartago, Inyo Co. **Fig. 16.** *P. emigdionis* colony site in Mojave River Wash near Victorville, San Bernardino Co. **Fig. 17.** Distribution and status of *P. emigdionis* colonies.

DISTRIBUTION

Colonies of *P. emigdionis* are known from a relatively narrow zone of overlap of the primary ranges of its *Atriplex* hosts and ant associates, chiefly at the western and southwestern margins of the Mojave Desert (Fig. 17). The elevation of known *P. emigdionis* colonies ranges from 490 m at the Cuyama River Bridge (San Luis Obispo County) to 1780 m at El Conejo Gate in the Coso Mts. (Inyo County). The *Atriplex* larval hosts are generally confined to xeric and/or saline/alkaline soil environments and are collectively widespread in Southern California from the deserts to the sea (Hickman, ed., 1993). Colonies of *F. francoueri* typically occur in relatively mesic habitats of cis-montane southern California, including riparian, chaparral, and coniferous forest communities. Although *F. francoueri* is rarely found in xeric habitats dominated by *Atriplex*, and is uncommon in the Mojave Desert Biome, it is nonetheless invariably present in association with *P. emigdionis* colonies.

Where *F. francoueri* colonies are associated with *P. emigdionis*, the ants may access soil moisture at some depth below the dry soil surface (*e.g*., dry creek washes), or rely on fluids from homopterous insects (various aphids and scales) associated with *Atriplex*. Limitations on the distribution of *P. emigdionis,* particularly its absence from cis-montane southern California, are speculative and may be related to intolerance of prolonged exposure to relatively cool, moist atmospheric conditions, such as often occur within the cis-montane fog belt below 1000 meters elevation. Coastal fog seldom penetrates inland to the Mojave Desert.

There are no recent records of *P.emigdionis* from the type locality, San Emigdio Canyon, Kern Co., CA, although patches of suitable host plants occur there. San Emigdio Canyon is a central feature of the Wind Wolves Preserve (WWP) bordering the south end of the San Joaquin Valley, The WWP is managed by the Wildlands Conservancy to conserve and rehabilitate habitat for native species. The canyon was subjected to intense cattle-grazing for many years, resulting in major impacts to the local ecology. In visits to this location (March and April 2015), a few clusters of *At. canescens* were found, primarily along the entrance road below the mouth of the canyon, at an ornamental garden near the administrative headquarters, and a short distance upstream from the mouth of the canyon and upslope from the creek wash. Neither *P. emigdionis*, nor any *F. francoueri* was found in association with the *Atriplex*.

WWP management staff indicated that *At. canescens* was heavily grazed and trampled by cattle, especially when other green foliage was scarce, and was likely more prevalent in the past. This suggests the possibility that the colony noted by Grinnell (1905) may have been extirpated by cattle grazing or other ranching activities. WWP management plans currently include re-establishing *At. canescens* at additional sites within the preserve, and potential future re-introduction of *P. emigdionis*. Another potential host plant for *P. emigdionis* at San Emigdio Canyon is *At. polycarpa*, which is prevalent on the canyon's lower alluvial fan (beyond the WWP boundary) and widespread on adjacent portions of the San Joaquin Valley. This plant is also abundant over much of the western Mojave Desert (Moe & Twisselman, 1995) where a few *P. emigdionis* colonies are widely scattered. The nearest (to San Emigdio Canyon) known extant colony of *P. emigdionis* is near Frazier Park, in Kern County (*ca* 26 air km SE of the mouth of San Emigdio Canyon). This colony site is currently proposed for conversion to recreational uses.

Elsewhere in Kern County, a few colonies of *P. emigdionis* have been observed in the Cache Creek drainage between the communities of Tehachapi and Mojave, and in the Kern River drainage between Onyx and Weldon. Two colonies along the middle reach of Cache Creek (vicinity of Cameron Road) apparently have been extirpated by a recent major debris flow (Ballmer and K. Davenport, personal observations). One extant colony of *P. emigdionis* is known (as of 2019) several km further upstream in Cache Creek Wash, along Sand Canyon Road. Other colonies of *P. emigdionis* in the watershed of the middle reach of the Kern River, as at Weldon and Onyx, appear to be suffering from drought, as few or no adult butterflies were observed during spring 2021 (K. Davenport, personal communication).

The northernmost known population of *P. emigdionis* occurs in the Alabama Hills, west of Lone Pine, Inyo Co. Two additional colonies of *P. emigdionis* in Inyo County are adjacent to US Highway 395 near the communities of Cartago and Olancha (Fig. 14), several miles south of Lone Pine. Further south, a previously observed colony of *P. emigdionis* near Sage Flat, west of Haiwee Reservoir, seems to be extirpated, as no *P. emigdionis* adults have been found there in recent years. The cause of this colony's demise is not known, and no overt physical change to the colony site is apparent. Another colony at El Conejo Gate in the Coso Mts. (Fig. 14), within the China Lake Air Naval Weapons Test Center, was still present in July 2014, but no adult *P. emigdionis* were observed when the site was last visited later in July and August 2014 (G.F. Pratt, personal communication). This colony seems to have undergone a dramatic population reduction compared to earlier years, although no obvious changes to the habitat have been noted (G.F. Pratt, personal communication). The status of another colony site adjacent to the Owens River, near Haiwee Reservoir, on land managed by the Los Angeles Department of Water and Power, is not open to the public and has not been assessed in recent years.

A few colonies of *P. emigdionis* are historically known from the hilly north-central region of Los Angeles County bordering the Mojave Desert. Some such colonies have been displaced by Los Angeles regional urban sprawl. The occurrence of *P. emigdionis* in the "Canyon Country" vicinity of Santa Clarita was noted in the course of a biological survey for a proposed large housing tract during the 1990s (G. Bruyea, personal communication). A colony formerly known from Solemint has been displaced by urban growth. Currently, one small colony (occupying *ca* one acre) is known to persist in Los Angeles County adjacent to Interstate Highway 5 in the general vicinity of Gorman *(*Fig. 13*)*. This colony is embedded in a modified coastal sage scrub community as described below.

The first reported colony of *P. emigdionis* (as *Lycaena Melimona),* was found in the 1880s on the south slope of the San Bernardino Mts. Wright (1906) described the location thus: "The locality of *Melimona* is a little open mesa on the southern slope of the mountain, at an altitude of 3,500 feet, and there I find it every year in June, but at no other time." The location of that site remains obscure, although a site resembling Wright's description exists near Waterman Canyon, is accessible by an old road, and is not far from Wright's former residence in San Bernardino. No colony of *P. emigdionis* is currently known from the San Bernardino Mts., but a colony was formerly reported to occur at Baldy Mesa, just to the north of the Cajon Pass. The Baldy Mesa area is currently subject to suburban sprawl, with extensive habitat alteration.

All known extant colonies of *P. emigdionis* in San Bernardino County occur at least several miles north-west of the San Bernardino Mountains, along the Mojave River. Small colonies are scattered along the river's dry wash margins over several miles between the communities of Victorville and Helendale (Fig. 16). These colonies occur in close proximity to elements of both riparian and Mojave Desert communities, as described below.

The westernmost known colony of *P. emigdionis* formerly occurred in the Cuyama River Wash, adjacent to the Highway CA 166 bridge, near Cuyama. Although technically in San Luis Obispo County, this site is very near the boundary of Santa Barbara County. The author (with G. F. Pratt) visited this colony to obtain life history material in 1988; it was apparently extirpated following subsequent bridge and highway reconstruction activities. When the site was re-visited in 2015 and 2016, a few *At. canescens* shrubs were observed adjacent to the road margin at the site of the former colony; but they were largely buried by debris from road construction activities and no *P. emigdionis* was found there. Nor was any *P. emigdionis* found in searches of numerous *At. canescens* shrubs up to 1 km both up- and down-stream from the former colony site. Nevertheless, several miles upstream (and about 300 m higher elevation) along the Cuyama River Wash in Ventura County, colonies of *P. emigdionis* occur along Lockwood Valley Road in the vicinity of Dome Spring (Fig. 13).

HABITAT STRUCTURE

Colonies of *P. emigdionis* are associated with various plant communities, mostly within or adjacent to the Mojave Desert Biome. Among the most diverse floral associations are those along the Mojave River where colonies of *P. emigdionis* frequently occur in the ecotone between desert and riparian communities. These colonies are associated with *Atriplex canescens*, *At. polycarpa*, and *At. torreyi* in proximity to riparian species, such as cottonwood (*Populus fremontii S. Watson*), various willows (*Salix* spp.), saltgrass (*Distichlis spicata* (L.)) and tamarisk (*Tamarix* spp.), as well as typical desert species including creosote bush (*Larrea tridentata* (D.C.) Coville), mesquite (*Prosopis juliflora* (SW.) D.C.), and rabbit brush (*Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird).

Plant communities which support colonies of *P. emigdionis* are often dominated by diverse trees and shrubs. Pinyon pine (*Pinus monophylla* Torr. & Frem*.)* and antelope bush (*Purshia glandulosa* Curran) are prominent at Dome Spring, Joshua tree (*Yucca brevifolia* Engelm) at El Conejo Gate, Coso Mts., canyon live oak (*Quercus chrysolepis* Liebm.), grape soda bush lupine (*Lupinus excubitus* M. E. Jones), and Great Basin sagebrush (*Artemisia tridentata* Nutt.) at Sage Flat. The colony near Gorman is in a modified Coastal Sage Scrub community with scrub oak (*Quercus* sp.), California juniper (*Juniperus californica* Carrieri), California buckwheat (*Eriogonum fasciculatum* (Benth.) Torr. & A. Gray), rabbit brush, bladderpod (*Peritoma arborea* (Nutt.) Iltis), basketbush (*Rhus aromatica* Aiton), and giant wild rye grass (*Elymus condensatus* J. Presl).

Adult *P. emigdionis* have been observed to imbibe nectar opportunistically from diverse floral resources. These include ephemeral annual spring flowers during the early flight period and various perennial floral resources later in the year. For example, at Helendale, San Bernardino Co., annual plant nectar sources used by *P. emigdionis*, such as *Amsinckia*,

Cryptantha and *Pectocarya* (Boraginaceae), are most apparent during March and April, while perennial nectar sources, such as *Heliotropium curassavicum* L. (Boraginaceae) become available later in the flight season. Nectar resources, when present, may extend the life span and reproductive capacity, of females.

HABITAT THREATS

The potential longevity, as well as fragility, of *P. emigdionis* colonies is exemplified by the Victorville colony site which provided material for the original life history description (Comstock & Dammers, 1932), as well as recent observations reported here. This colony is well known to lepidopterists due to its convenient location adjacent to Interstate Highway 15 where it crosses the Mojave River. But as of spring 2016, a major portion of this colony was buried during construction of expanded bridge and highway infrastructure.

Other colonies of *P. emigdionis* are (or were) equally vulnerable to extirpation. The colony adjacent to the CA State Route 166 bridge over the Cuyama River (San Luis Obispo County) was apparently destroyed by highway construction activities, as noted above. The Dome Spring population (Ventura County) is also concentrated near the paved highway and therefore at risk should road widening activities occur. This site is further at risk from damage by cattle which frequently graze the surrounding National Forest land and have been observed to both eat and trample the *Atriplex canescens* host plants colonized by *P. emigdionis* (GRB, personal observations). The Cartago colony, adjacent to highway US 395 in Inyo County (Fig. 15), was largely damaged by a local brush fire caused by a motor vehicle crash in 2017. As noted above, colonies of *P. emigdionis* in the so-called "Canyon Country" of Los Angeles County have been displaced by urban growth, while the single known remaining colony in Los Angeles County (vicinity of Gorman) is also vulnerable to potential expanded highway construction and related activities. The site of the *P. emigdionis* colony near Frazier Park is currently proposed for conversion to commercial recreational use.

Competitive displacement of *Atriplex* host plants by invasive exotic plants has been observed, as by tamarisk (*Tamarix* spp.) at the Mojave River and Cache Creek localities. Non-native giant reed (*Arundo donax* L.) also has potential to displace *Atriplex* spp. along the Mojave River, while both that species and tamarisk may present wildfire threats, as well. It is also notable that exotic grasses (chiefly *Bromus diandrus* Roth. and *B. madritensis* L.) have invaded virtually all localities where *P. emigdionis* occurs and can contribute to ignition and spread of wildfires.

Natural environmental stochasticity can also contribute to the demise of *P. emigdionis* colonies. The loss of two colonies along Cache Creek (Kern County) following a debris flow from a locally intense storm was discussed above. Recent extreme drought conditions may have been a factor in the apparent extirpation of the Sage Flat colony, as well as the apparently diminished, if not extirpated, El Conejo Gate colony, as noted above. Additionally, ongoing climate change can be expected to affect all colonies of *P. emigdionis* to a still unknown degree. The distribution of existing known *P. emigdionis* colonies may be interpreted as relicts of a Pleistocene distribution when climate was probably cooler and generally moister in the Mojave

Desert region. Thus, a predicted warmer and drier climate in response to "global warming" may cause greater pressure on survival of remaining colonies.

The potential threat from insect collectors cannot be ignored, though it should be noted that the *P. emigdionis* colony where Highway I-15 crosses the Mojave River has been well known among lepidopterists at least since the 1930s and continues to persist. The major threat to that colony has been habitat destruction, as noted above, when recent expansion of the bridge and related highway infrastructure obliterated a substantial portion of the colony. Similarly, wanton and/or inadvertent destruction of that and other colonies of *P. emigdionis* along the Mojave River (and elsewhere) are possible through ignorance or indifference of the relevant public and private land owners and land use agencies. It is notable that extensive portions of the Mojave River Wash's natural communities have been supplanted by agricultural and pastoral uses, as well as by residential conversion. Thus, insect collecting appears to be a far less important cause of past and likely future *P. emigdionis* colony extirpation than habitat loss and degradation from other anthropogenic causes.

COLONY MANAGEMENT

While the preferred strategy for species conservation ordinarily entails preservation of intact habitat, the current specter of rapid and dramatic climate change indicates that active management may be required in the future. Although *P. emigdionis* has apparently survived multiple periods of climatic extremes, particularly ice-age cold, likely prospects of future extreme heat and extended drought, as well as changes in land use and wild lands management, and spread of invasive species, pose additional challenges to *P. emigdionis* survival. Active habitat management and/or transplantation of *P. emigdionis* colonies to more favorable locations may be advisable. And, while captive breeding (if it were to become practical) may be useful in augmenting colonies, it cannot substitute for self-sustaining colonies.

Critical factors in need of further study to inform colony management include the value of nectar sources to adult *P. emigdionis* longevity and fecundity, food resources (including homopterous insects) and soil moisture needs of *F. francoueri*, as well as soil moisture, land disturbance, and plant competition affecting host plants. The status of managed *P. emigdionis* colonies should be monitored annually by butterfly census and perhaps other factors relating to host plant viability and ant presence, such as pesticide contamination, changes in soil chemistry, etc. Where augmentation of host plants is deemed necessary, propagules should be obtained from sources onsite or as near as possible. Adaptive management should consider all aspects of colony health and be prepared to implement changes, as needed, with respect to unique features of each colony site.

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