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THREE BIOTYPES OF *APODEMIA MORMO* (RIODINIDAE) IN THE MOJAVE DESERT

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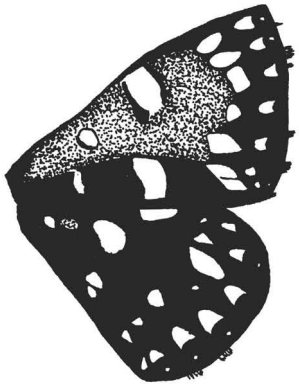
ABSTRACT: Along the western edge of the Mojave Desert and southeastern Sierra Nevada there occur three sympatric biotypes of *Apodemia mormo* (Felder & Felder) (Riodinidae). One is multivoltine and uses a wide variety of larval food plants, but most often selects and feeds on *Eriogonum inflatum* Torr. & Frem. (Polygonaceae). The other two are univoltine; one flies in the spring and feeds on *Eriogonum fasciculatum* Benth.; the other flies in late summer and eats various late-blooming, perennial *Eriogonum* species. These biotypes maintain different developmental patterns when reared under laboratory conditions. Various populations of the univoltine biotypes differ independently in adult wing patterns. The multivoltine biotype varies little throughout this area. These three biotypes may comprise distinct species.

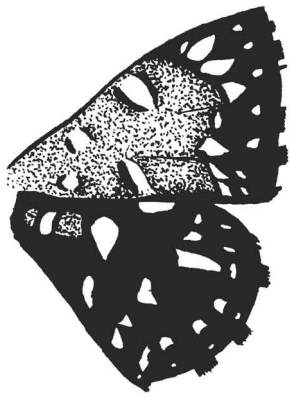
Additional key words: *Eriogonum*, Polygonaceae, diapause, California, food plants.

Apodemia mormo ranges throughout western North America from northern Mexico to southern Canada (Scott 1986). Throughout its range, there is pronounced geographic variation in adult wing pattern such that five allopatric species were once thought to exist (Opler & Powell 1961). Stichell (1911), however, reduced these to subspecies rank and since then four new subspecies have been recognized (Opler & Powell 1961).

We have found that three biotypes of *A. mormo* occur in an area bordering the western Mojave Desert and southeastern Sierra Nevada in California. This area includes the Little San Bernardino Mts., the northern slopes of the San Bernardino and San Gabriel Mts., and the southeastern slopes of the Sierra Nevada. Characteristics of the three biotypes are: (Type 1) multivoltine and most often ovipositing and feeding on *Eriogonum inflatum* Torr. & Frem. and various annual *Eriogonum* species (Polygonaceae); (Type 2) univoltine, spring-flying, and with *E. fasciculatum* Benth. as the sole larval food plant; (Type 3) univoltine, late-summer-flying, and with various late-blooming, perennial *Eriogonum* species as larval food plant. Although the two univoltine biotypes display geographic variation in wing characters, they can be distinguished wherever they are sympatric. The late-summer population (Fig. 1b, d) has either more dorsal orange or smaller white



a



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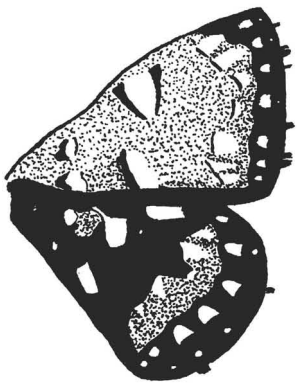

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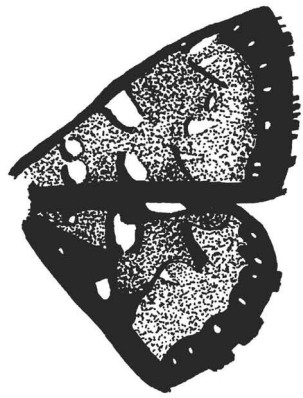

d

FIG. 1. Adult 'phenotypes' of the various *Apodemia mormo* populations found in the Mojave Desert. Basically, there are three colors on the dorsal wing surface: black, white, and orange (stippled area). The phenotypes are as follows: the near *dialeuca* phenotype (a) from Eureka Peak (Joshua Tree National Monument) (Type 2); the subspecies *mormo* (b) from Covington Flat (Joshua Tree National Monument) (Type 3); the near *virgulti* phenotype (c) from Pinyon Mt. (Type 2); and the subspecies *cythera* (d) from Mojave River Forks (Type 3).

macules than the spring population (Fig. 1a, c). The multivoltine biotype shows little variability throughout the area and resembles the late summer population of Covington Flat (Fig. 1b).

To determine whether these different biotypes are due to seasonal or host-related factors or to genetic differences, we reared a number of populations under similar laboratory conditions.

MATERIALS AND METHODS

Larvae of *A. mormo* representing five populations from southern California (localities numbered 1–5 as shown in Figs. 2 & 4) were reared in the laboratory in screened 1-liter plastic containers (two 25 cm^2 screened windows on the sides and complete screening on the top) on fresh *E. fasciculatum* (with branches set in water) at ca. 25°C. The *E. fasciculatum* was changed every 4–5 days or when needed. Egg and larval stage durations were recorded. Statistical differences in development times between the populations were determined by Duncan's Multiple-Range Test. The stages of development at various times of year for most subspecies of *A. mormo* were determined from field observations of adults, pupae, larvae, and ova. The eggs were measured to the nearest 0.01 mm using a dissecting scope with an ocular micrometer that was calibrated with a ruler.

Apodemia mormo females from the following populations were allowed to oviposit in screened 1-liter plastic containers on their *Eriogonum* larval food plant (host) or on *E. fasciculatum*: Eureka Peak, Little San Bernardino Mts., Riverside Co., California (Fig. 2, site 1) (adults mid-May)—host: *E. fasciculatum*; Juniper Flat, northwest slopes of the San Bernardino Mts., San Bernardino Co., California (Fig. 2, site 2) (adults mid-May)—host: *E. fasciculatum*; Pinyon Mt., southeast slopes of the Sierra Nevada, Kern Co., California (Fig. 2, site 3) (adults late-May)—host: *E. fasciculatum*; Mojave River Forks, northwest slopes of the San Bernardino Mts., San Bernardino Co., California (Fig. 4, site 4) (adults mid-August)—hosts: *E. fasciculatum* and *E. wrightii*; Old Woman Mts., San Bernardino Co., California (Fig. 4, site 5) (adults late-September)—host: *E. heermannii* Dur. & Hilg. All of the hosts were determined by adult association. Adult association was determined by observing adults (particularly females) land on the plants and wander through the branches and by correlating the distributions of the butterflies to the distributions of the plant (many *Eriogonum* species have patchy distributions as do the butterflies). These same plant species have been identified as larval hosts (by presence of larvae or eggs) of other neighboring populations of the same subspecies or phenotype of *A. mormo* (Pratt & Ballmer unpubl. data).

RESULTS

Among Type 2 populations along the southwestern margin of the Mojave Desert, there is a southeast-northwest clinal gradient in adult characters (Fig. 2). At the southeast end of this cline (Eureka Peak in the Little San Bernardino Mts.) adults have wings that have a dark black ground color with the dorsal orange restricted to a small area of the forewing and with large white macules (Fig. 1a). These populations resemble *Apodemia mormo dialeuca* Opler & Powell and the near *dialeuca* from above 2400 m on Sugarloaf Mt. in the San Bernardino Mts. (Stanford 1973). At Pinyon Mt., Nine Mile Canyon, and Walker Pass (>100 miles northwest of Eureka Peak), other Type 2 populations are lighter, with orange extending through much of the forewing and into the hindwing, and resemble *A. m. virgulti* (Fig. 1c). Between these areas, along the north slope of the San Gabriel Mts. and the northwest slope of the San Bernardino Mts. (examples: Juniper Flat and Cajon Pass), Type 2 populations are variable, exhibiting both the eastern and western extremes in wing pattern as well as various intermediates. Probably this is a blend zone between *dialeuca* and *virgulti* phenotypes, rather than blend zone between a dark *A. m. mormo* phenotype and *A. m. virgulti* as proposed by Opler and Powell (1961).

The phenotypes of the adult *A. mormo* reared from ova or larvae collected from *Eriogonum inflatum* at various sites (Kern Co.: Jawbone Canyon and El Paso Mts.; San Bernardino Co.: Danby, Granite Mts. near Victorville, Kramer Hills, Morongo Valley, Queen Mt. in Joshua Tree National Monument, and Yucca Valley) exhibited little variability and resembled Fig. 1b. In these adults the dorsal orange was restricted to the basal two thirds of the forewings and the white macules tended to be larger than in *cythera*, but smaller than in the near *dialeuca* phenotype from the Little San Bernardino Mts. Additional localities of this Type 1 *A. mormo* are shown in Fig. 3.

The phenotype of the Type 3 populations (from the southeastern slopes of the Sierra Nevada down to the northern slope of the San Gabriel Mts. and east to the north slopes of the San Bernardino Mts.; Fig. 4) is very orange dorsally, with orange extending beyond the basal two thirds of the forewing as well as into the hindwing (subspecies *A. m. cythera*—Fig. 1d). This orange tends to be browner and the dorsal white macules tend to be smaller than that of the sympatric spring-flying *A. mormo* nr. *virgulti* Type 2 populations (Fig. 1c). To the east (starting from Cactus Flat just north of Baldwin Lake) along the northeast slopes of the San Bernardino Mts., the phenotype of the Type 3 populations (Fig. 1b) is darker, with the dorsal orange usually restricted to the basal two thirds of the forewing, much like *A. m. deserti* (some

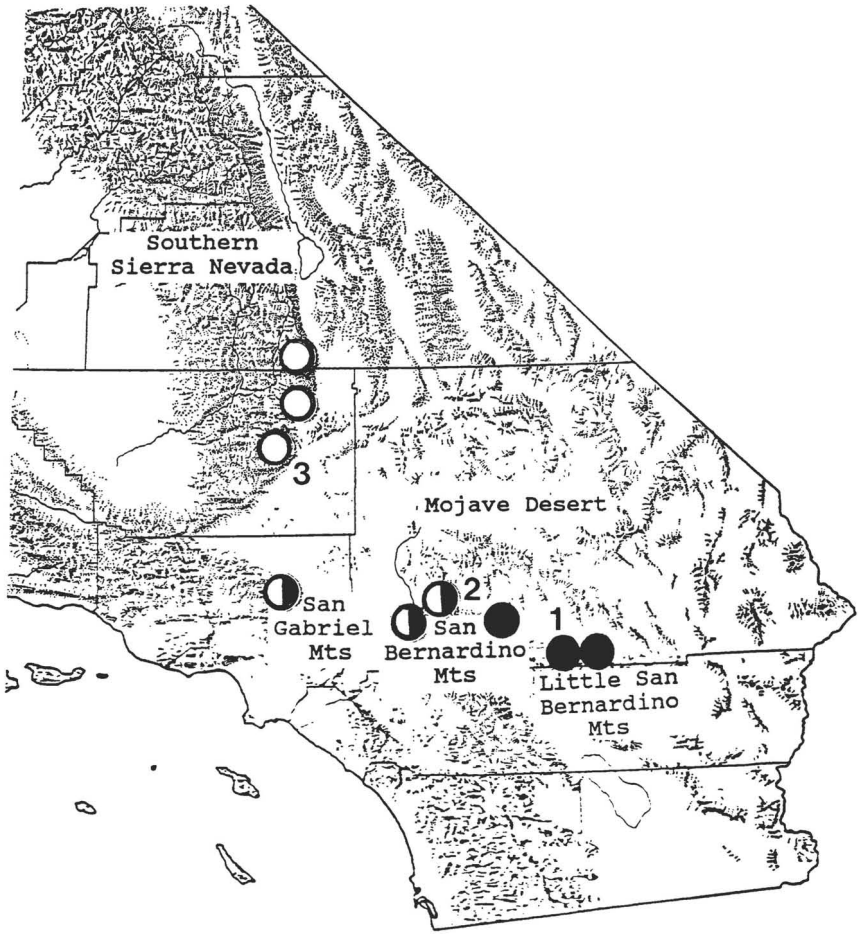

FIG. 2. Map of southern California showing locations of Type 2 populations found along the edge of the Mojave Desert. The closed circles are localities where the near *dialeuca* phenotype (a in Fig. 1) is found, the open circles are localities where the near *virgulti* phenotype (c in Fig. 1) is found, and the half closed circles denote populations with various intermediates between these two phenotypes. The localities in Table 1 are as follows: 1 is Eureka Peak, 2 is Juniper Flat, and 3 is Pinyon Mt.

individuals exhibit more extensive orange scaling that extends weakly into the hindwing).

The three biotypes had different development times under identical laboratory conditions. Populations from the western Mojave Desert reared from ova, collected from *E. inflatum*, exhibited a Type 1 life history with ova hatching 10 days after oviposition and larval durations of approximately 70 days. These populations (*Apodemia mormo deserti*

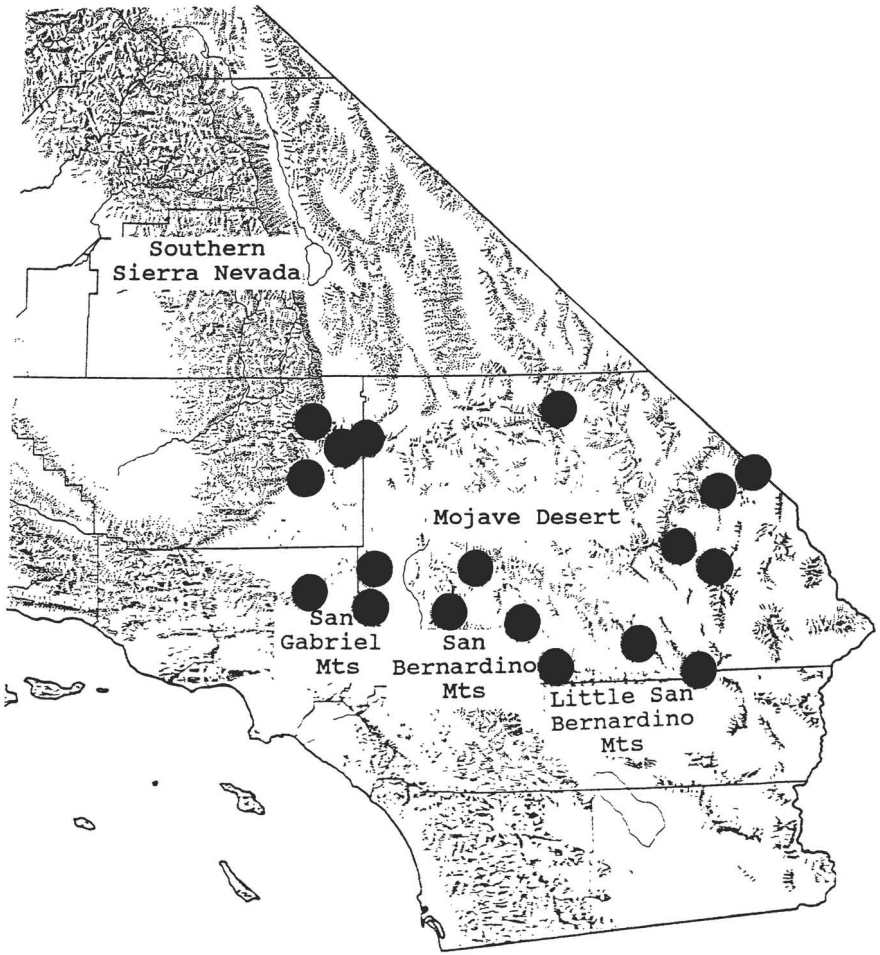

FIG. 3. Map of southern California showing locations of Type 1 populations (*A. m. deserti*) in the Mojave Desert. The phenotype of this subspecies is much like b in Fig. 1.

Barnes & McDunnough) were found at the following locations: Kern Co., California, El Paso Mts.; San Bernardino Co., California, Danby, Kramer Hills, and Sheephole Pass.

Type 2 populations exhibited long larval development times in the laboratory. Populations from Eureka Peak, Juniper Flat, and Pinyon Mt. (Table 1) had mean larval stage durations of 182, 231, and 156 days, respectively. We have observed similar long development times (>150 days) under laboratory conditions for populations of *A. mormo* from Holcolmb Valley, San Bernardino Co., California (host—*E. wrightii*

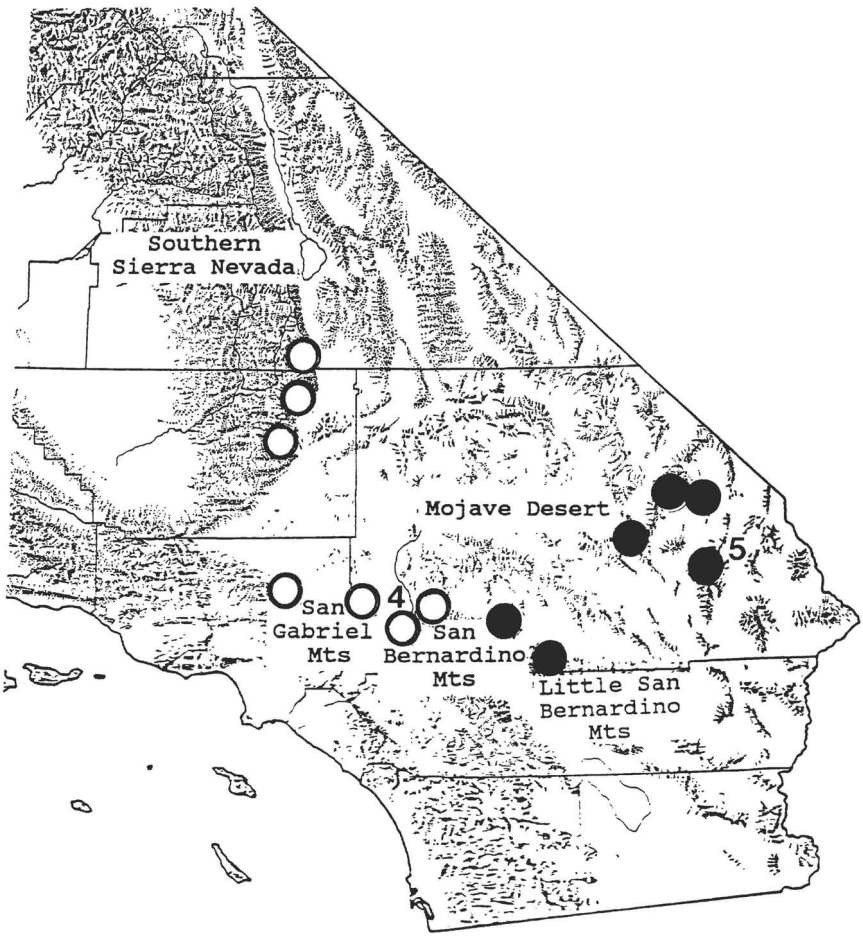

FIG. 4. Map of southern California showing locations of Type 3 populations in the Mojave Desert. The open circles indicate populations of the subspecies *cythera* (d in Fig. 1) and the closed circles denote populations of the subspecies *mormo* (b in Fig. 1). The localities used in Table 1 are as follows: 4 is Mojave River Forks and 5 is Covington Flat.

& *E. kennedyi* Porter ex Wats.); Dome Spring (*A. m.* nr. *virgulti*), Ventura Co., California (host—*E. fasciculatum*); and Nine Mile Canyon (*A. m.* nr. *virgulti*), Inyo Co., California (host—*E. fasciculatum*). All of the above larval host plants were determined by adult association (as described in the Materials and Methods), except for *E. kennedyi* from Holcolmb Valley, which was also determined from a collected larva (Table 2).

Type 3 populations differed from those of Types 1 and 2 by having a longer and more variable egg stage, and from Type 2 by having a

TABLE 1. Egg size and development times of *A. mormo* populations from the western Mojave Desert and southeastern Sierra Nevada.

Locality	Size mm	Eclos. mean (days)	Range	n	Dev. mean (days)	SD	Range	n	Life history type
Eureka Pk.	<0.90	10 C*	10	28	182	41 B*	111–253	28	2
Juniper Ft.	<0.90	10 C	10	10	231	42 A	151–290	10	2
Pinyon Mt.	<0.90	10 C	10	13	156	17 C	123–180	13	2
Mojave R F	>0.95	19 B	16–33	146	52	7 E	42–70	52	3
Old W. Mts.	>0.95	34 A	20–64	51	75	18 D	52–104	27	3

The development times for *A. mormo* populations are described in Materials and Methods in days at 25°C. All larvae were reared on fresh shoots of *Eriogonum fasciculatum*.

* The development times of those populations followed by a different letter were significantly different ($P > 0.001$) according to Duncan's Multiple-Range Test.

[Note: J. F. Emmel (pers. comm.) has reared the Type 3 biotype under outdoor conditions at Hemet (elev. 600 m), Riverside Co., California, where they take 130 to 150 days to hatch. Thus under natural conditions Type 3 ova do not hatch until February to June of the following year, depending on elevation and local climatic conditions.]

relatively short larval stage. The mean egg stage durations of Type 3 populations from Mojave River Forks (*Apodemia mormo cythera*) and Old Woman Mts. (*A. m. mormo*), were 19 and 34 days, respectively (Table 1).

The ova of most Type 3 populations are larger than those of the other two biotypes, a characteristic useful in discriminating fall-flying multivoltine populations of *A. m. deserti* (eggs < 0.9 mm, Type 1) from *A. m. mormo* (eggs > 0.95 mm, Type 3), which are phenetically very similar as adults, but often use different *Eriogonum* hosts. Differences in the three life history types are summarized in Fig. 5.

The larval food plants of the various *Apodemia mormo* subspecies and their localities in the Mojave Desert and along its western edge are presented in Table 2. Some taxa (*A. m.* nr. *dialeuca* and *A. m. virgulti*) appear to feed on only one species of *Eriogonum*, whereas others (*A. m. cythera* and *A. m. mormo*) utilize various late-summer blooming, perennial *Eriogonum* species, and one (*A. m. deserti*) feeds on many plant species. Although *A. m. deserti* was not observed to oviposit on *Krameria* (Krameriaceae), several females at Sheephole Pass were seen wandering through *Krameria* plants as though searching to oviposit. Larvae from Sheephole Pass have been reared to adults on the *Krameria* that occurs there. *Krameria* is recorded as a larval host for *A. m. mejicanus* (Behr) in Texas (Kendall 1976) and is a suspected host for *A. m. duryi* (Edwards) in New Mexico (G. S. Forbes pers. comm.).

DISCUSSION

The population that flies synchronically with both Type 2 and Type 3 populations along the northwest slopes of the San Bernardino Mts. and the northern slopes of the San Gabriel Mts. is *A. m. deserti*. If blending between *A. m. deserti* and the two other biotypes were oc-

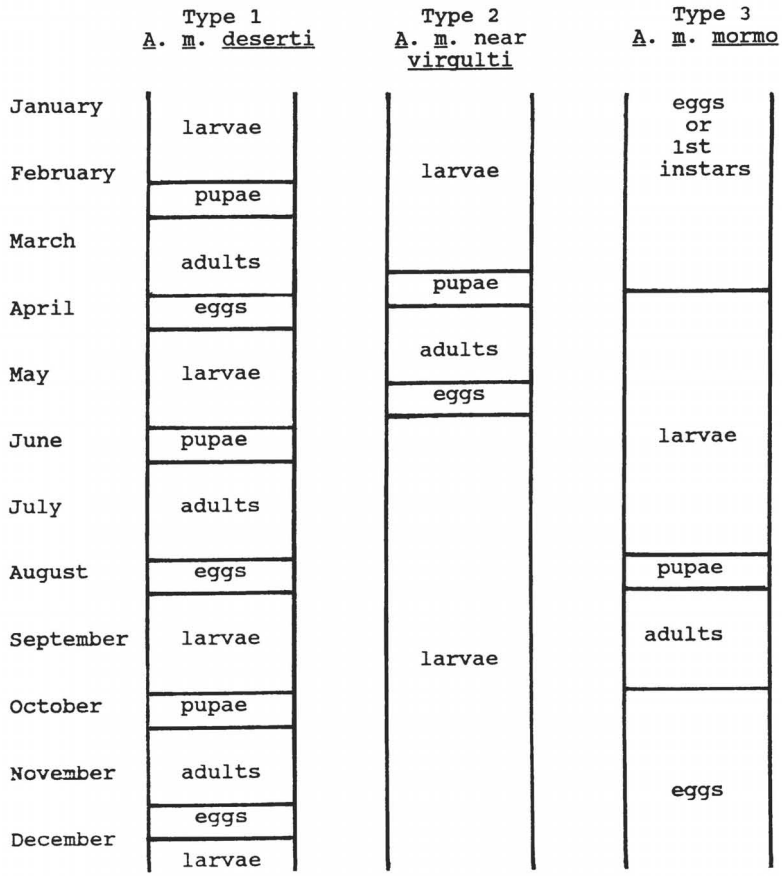

FIG. 5. Life history types showing distribution of stages throughout the year.

curring, one would expect a continuous blend zone, or a gradation of both extremes in pattern, throughout the desert edge (not one limited to the Cajon Pass area and areas just east and west of the pass as occurs with Type 2 populations), because both Types 2 and 3 come into contact with *deserti* mainly along the desert's edge (Figs. 2–4). *Apodemia mormo deserti* seems to be restricted to the lowland areas below 1500 m in the Mojave Desert, whereas both Types 2 and 3 populations of *mormo* seem to be largely restricted to above 900 meters along the desert edge (Figs. 2–4). Only populations of Type 3 can be found away from the desert's edge, on the slopes of the moister higher mountains where their late-summer blooming perennial hosts are found (Little San Bernardino Mts., Old Woman Mts., Granite Mts. southwest of Kelso, New York Mts., Providence Mts., Hackberry Mt., and Westgard Pass

TABLE 2. Life histories and host plants of *A. mormo* populations from the western Mojave Desert.

Taxon	†Life history type	*Larval host plant	Localities
cythera (Edwards) 1873	3	*Eriogonum microthecum* Nutt.	Kern Co.: Pinyon Mt.
		E. umbellatum Torr.	Mono Co.: Sherwin Summit
		E. wrightii Torr. ex Benth. in DC.	San Bernardino Co.: Big Pines Flat
deserti Barnes & McDunnough 1918	1	*E. inflatum* Toff. & Frem.	Kern Co.: El Paso Mts., Randsburg, Jawbone Canyon; Los Angeles Co.: Pearblossom; San Bernardino Co.: Danby, Sheephole Pass, Queen Mt, Morongo Canyon, Pinyon Hills, Granite Mts. near Victorville.
		E. nudum Dougl. ex Benth.	Kern Co.: El Paso Mts., Randsburg
		E. deflexum Torr. in Ives	San Bernardino Co.: Danby dry lake
		E. insigne S. Wats.	San Bernardino Co.: 7.5 miles east of Ludlow
		Oxytheca perfoliata Torr. & Gray	Kern Co.: El Paso Mts.
nr. *dialeuca*	2	*E. kennedyi* Porter ex Wats.	San Bernardino Co.: Holcolmb Valley
nr. *virgulti*	2	*E. fasciculatum* Benth.	San Bernardino Co.: Pinyon Hills
mormo (Felder & Felder) 1859	3	*E. wrightii* Torr. ex Benth. in DC.	San Bernardino Co.: Covington Flat, Joshua Tree National Monument
		E. heermannii Dur. & Hilg.	Inyo Co.: Westgard Pass

† Types of life histories are shown in Figure 5.
* The host plants were determined by field collection of larvae or eggs.

for the *mormo* phenotype; Hunter Mt., Coso Mts., and Inyo Mts. for the *cythera* phenotype). There appear to be no Type 2 populations feeding on *E. fasciculatum* in the Mojave Desert (even though the plant is present), except in the Little San Bernardino Mts., along the northern slopes of the San Bernardino and San Gabriel Mts., and the southeastern slopes of the Sierra Nevada (Fig. 2).

There is another reason that a north slope blend zone between *A. m. virgulti* and *A. m. deserti* is unlikely. Both taxa are multivoltine with Type 1 life histories. It would be surprising if a blend zone between these two taxa would yield a population that is univoltine with a Type 2 life history. Instead, it seems probable that this blend zone is between

the *dialeuca* and near *virgulti* phenotypes, both of which have a Type 2 life history.

The phenotypes of these three biotypes are the most distinctive along the northwest slopes of the San Bernardino Mts. Under laboratory conditions the spring population (Juniper Flat) can be made to complete development in the fall. Normally the host plant, *E. fasciculatum,* becomes dormant during the summer, so in nature these larvae probably can not complete development until spring. When reared on plants allowed to desiccate, before being replaced with fresh branches, larvae often go into dormancy and will not readily feed when subsequently given fresh branches. The adults that emerge under laboratory conditions are different from the late-summer-flying populations and are identical to the parent spring brood. The late-summer-flying population from Mojave River Forks, only a few miles west of Juniper Flat, has more dorsal orange than does the spring phenotype (which resembles the Type 2 Juniper Flat population). When this late-summer population was reared in the laboratory on *E. fasciculatum,* adults that emerged in late-winter and early-spring were identical to *A. m. cythera,* rather than to the spring population. These results suggest that these phenotypes in the field are not seasonally or host plant induced.

These three biotypes are biologically adapted to their larval food plants' phenology. Type 1 populations, which feed on various annuals as well as the short-lived *E. inflatum,* are adapted to the variable and often short growing season of the desert by developing rapidly from oviposition to pupation. Type 2 populations, which are adapted to *E. fasciculatum* along the desert edge, exhibit a long larval development period, probably because the food plant usually goes dormant during the summer and doesn't resume growth until late-fall or early-winter rains. On the other hand, the food plants of the Type 3 populations do not bloom until late summer, so that food plant is available for larval development throughout the summer. Also, because these plants bloom in late-summer, they are nectar sources for the adults in areas where nectar can be unreliable at that season.

Although the eggs of the Type 3 populations had mean eclosion times of 19 and 34 days, these were obtained under a constant temperature of 25°C. In the field these ova would be exposed to lower temperatures and remain in diapause longer (J. F. Emmel pers. comm.). The larvae probably benefit from the ova remaining in diapause, because most of these late blooming food plants go dormant shortly after blooming or just after the females finish ovipositing.

Apodemia mormo is a complex species with nine described subspecies. Some populations (particularly in southern Arizona) are extremely variable in wing pattern, yet do not follow the "blend zone" concept

as postulated by Opler and Powell (1961) (Forbes 1979). This suggests that morphology, particularly wing pattern, may be of little value in organizing the relationships of the different *A. mormo* taxa. Perhaps these three biotypes, which occur sympatrically, are distinct species. Their differences as described here, along with other characters such as enzyme polymorphisms, may help sort out the taxonomy of *Apodemia mormo* outside the Mojave Desert. For instance, *A. m. duryi* and *A. m. mejicanus* share with *A. m. deserti* a Type 1 life history (as probably does *A. m. maxima*); both are multivoltine with a short egg and larval development period and may be more closely related to each other than to other taxa of *A. mormo*. *Apodemia m. langei* has a Type 3 life history (eggs take more than 30 days to eclose), which may place it with *A. m. mormo* and *A. m. cythera*. Although *A. m. virgulti* is multivoltine and therefore does not have a Type 2 life history, it does share with Type 2 the same larval food plant not used by the other biotypes. Those populations of *A. mormo* that occur on the northern slopes of the San Bernardino Mts. and further north may have evolved in response to the shorter growing season experienced by desert populations of *Eriogonum fasciculatum*.

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