

The endangered quino checkerspot butterfly, *Euphydryas editha quino* (Lepidoptera: Nymphalidae)

Rudi Mattoni,¹ Gordon F. Pratt,² Travis R. Longcore,¹ John F. Emmel,³ and Jeremiah N. George^{1,2}

¹Urban Wildlands Group, UCLA Department of Geography, Box 951524, Los Angeles, California 90095-1524

²Department of Entomology, University of California, Riverside, California 92521

³Hemet, California

Abstract. With the listing of the quino checkerspot butterfly, *Euphydryas editha quino*, as a federally endangered species, research into its ecology and conservation is necessary to allow for recovery planning and management. We review systematics, distribution, natural history, and conservation prospects, with reference to pertinent literature about other *E. editha* subspecies. Additional information is presented from museum specimens and ongoing research on the species.

Keywords. Quino checkerspot butterfly, *Euphydryas*, endangered species, conservation

INTRODUCTION

The quino checkerspot butterfly, *Euphydryas editha quino* (Behr) 1863 (QCB or *quino*), was listed as an endangered species on January 16, 1997 (62 Federal Register 2313). The basis for the listing was habitat loss, degradation, and fragmentation, recognizing additional negative effects from fire management practice. All factors are the results of intensive human economic development of ever diminishing resources. Recent loss of the distribution area of *quino* was estimated as 50–75%, with “seven or eight populations” known in the United States with “all but three populations” consisting of fewer than five individuals (Nelson 1997). Surveys over the past year indicate that although QCB may not seem in as dire circumstance as the listing package indicated, with at least two robust metapopulations found in two counties and numbering thousands of individuals, we believe the species was correctly assessed as near extinction. QCB appears headed toward becoming the “passenger pigeon” butterfly — a once common widespread species crashing to extinction over a few decades. This would be especially remarkable because an average female QCB lays over 500 eggs in a season compared with two eggs for the passenger pigeon. We summarize herein all pertinent data regarding QCB, discuss our reasoning for projecting its imminent disappearance in the absence of substantial effort, and emphasize the rather unique event this disappearance will be among the set of all U.S. endangered butterfly species.

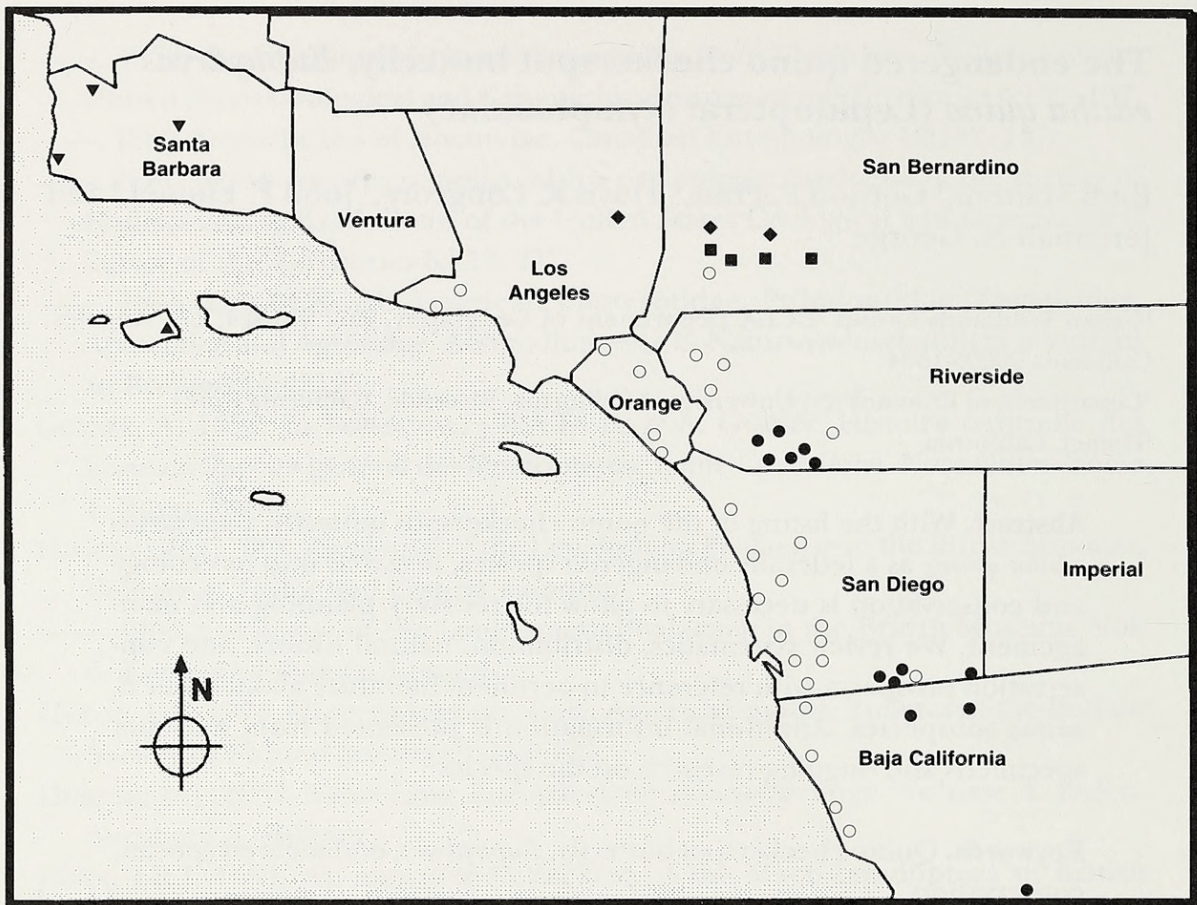


Fig. 1. Historic and current distribution of Quino checkerspot butterfly in southern California and Baja California, showing distribution of nearby subspecies of *Euphydryas editha*. Legend: ○ *quino* pre-1990, ● *quino* post-1990, ▲ *insularis*, ■ *augustina*, ◆ new subspecies, ▼ *editha*.

SYSTEMATICS

The QCB is one of over 20 recognized subspecies of *Euphydryas editha* (Miller & Brown 1981). *Euphydryas editha quino* is the most southwesterly distributed taxon and is parapatric with three other subspecies (Fig. 1): *editha* (Boisduval) 1852, *augustina* (W.G. Wright) 1905, and a new subspecies on the desert slopes of the Transverse Range to the southern Sierra Nevada. A fourth subspecies, *insularis* (Emmel & Emmel) 1974, occurs in southern California on Santa Rosa Island.

In adult appearance the QCB is distinguishable from all other subspecies by size and relative cover of red, yellow, black, and white scaling forming both upper- and underside maculation (Fig. 2). In nominotypical *editha*, black scaling predominates on the uppersides of the wings, covering approximately 50% of the wing surface, with cream spots covering about 25–30% and orange/red scaling covering about 20–25% of the wing surface. *E. e. quino* is similar to nominotypical *editha* in size, but differs in that the orange/red scaling is increased and cream spots are slightly larger. *E. e. augustina* is markedly smaller than *quino* and is similar in maculation to *quino* except that there is greater development of orange/red scaling in *augustina*. The desert slope Transverse Range segregate is intermediate in size between

quino and *augustina*, and tends to have greater development of both orange/red and cream scaling than either of these taxa. *E. e. insularis* is similar to nominotypical *editha* in size but differs from that subspecies by greater development of black scaling and greater reduction of the orange/red scaling relative to the cream scaling.

There are additional defining larval characteristics, but these have not been systematically described for all subspecies (D. Murphy & G. Pratt, unpub. data). Foodplant utilization by QCB in the wild is restricted to *Plantago erecta* E. Morris, possibly *P. ovata* Forsskal [= *P. insularis* Eastw.], and *Castilleja exserta* (A.A. Heller) Chaung & Heckard [= *Orthocarpus purascens* Benth.]. Among *E. editha* subspecies, this foodplant utilization pattern is shared with nominotypical *editha* and *insularis*. In a study that did not include *insularis*, Baughman et al. (1990) presented genetic evidence that *quino* is more closely related to *editha* than other subspecies.

A contrasting view of *E. editha* was given by Scott (1986), who recognized only three subspecies: *editha*, *nubigena*, and *beani*, and stated that “Dozens of localized races have been named, but they all fit into these three ssp.” In our opinion Scott’s view under-represents variation (see also Baughman & Murphy, in press).

There have been two recent nomenclatorial changes with the taxon. The first was assignment of *editha* to the genus *Occidryas* (Higgins 1978). However, the erection of *Occidryas*, although accepted by a few uncritical authors (e.g., Miller & Brown 1981), was unsubstantiated by morphological or genetic evidence. All objective authorities synonymized it to *Euphydryas*. The other matter was recognition of *quino* as the correct available name for the taxon which earlier had been referred to as *wrighti* (Emmel et al., in press, a). Although Gunder (1928) associated the name *quino* with the *Euphydryas chalcona* complex, a critical examination of Behr’s description as well as the geographic parameters of collecting in the 1860s places *quino* with the *E. editha* species complex. A neotype for *quino* has been designated and the type locality fixed as San Diego, San Diego County, California.

The following summarizes the nomenclatorial treatment of *quino* and the three other named subspecies in southern California (format based on Miller & Brown 1981).

***EUPHYDRYAS* Scudder**

editha (Boisduval) *MELITAEA*.

a. ***e. editha*** (Boisduval) *MELITAEA*. Ann. Soc. Ent. France, (2) 10:304 (1852). Type locality restricted to Twin Peaks, San Francisco, California, and lectotype designated, in U.S. National Museum, by Emmel et al. (in press, b).

= *bayensis* Sternitzky. Canadian Ent., 69:204–205 (1937). Type locality

Hillsborough, San Mateo Co., California. Syntypes in California Academy of Sciences, San Francisco.

b. *e. augustina* (W.G. Wright) *MELITAEA*. Butts. W. Coast: 154 (1905). Type locality San Bernardino Mtns., San Bernardino Co., California. Holotype in California Academy of Sciences, San Francisco.

c. *e. insularis* T. Emmel & J. Emmel. J. Res. Lepid., 13:131–136 1974(1975). Type locality Santa Rosa Island, Santa Barbara Co., California. Holotype in Los Angeles County Museum.

d. *e. quino* (Behr) *MELITAEA*. Proc. California Acad. Nat. Sci., 3:90 (1863). Type locality restricted to San Diego, San Diego Co., California, and neotype designated, in California Academy of Sciences, San Francisco, by Emmel et al. (in press, a).

= *augusta* (W.H. Edwards) *MELITAEA*. Canadian Ent., 22:21–23 (1890). Type locality vic. San Bernardino, San Bernardino Co., California. Lectotype in Carnegie Museum, designated by F.M. Brown, Trans. American Ent. Soc., 92:371 (1966).

= *wrighti* (Gunder). Pan-Pac. Ent., 6:5 (1929). Type locality San Diego, San Diego Co., California. Holotype in American Museum of Natural History, New York.

The name *augusta* has been applied to the *E. editha* populations in the San Bernardino Mountains since Comstock's publication of *The Butterflies of California* in 1927. However, examination of the lectotype specimen as well as consideration of the type locality (vicinity of San Bernardino, specifically Little Mountain northwest of the city; see Coolidge 1911, for a description of a day collecting on Little Mountain with W.G. Wright, during which he was told that this was the type locality for *Melitaea augusta*) clearly places the low elevation, phenotypically large *augusta* with *quino*. The name *augustina* is based on an aberrant specimen from the San Bernardino Mountains; because Wright considered it a new variety (his term for subspecies), the name can be used in a subspecific sense for the small phenotype, higher elevation San Bernardino populations of *E. editha*.

Populations of *E. editha* on the desert slope of the Transverse Ranges (San Bernardino and Los Angeles counties) that use *Castilleja plagiotoma* Gray as a larval host represent an undescribed subspecies; this taxon is being described by Baughman and Murphy (in press).

In spite of the importance of *E. editha* to population biology theory, there has been no recent revision of the overall species group. However, the patterns of variation and approximate phylogenetic relationships of the taxa surrounding *E. editha quino* are fairly well defined. Because of the sensitivity of *E. editha* *senso lato* to a suite of anthropocentric environmental im-

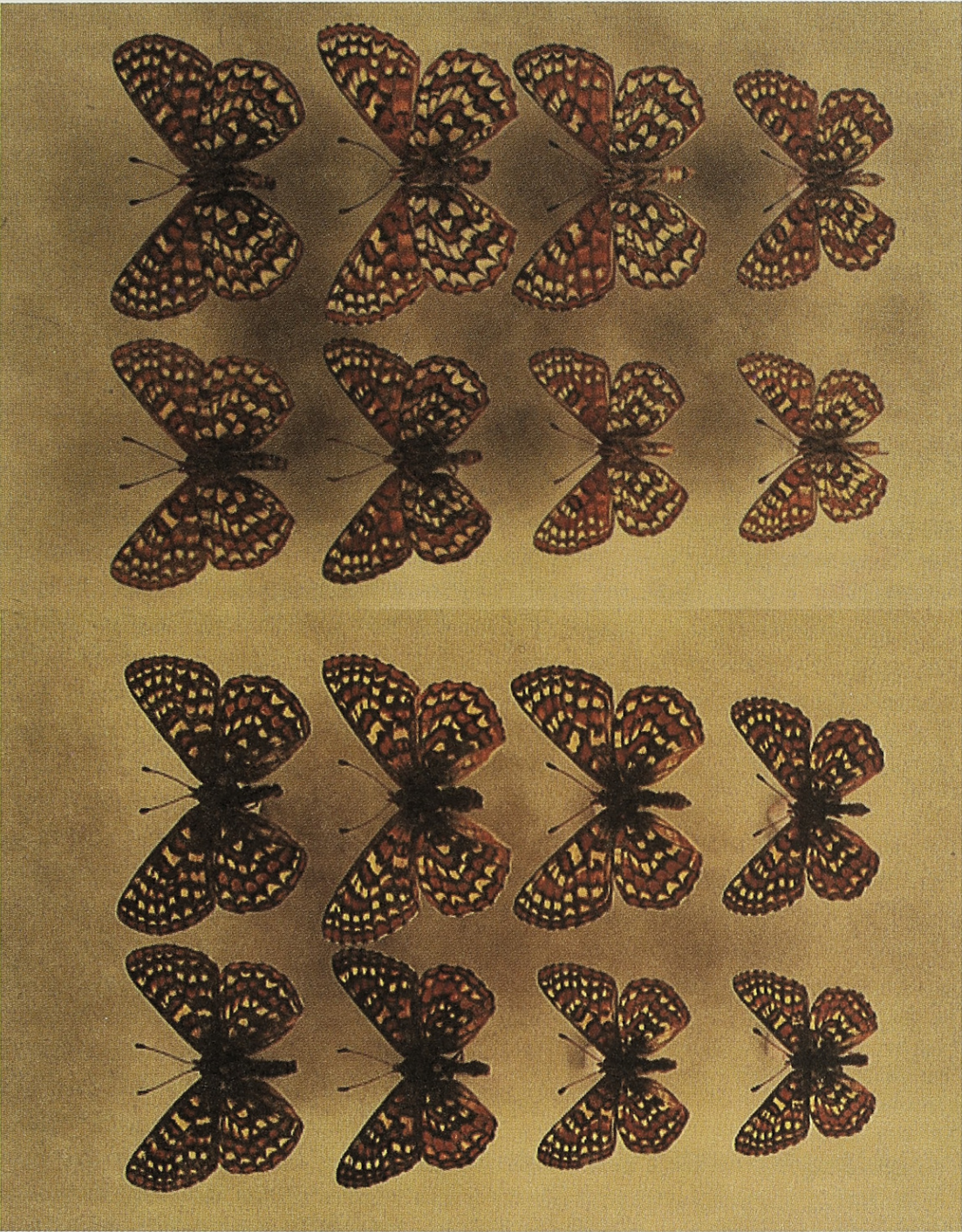


Fig. 2. *Euphydryas editha quino* and parapatric subspecies. Columns across: ♂ upperside, ♀ upperside, ♂ underside, ♀ underside. Top row: *editha*, ♂ CA: San Luis Obispo Co., Foothill Rd. near Los Osos, 29.IV.1976, ♀ same. Second row: *quino*, ♂ CA: San Diego Co., hills S of Lake Jennings, 25.III.1981, ♀ CA: San Diego Co., Dictionary Hill, 23.III.1975. Third row: new species, ♂ CA: San Bernardino Co., near Bowen Ranch SE of Hesperia, 14.IV.1987, ♀ same. Bottom row: *augustina*, ♂ CA: San Bernardino Co., Cienega Seca Crk., ♀ same. *E. e. insularis* is illustrated in Emmel & Emmel (1975).

Table 1. Localities for *Euphydryas editha quino* and most recent date of collection or observation. A list of museum specimens is available from the authors upon request.

Mexico

Estrado de Baja California

N of Ensenada	1935	Spring Valley	1969
Las Animas Canon	1935	SE of El Cajon	1970
Mosquito Springs	1936	Proctor Valley	1971
Rodriguez Dam, Tijuana	1977	Otay Lake	1973
S of Salsipuedes	1979	Mt. Palomar	1975
N of Sordo Mudo	1979	San Diego	1976
Table Mt. (near Rosarita Beach)	1979	Chula Vista	1978
Turn off to Ojos Negros	1981	Little Cedar Canyon	1979
Valle de La Trinidad, Aquaito Spring	1994	Mesa E of Otay Reservoir	1979
N of El Testero	1996	Otay Mesa	1980
S of El Condor	1996	Dictionary Hill	1981
		Brown Field	1997

California

San Diego County

San Francisquita Pass	1914	Otay Mt., ridge S of O'Neal Canyon	1997
Warner's Dam	1916	South Otay Mt., Marron Valley	1997
South San Diego	1917	Jacumba	1997
Santa Fe Ranch	1930	North slopes of Tecate Peak	1997
Lake Hodges	1932	Riverside County	
Rancho Santa Fe	1933	Sage	1951
Alta Vista	1934	Lake Elsinore	1983
Adobe Falls, San Diego	1948	Gavilan Hills	1985
Division Street, San Diego	1948	Murrieta Hot Springs	1997
Vista	1951	Aguanga	1997
Dehesa	1957	Oak Mountain	1997
San Miguel Mt.	1957	Temecula	1997
El Cajon	1958	Lake Skinner	1997
La Presa, San Diego	1958	Orange County	
Miramar	1960	Hills E of Orange Co. (Irvine) Park	1917
Mission Gorge	1960	Anaheim	1930
Tecate Mt.	1961	Laguna Lakes	1931
Fletcher Hills near El Cajon	1963	Hills N of Orange Co. (Irvine) Park	1934
Sweetwater Dam/Reservoir	1969	Dana Point	1936
Encanto	1969	Irvine Park	1937
Kearney Mesa	1969	Hidden Ranch	1967
Paradise Mesa, National City	1969	Los Angeles County	
		Tapia Camp, Santa Monica Mts.	1947
		Pt. Dume	1954

pacts now entrained, it would be well to document geographic variation patterns and correlated natural history characteristics into a formal revision as quickly as possible.

DISTRIBUTION

The few known persistent populations of the QCB are large in area, distributed as complex metapopulations. In attempting to reconstruct historic QCB distribution, this hypothesis implies that specimens collected prior to 1940 most likely represent samples of extensive, and not small refugial, populations. Maps of presumed historic vegetation communities (e.g., K  chler 1977) and documented specimen localities indicate that the QCB may have had an almost continuous distribution across cismontane south-

ern California from the westernmost Santa Monica Mountains, where dense but local concentrations of *Plantago erecta* still persist, across the Los Angeles plain and margins of the Transverse Ranges into the desert in upper Anza-Borrego and thence south into Baja California to about the northern San Pedro Martir (Fig. 1; Table 1). It was abundant on coastal bluffs in Point Dume in western Los Angeles County, Orange County (John Johnson, in litt. 1989 and see Orsak 1977), and the northern Baja California coast (Brown et al. 1992). All the coastal bluff populations have probably been destroyed with the possible exception of refugial colonies in the inaccessible coastal region between Ensenada and Cabo Colonet. During the past 20 years most of the coastal Baja terraces have been converted to high density agriculture.

By reasonable extrapolation, the first European missionaries to southern California made large negative impacts that are now immeasurable. In addition to direct land conversion, they caused many destructive secondary effects including introduction of grazing animals and many preadapted invasive Mediterranean plant and invertebrate species, introduction of destructive agricultural practices, general resource depletion, and modification of native American lifestyles. With open grass- and forb lands in the general scrub communities taking the brunt of habitat destruction, the QCB from that moment forward likely suffered more than any butterfly species of southern California. The importance of harvested *Plantago erecta* as a major grain resource of Native Americans provides some insight as to the quantities of this plant that were available, but are now more restricted. From the initial missionary invasion in the 1770s, the tide of acculturated humanity has unceasingly brought on natural habitat degradation by outright destruction, fragmentation, soil ecosystem disturbance, and explosions of nonnative species. Nevertheless, as recently as the early 1900s, two flora of Los Angeles reported that *P. erecta* was "Very common on dry plains and in the foothills throughout our range [Los Angeles and Orange counties]" (Abrams 1903) and "On dry hillsides throughout the south; the common species" (Davidson & Moxley 1923).

Any reconstruction of the former distribution of QCB is complicated by relying on museum specimens, which provide only presence data, and then only for localities frequented by collectors. Our recent discovery of populations across the southern slope of Otay Mountain and north of Tecate Peak indicates that previous collection localities were far from exhaustive. Casual collections rather than systematic surveys are the norm for our knowledge of historic butterfly distributions. The geographic extent of collection records, taken with the historic abundance of foodplant, leads to the presumption that *quino* was once commonly, if patchily, distributed from Point Dume to Ensenada and inland up to 60 miles (100 km).

Recently, Parmesan (1996) surveyed *Euphydryas editha* populations across the entire species range, sans the Rocky Mountain populations, to test the hypothesis that global warming should cause "net extinctions to increase in the south and at low elevations and to decrease in the north and at high

elevations.” After censusing 151 previously recorded populations, she concluded that there indeed was a correlation, acknowledging that the relationships expected were complex, particularly with regard to habitat destruction and its effect on recolonization. Given the complex population structure of *E. editha*, and our observation that human impacts were almost always involved in local extirpations in southern California (even for those areas that may seem to still have “suitable habitat”), the role of global warming as the proximate cause of extinction of *E. e. quino* populations must be carefully evaluated. We suspect that warming is perhaps an exacerbating factor, but that increased extinction rates in southern California are primarily caused by more direct anthropogenic forces.

NATURAL HISTORY

The studies of Paul Ehrlich and his many students and colleagues have produced a large body of information about *Euphydryas editha* as a species, mostly concerning the bay checkerspot, *Euphydryas editha editha* [=bayensis] (BCB). Most of this work is applicable to the QCB (e.g., Ehrlich 1965, Labine 1965, Ehrlich et al. 1975, 1980, Ehrlich & Murphy 1987, Ehrlich & Wheye 1984, 1986, 1988, Launer & Murphy 1994, Murphy et al. 1983, Murphy & Weiss 1988, Singer 1971, 1983, Singer & Thomas 1992, Baughman et al. 1990, Dobkin et al. 1987, White 1986, Weiss et al. 1987, 1988).

Life cycle

The QCB is univoltine with adults usually flying from late February into April (but see anomalies in phenology below). Females usually mate only once, and are “plugged” by males, which inhibits multiple copulations (Labine 1964). Shortly thereafter gravid females begin laying egg masses of 120–180 eggs (Ehrlich et al. [1975] record a minimum of 39 eggs per mass for *quino* in the field), which hatch in 7–10 days. Murphy et al. (1983) experimentally demonstrated in BCB that nectar feeding is essential to maximize egg mass production beyond the initial two masses, and in all cases subsequent egg number per mass decreased. Total egg production ranged from about 400–800 per female. The emergent prediapause larvae undergo two or three obligate moults, depending perhaps on the quality of the foodplants, and then enter an obligate diapause as either third or fourth instar larvae (G. Pratt, unpub. data). The prediapause larvae are gregarious, usually spinning a communal web, whereas postdiapause larvae are solitary.

Surviving larvae break diapause after winter rains of the next season are sufficient to germinate and establish foodplant. These postdiapause larvae go through three to perhaps seven or more additional instars and then pupate, usually among low plants near the ground or under rocks if such occur (G. Pratt, unpub. data, White 1986). Pupae mature and eclose in about ten days. Once larvae enter diapause their survival rates likely increase given that postdiapause larvae can repeat diapause at least once, and perhaps several times (D. Murphy & G. Pratt, unpub. data). There is also variation

in larval coloration that may be geographic. White (1986) discusses several less studied aspects of the life history of *E. editha* subspecies.

Because of their dependence on annual foodplants that senesce and dry rapidly following the last rain of a season, prediapause larvae are the stage most susceptible to mortality. If neonate larvae cannot find foodplant within 10 cm of the egg masses, they will starve (Singer 1972, Singer & Ehrlich, 1979). Singer found approximately 99% mortality in the prediapause cohort leaving little room for other factors, at least in the seasons of the years studied. Singer and Ehrlich concluded that the major population regulators were density independent, highly variable weather conditions. Prediapause larvae (BCB) survived under three different conditions: 1) if eggs were laid when *P. erecta* would remain green for five more weeks, 2) if eggs were laid on *P. erecta* in soil tilled by pocket gophers (*Thomomys bottae*), which plants have deeper root systems and are generally more robust (see Hobbs & Mooney 1985), or 3) if larvae were able to locate the larger secondary foodplant *Castilleja exserta* (Singer 1972, Ehrlich et al. 1975).

Foodplants and nectar sources

Under field conditions the QCB essentially is restricted to the two larval foodplants, *Plantago erecta* and *Castilleja exserta*, throughout its range. Where present, *Plantago ovata* may be used although these plants are not usually abundant in QCB territory. *P. ovata* may be a long-naturalized exotic species from the Mediterranean region (Dempster in Hickman 1993). One larva was observed on *Keckiella antirrhinoides* (Benth.) Straw (G. Ballmer, unpub. data), a plant not common in QCB range. In the laboratory females oviposit and larvae feed on other *Plantago*, *Keckiella*, and *Penstemon*, including plant species found at QCB localities that are not used in nature. Although the patterns of *Euphydryas editha* oviposition choice and larval foodplant specificity have been elucidated in geographical context by Singer (1971, 1982, 1983), the physiological significance remains unknown. Experimental trials have not been conducted on *quino* to determine host preference.

Nectar sources are almost entirely small annuals that flower in synchrony with appearance of adult QCB. These include *Lasthenia* spp., *Cryptantha* spp., *Gilia* spp., *Linanthus dianthiflora*, *Salvia columbariae*, and annual *Lotus* spp. Most perennial plants are not in flower during the average QCB flight period. However, we observed QCB nectaring at *Eriodictyon* spp. late in the season.

Phenology and microclimate

Murphy and Weiss (Murphy & Weiss 1988, Weiss & Murphy 1988; see also Weiss et al. 1993) provided a detailed study of fine scale distribution of the BCB in terms of relative densities of both larvae and adults to slope and exposure (microtopography) and the resultant microclimates produced by insolation effect. They showed that the distribution of larvae, which were highly clumped, changed between years depending on weather patterns, and also moved in response to climatic factors. Position of larvae across the

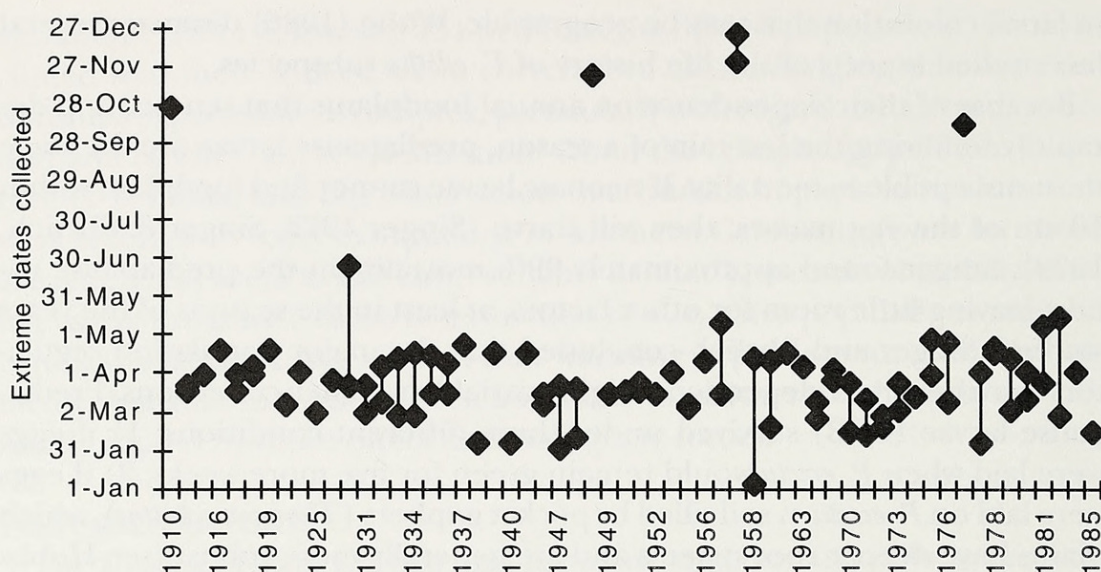


Fig. 3. Extreme collection dates of *Euphydryas editha quino* from museum specimens. Lines connect dates assumed to be within the same flight season. Note the fall emergence of adults in 1910, 1948, 1957, and 1976. All of these years had significantly greater than normal rainfall in September and October; 1957 and 1976 were El Niño years.

microclimatic strata affected their phenology and the timing of adult emergence. They also determined during the four-year study that population density centers shifted, with resultant variability in rates of postdiapause larval development to pupation and eclosion. The complex pattern of adult emergence, oviposition, and foodplant status (senescence) is described in terms of “phasing” to weather patterns in any season (Dobkin et al. 1987). These results illustrate that persistence of complex metapopulations depends on maintaining large and variable habitats with a broad range of microenvironments that may not be obvious at a glance.

Adults usually fly from February through April, but substantial variation has been recorded. Known adult flight dates are shown in Fig. 3, tabulated from museum specimens. Late fall adult emergence in 1910, 1948, 1957, and 1976 is correlated with significantly greater than normal rainfall during September and October (measured in San Diego) of those years, which may or may not be associated with an El Niño/Southern Oscillation event (1957 and 1976 were El Niño years). These extreme emergence dates suggest that larval phenology is plastic; larvae are able to break diapause virtually anytime in response to rain sufficient to establish foodplant. However, early adult emergence dates also require sufficiently warm weather as to not slow larval development. Dobkin et al. (1987) suggested that El Niño years were in fact detrimental to *editha*, because larval development and subsequent adult emergence were delayed by the cool, damp thermal regime more than foodplant vigor was prolonged — the butterfly and the foodplant were “out of phase.” For El Niño, this condition may have been unique to the Jasper Ridge colony studied, because the serpentine soil is

extremely porous and excess rainfall drains quickly. Drought, too, was shown to be detrimental to *editha* populations (Ehrlich et al. 1980, Ehrlich & Murphy 1987). In sum, weather conditions may cause the time of adult flight to vary anywhere from October to June.

Predators, parasitoids, and disease

Quantitative data on predation are available for the BCB, where mortality from parasitism in mature larvae was about 5% and in pupae about 50% (Weiss et al. 1988, White 1986). The only QCB data are for 200 larvae collected at Lake Skinner, of which three were parasitized by tachinid flies (K. Osborne, pers. comm.). No other field data concerning predation or disease are available, although ground dwelling larvae must be vulnerable to a number of spiders, ants, and carabid beetles. Nothing is known about QCB diseases.

Mating behavior and hilltopping

Mating behavior is an important factor in population dynamics. At locations with high population densities of the QCB, mate locating usually involves actively flying males seeking perched females. Females rest on the ground or low plants near where they eclosed, with wings spread, awaiting males. At locations where there is topographic relief combined with dispersed nectar and foodplant resources, females frequently move to high points, ridges and hilltops, where they encounter perching males (see Ehrlich & Wheye 1984, 1986, 1988). Here, males await females and usually defend small territories.

The latter phenomenon, hilltopping, has been described and documented for butterflies by Shields (1967) and is defined as “a phenomenon in which males and virgin or multiple-mating females instinctively seek a topographic summit to mate.” According to this theory, high ground, ridges, hilltops, or even rock formations serve as visual beacons for sexual encounters. Larval foodplant or adult nectar sources may or may not be present, but males usually defend perches and/or patrol territory. At sites where both nectar and foodplant resources are also associated with “hilltops,” butterfly occurrence is adventitious and is not necessarily hilltopping unless mating can be shown to be the purpose of butterfly presence. Nor is it the case where hilltop presence is the result of “random” movement across high ground. Unequivocally discriminating mate location from resource occurrence (and resource seeking) on “hilltops” requires statistical analysis. Shields provided quantitative data for one species, *Papilio zelicaon*, whereas a summary table of species he presents as hilltopping (including *quino*) is not supported by documented evidence. Regardless, however, there is a clear tendency among many volant insects to congregate at high ground regardless of sex or resources (see refs. in Shields 1967).

While Ehrlich and Wheye (1984, 1986, 1988) presented evidence supporting hilltopping in *E. editha*, Singer and Thomas (1992) disagree. They argue that hilltopping, defined as a behavioral preference for a resource, can-

not be distinguished using measures of resource use (e.g., sex ratio on hilltops). Rather, to show hilltopping, one must observe a tendency in individual males or virgin females to move toward hilltops, or a trend for mating location to be closer to hilltops than emergence location, neither of which has been shown for any *E. editha* subspecies (Singer & Thomas 1992). Singer and Thomas' argument does not suggest that butterflies are not found on hilltops; it only questions the explanation for their presence. However, determination of the ecological and evolutionary role of the distribution of *E. editha*, especially *quino*, on hilltops is of important conservation value. If indeed *quino* congregate on hilltops to mate, the conservation value of those hilltops will be great.

Our observations across southern San Diego County during spring 1997 (Pratt et al. 1997) provided evidence of QCB using hilltops, although insufficient data were collected to prove hilltopping as prescribed by Singer and Thomas (1992). Our survey team found virtually all QCB as "hilltoppers" in the sense of appearing to be concentrated on ridges and peaks. Across the slopes of Otay Mountain and Tecate Peak, individuals (mostly ovipositing females) were found infrequently on lower slopes in comparison with ridges. By contrast, QCB populations across extensive flat grasslands, as in the vicinity of Murrieta, are found where there is little or no relief that provides hilltops (G. Ballmer, pers. comm.). There are also large expanses of *Plantago erecta* and *Castilleja exserta* with abundant nectar from sites where the species has been extirpated (Gavilan, March AFB, etc.), sites both with and without relief. Dense, shrub-covered areas, including high relief sites, do not have QCB populations. Thus the determination of whether a specific upland, ridge, rock outcrop, or hill serves for hilltopping behavior remains subject to interpretation and depends on the areography of the *quino* aggregates in question, their place in the vegetation matrix, and population density.

Population cycles and structure

Long-term studies initiated by Paul Ehrlich on the BCB in 1959 provided quantitative data showing large fluctuations in population density from year to year. As his work progressed it became apparent that the fluctuations were caused primarily by weather patterns, principally rainfall quantity and timing. After the major drought years, populations crashed, then variably recovered with return of favorable rains (Ehrlich et al. 1980). In the past two years, however, his major study population at Stanford's Jasper Ridge seems to have been extirpated. Although there are only anecdotal records on the QCB, cyclic fluctuations have been recorded.

The late John Johnson (in litt. 1989) observed *quino* for over 60 years in Orange County and noted significant changes in densities over time. The QCB was collected in abundance at Irvine County Park between 1917 and 1922 and then apparently almost disappeared until 1928. In 1933 and 1934 the species was again common, but vanished thereafter and was never seen again. A nearby colony about 0.5 miles (0.8 km) southwest of Hidden Ranch

in Black Star Canyon, Santa Ana Mountains, was known from the 1920s to 1930s. After two decades without records James Mori found the butterfly abundant in March 1967. A severe fire in November 1967 burned the area and the butterfly has not been seen since. Two large reservoirs were constructed near Irvine Park and the whole area has been subjected to ever-increasing trampling over the 30 years since Mori found the last QCB in this part of the Santa Ana Mountains.

Harrison (Harrison et al. 1988, Harrison 1989) has proposed a metapopulation model for the BCB, a description which probably also fits the QCB. A metapopulation is a set of populations that are usually demographically independent (as Ehrlich found among the three populations of BCB at Jasper Ridge, 1965), but that are “interdependent over ecological time” (Harrison 1988). The evidence from *editha* is that local populations vary independently and occasionally suffer extinctions, but are recolonized from other populations. At Morgan Hill, there is a “reservoir” population that is large, stable, and much less likely to suffer extinction, even during a bad year. Surrounding smaller patches are periodically recolonized from the reservoir population. Because of the sedentary nature of *E. editha*, these small patches of once-occupied habitat may remain unoccupied for long periods before being recolonized (Harrison 1989).

Current data are insufficient to describe conclusively the population structure of *quino*, but observed patterns and anecdotal evidence suggest that it is similar to that of BCB. The distribution observed during 1997 surveys on Otoy Mountain was patchy, with the butterfly exploiting temporally limited resources in some localities (post-fire chaparral, see below). Localities are separated by several to tens of kilometers, and can be assumed to be demographically isolated. The existence of a reservoir population has yet to be shown. QCB could have a true metapopulation structure (small patches, low dispersal) or a core-satellite structure typified by a reservoir population and smaller outlying habitats.

In the Gavilan Hills, Riverside County, anecdotal accounts of *quino* abundance and distribution seem to be consistent with a core-satellite population structure. At one location, on private land near Harford Spring Park, *quino* was abundant and always present, according to accounts from collectors reaching back to the 1930s. QCB were also found on outlying patches as far as 5 miles (8 km) distant (G. Pratt, unpub. data), but never in the numbers or consistency as adjacent to Harford Spring Park. In 1984 the landowner disked the presumptive reservoir population, completely destroying its habitat value. The butterfly subsequently disappeared in the surrounding region.

Plant community associations

The QCB is not associated with a single plant community, as are many butterflies, but instead with open spaces within several communities. Furthermore, QCB resource and climatic requirements are met, over the long term, by dynamic relationships that we can only generally recognize and at

present describe rather imprecisely. The butterfly is found within several plant community types from scrub on coastal bluffs, through coastal sage scrub, chaparral, oak woodland, to desert pinyon-juniper woodland. In all these communities, however, it is only found in openings within the dominant plant community where there is sufficient local cover of the larval foodplants, which usually co-occur with the annual forbs that provide most nectar for adults. Sufficient foodplant density has yet to be determined; at Lake Skinner, QCB have occupied areas with foodplant densities as low as one plant per square meter (K. Osborne, pers. comm.). The butterfly does not occur in extensive open grasslands, nor does it occur in dense (without small clearings) coastal sage scrub, chaparral, or oak woodland. Plant community structure, and not dominant species composition, is the critical factor for QCB populations. The optimum habitat for oviposition and larval development consists of patchy shrub or small tree landscapes with openings of several meters between large plants. Landscapes with alternating open swales and dense shrub patches also provide habitat.

Among known colonies, there is usually some topographic relief such as raised mounds, low to high hills, slopes, and ridges. The species was common on Otay Mesa before urbanization; the natural landscape was one of vernal pool depressions alternating with a relief of mima mounds. Prior to widespread habitat destruction, the species was apparently abundant on coastal bluffs, which were characterized by sparse low vegetation.

Plant community identity as normally construed (i.e., dominant cover) is less helpful in defining *quino* habitat than is consideration of larval foodplant abundance and distribution, nectar source availability, and microtopography. In addition, cryptobiotic crusts and episodic disturbances such as fire and light grazing contribute both to creating and maintaining suitable habitat.

Cryptobiotic crusts. In surveys for stands of *Plantago erecta* on Otay Mountain, we observed that the species was correlated with the presence of undisturbed cryptobiotic crusts (also called cryptogamic or microbiotic crusts, St. Clair & Johansen 1993). Cryptobiotic crusts are formed in soils in arid environments by blue-green algae, lichens, mosses, and other lower plant species, as well as fungi and bacteria (Belnap 1993). Research has shown that cryptobiotic crusts increase the ability of the soil to hold moisture and decrease its susceptibility to erosion through the adhesive qualities of mucilaginous polysaccharides exuded by certain blue-green algae and fungi (Belnap & Gardner 1993). They also improve the availability of essential minerals (N, P, K, Ca, Mg, Fe) for higher plants and provide conditions that promote mycorrhizal associations (Harper & Pendleton 1993). Crusts are easily disturbed by trampling, especially by cattle. At Otay Mountain, we observed that *P. erecta* and other native annual species (e.g., *Lasthenia* sp., *Castilleja* sp., *Lepidium* sp.) were more often found in areas that had crusts intact, as identified by their characteristic patina and the presence of small mosses. In general, the proportion of native to exotic plant species was observed to be larger in areas with intact crusts. We speculate that crusts serve the role of "gatekeeper," allowing the germination of native species and

perhaps inhibiting exotic species. However, crust areas have more “bare” ground (actually occupied by lichens, small mosses, algae, etc.) than non-crust areas, a characteristic preferred by the QCB. Cryptobiotic crusts are also usually darker (and thereby warmer) than surrounding soils (Harper & Pendleton 1993), making them attractive locations for QCB thermoregulation. The combination of native annuals (foodplant and nectar sources) and open ground may be encouraged by different edaphic factors (e.g., high clay content) in other areas. The BCB is found in grasslands defined by serpentine soils, which, much like crusts, support sparse native vegetation.

Grazing. In areas of heavy grazing, the annual plant cover at Otay Mountain was largely dominated by *Erodium* spp. (mostly *E. botrys*). In grazed areas, *Plantago erecta* was absent, all available space being preempted by the prostrate storksbills. *P. erecta* tended to occur in areas that would be less accessible to cattle, such as steep or rocky areas. Our observations about cryptobiotic crusts suggest a pathway of replacement wherein trampling by cattle disrupts the crusts, allowing establishment of the exotic *Erodium*, which in turn excludes *P. erecta*. Cattle also disperse *Erodium* seeds, thus further facilitating the invasion. Such animal-mediated disturbance has been implicated elsewhere in the spread of alien plants (Schiffman 1997a), and the quantity of seed dispersed by cattle has been shown to be enormous (Malo & Suárez 1995). However, light grazing may serve to maintain QCB habitat by promoting forb-dominated, intermediate successional grassland stages, as discussed for the southern habitat patches of the BCB by Murphy and Weiss (1988). But too much grazing has been implicated in local extirpations (Murphy & Weiss 1988). Light grazing by native ungulates was historically present throughout the QCB range, and emulation of it may indeed be necessary to maintain stable habitat areas. Also, regular disturbance by fossorial rodents may have contributed to maintaining areas dominated by annuals (Schiffman 1997b, Longcore, in prep.). Such disturbance by pocket gophers has already been shown to contribute to foodplant quality and BCB larval survival (Hobbs & Mooney 1985, Ehrlich & Murphy 1987).

Fire. Areas on the western side of Otay Mountain occupied by QCB in 1997 were in early post-burn succession. Adult QCB, *Plantago erecta*, and ample nectar sources were found throughout recently burned areas. QCB distribution was limited by the edge of the burn, which was marked by dense, mature chaparral. Although in some areas *P. erecta* distribution is stable, it can also be found tracking disturbance, with a distribution variable in both space and time. Like other “fire-followers,” *P. erecta* grows well following disturbance (usually fire, but also other one-time events), sets large amounts of seed, and then thins out as the canopy is closed by the regenerating shrub layer. The regionally dynamic metapopulation structure of the QCB is adapted to such geographic and temporal variation in foodplant distribution.

The variable and synergistically interacting factors that contribute to appropriate *quino* habitat make defining essential areas for species survival

difficult. What is one year closed canopy chaparral may the next year be covered with foodplant and flowering annuals, posing a special challenge to conservation efforts. Protecting sufficient habitat may mean protecting large enough areas to allow for a natural fire regime to maintain a shifting mosaic of habitat patches.

CONSERVATION PLANNING

With exception of the QCB and the BCB, all Nearctic butterflies listed under the Endangered Species Act have restricted distributions and/or highly specific habitat requirements. The threatened Karner blue butterfly (*Lycaeides melissa samuelis*) has a 1,000-mile wide geographic distribution, but is restricted to small dynamic successional habitat patches that support its one foodplant. The highest extinction probability is for species found only at single small sites. One limited catastrophe could destroy them: e.g., Lange's metalmark (*Apodemia mormo langei*) and Palos Verdes blue butterfly (*Glaucopsyche lygdamus palosverdesensis*).

By contrast, the QCB had a large range (ca. 200×60 miles [320×100 km], now reduced by over half), occurring over a continuum of climatic regimes from wet coastal to high desert; it is still found in several plant communities although it has only two hostplants, and likely maintains substantial genetic variation both hidden and expressed by local ecotypes. The key to its conservation will be management of the surviving populations under the assumption that they conform to a classic metapopulation structure. The fundamental feature of this scenario is the vulnerability of any metapopulation following the permanent loss of any of its demes (subpopulations) or fragmentation that would destroy dispersal patterns that connect them.

To ensure the conservation of the QCB, there must be some critical number of interconnected demes to provide a population structure with sufficient habitat variation that a viable effective population size is always maintained in some part of the metapopulation unit (Murphy & Weiss 1988). Available data do not permit even one metapopulation to be circumscribed even though at present there are three fairly large (each ca. 40–150 square miles [$100\text{--}390$ sq. km]) areas of distribution that may support at least one metapopulation: Otay Mountain, Temecula-Oak Mountain-Anza, and north central Baja. Although small refuge colonies may yet be found in parts of the historic range, as in Orange County and northern San Diego County, these colonies will be at high risk unless appropriate management plans are implemented to assure their survival, which may include providing corridors.

Murphy and Noon (1992), using the northern spotted owl as an example, provided a useful exercise in applying rigorous hypothesis tests to reserve planning. Their approach, which was to identify the minimum number of populations necessary to ensure species persistence, was a pioneering attempt to offset the usual socioeconomic constraints in conservation planning. Their first task was to determine if the data supported rejection of

the null hypothesis that the finite rate of population change (λ) was > 1.0 . The null hypothesis was rejected, leading to the recognition that their target species was in fact on the path to extinction (data concerning the QCB concur). Murphy and Noon then proceeded to test nine more hypotheses and concluded with a conservation map and strategy that were logically consistent.

Unfortunately, field data currently available are insufficient to provide a testable set of null hypotheses from which to design a reserve and management program for the QCB. The only operable current reserve design approach will be to maintain large contiguous parcels of land that will contain most, if not all, of the remaining metapopulations. The extent to which *quino* can tolerate limited development on these parcels currently cannot be assessed without further research on the autecology of the species. Tentative conservation requirements must include care to not overgraze, attention to the fire regime, and security of core cryptobiotic crust areas to preclude trampling. Whether sufficient land to preserve the species can be set aside, either through public ownership or voluntary conservation agreements with private landowners, remains to be seen.

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