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ECOLOGY AND DISTRIBUTION OF A NEWLY DISCOVERED POPULATION OF THE FEDERALLY THREATENED *EUPROSERPINUS EUTERPE* (SPHINGIDAE)

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ABSTRACT. We discovered a new locality of the federally threatened sphingid *Euproserpinus euterpe* at the Carrizo Plain National Monument in San Luis Obispo County, California. We verified the determination of the species using voucher specimens and diagnostic larval characters. During surveys of the Carrizo Plain, we located the moth along three sandy washes supporting the host plant *Camissonia campestris*, and identified probable individuals at two other sites. The timing of the adult flight was approximately one month earlier than the previously known locality at Walker Basin, spanning late January through February in 2003, but this observation compares different years. Females were observed to oviposit on a pebble and an unpalatable annual plant, which, combined with observed mobility of first instar larvae, leads to the conclusion that oviposition on the exotic weed *Erodium cicutarium* is not maladaptive as has been previously maintained. We hypothesize that natural hydrogeomorphological disturbance is important to maintain habitat features such as young, alluvial sandy soils and dense foodplant along washes. Disturbance from grazing, especially by sheep, appears to harm or destroy habitat, but further research is warranted.

Additional key words: Endangered species, phenology, *Camissonia campestris*, invasive species, *Erodium cicutarium*, grazing, Kern Primrose Sphinx Moth

Euproserpinus euterpe has been listed as threatened under the U.S. Endangered Species Act since 1980 (U.S. Fish and Wildlife Service 1980). The species was originally known as the Euterpe Sphinx (Holland 1903), and later as the Kern Primrose Sphinx Moth (see Osborne 2005). In recent times, it has been known to exist only at one site in the Walker Basin of Kern County, near Bakersfield, California. In 2002, PMJ and Tom Dimock discovered *Euproserpinus euterpe* at two localities within the Carrizo Plain National Monument in San Luis Obispo County, California, over 120 km west of Walker Basin. The discovery of new localities for *Euproserpinus euterpe* provides an unexpected opportunity to secure and manage this threatened species on public land.

Sphingids in the genus *Euproserpinus* are found in arid environments of Alta and Baja California and the Intermountain West. *E. phaeton* is relatively widespread, *E. wiesti* is rare throughout its range across three western states, and *E. euterpe* was thought to be endemic to Kern County in California. The three species are not known to be sympatric at any location (Tuskes and Emmel 1981). Adult *E. euterpe* fly in early spring, with a flight period previously known to range between late February and early April. Longevity of adults is unknown. Females mate soon after eclosion and lay eggs on low-growing forbs and other substrates such as pebbles. Pupation occurs underground, and pupae may remain in diapause for multiple years, a common phenomenon for species of arid landscapes with erratic climates (Powell 1987).

IDENTIFICATION

Euproserpinus euterpe has never before been recorded in the Carrizo Plain, nor indeed anywhere but in the Walker Basin of Kern County (Tuskes and Emmel 1981). Edwards (1888) described the type locality for the species as "San Diego" but this was almost certainly an error (Tuskes and Emmel 1981). The population at Carrizo Plain represents a significant range extension and requires certain proof that the population is *Euproserpinus euterpe*. This requires careful analysis of adult and larval characters.

Two adults from the Carrizo Plain were collected, mounted, and labeled (Fig. 1: Row 1) (currently deposited in the Natural History Museum of Los Angeles County). Moths from the Carrizo Plain share diagnostic characters with those from the Walker Basin (Fig. 1: Row 2), including mixed pale and dark gray scaling on the labial palpus instead of the uniform scales of *E. phaeton* (Hodges 1971). *E. phaeton* shows black scaling of the dorsal surface of the antenna, while

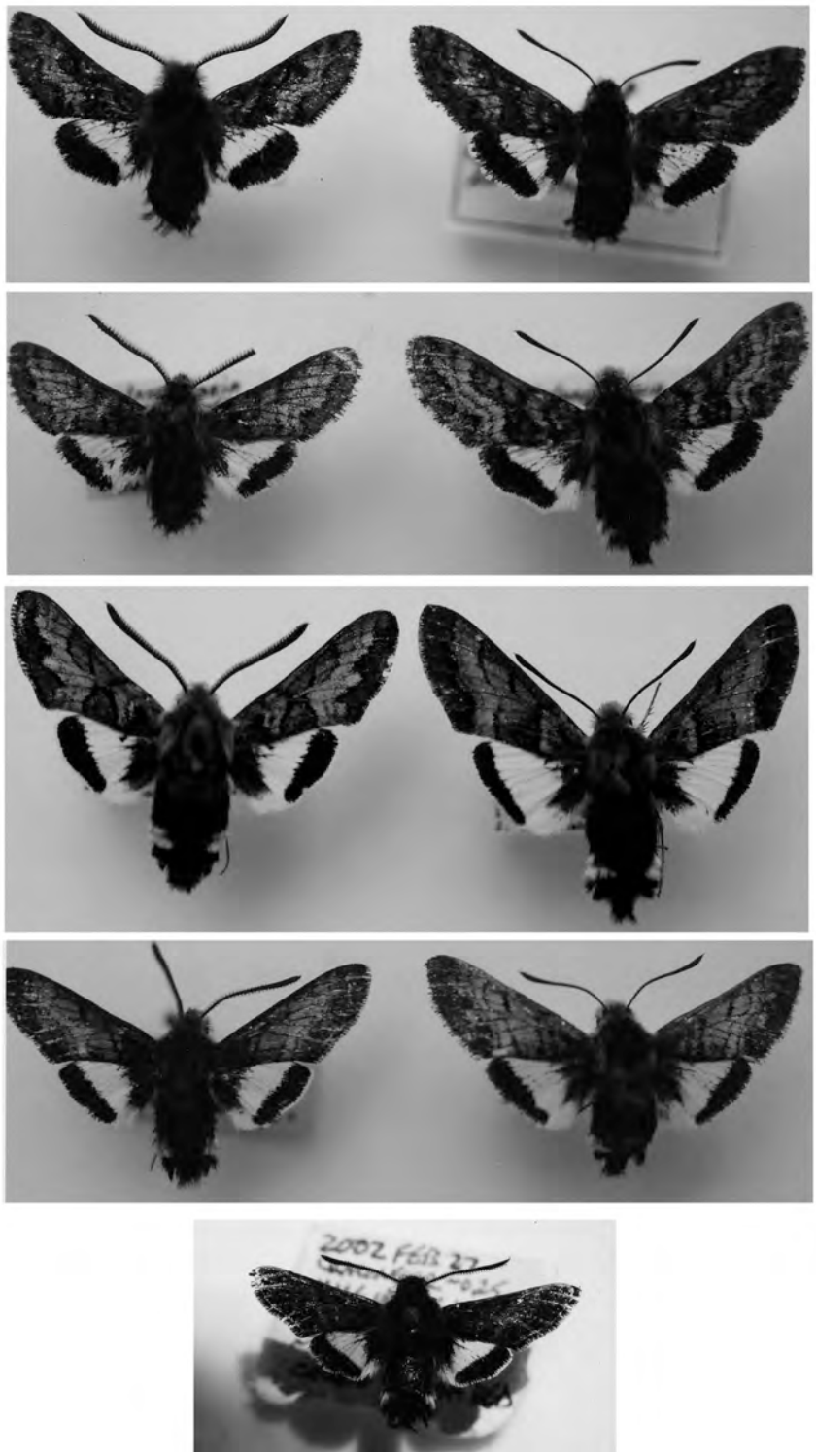

Fig. 1. *Euproserpinus* species, females on left, males on right. Row 1. *Euproserpinus euterpe* - Carrizo Plain population, San Luis Obispo Co., CA. Row 2. *Euproserpinus euterpe* - Walker Basin population, Kern Co., CA. Row 3. *Euproserpinus phaeton* - Mojave Desert population, CA. Row 4. *Euproserpinus phaeton* - Atascadero population, San Luis Obispo Co., CA. Row 5. *Euproserpinus phaeton,* ♂ - Chalone Creek, Pinnacles National Monument, San Benito Co., CA.

scaling is white in *E. euterpe*. White banding on the abdomen is larger and more contrasting in *E. euterpe* than *E. phaeton*. Sensilla chaetica of the antenna are longer in *E. euterpe*. The costal margin of the forewing and hindwing are more convex in *E. euterpe* compared with the flatter and straight margin of *E. phaeton* (K. Osborne, pers. comm.). Based on these adult characters, the two *Euproserpinus euterpe* populations are distinct from the more common *E. phaeton mojave* (Fig. 1: Row 3) found throughout the Mojave Desert and the more coastal *E. phaeton phaeton* (not figured) of Riverside and San Diego counties. A third population of *Euproserpinus* ranges from Atascadero, San Luis Obispo County (Fig. 1: Row 4) at least north to Pinnacles National Monument, San Benito County (Fig. 1: Row 5). Adults of these moths have *E. phaeton* characters, but the larvae exhibit mixed characters: the first instar lacks the black thoracic shield diagnostic of *E. euterpe*, but the fifth instar exhibits typical coloration and pattern of *E. euterpe* from the Carrizo Plain (see below). Pending further analysis, we do not believe that this population is conspecific with *E. euterpe*.

Larvae of the moths at Carrizo Plain exhibit additional diagnostic characters. Tuskes and Emmel (1981) reported that the first instar larva of *Euproserpinus euterpe* is divergent from its congeners, *E. phaeton* and *E. phaeton mojave*. They report that "[t]he thoracic shield, anal horn, and patches on the prolegs are heavily sclerotized and dark brown or black in *euterpe*, but are not sclerotized and green in *phaeton*." First instar larvae from the Carrizo Plain exhibit the *euterpe* character (Fig. 2: Row 1). A second diagnostic character is found in the illustrations of larval forms by C. M. Dammers archived at the Natural History Museum of Los Angeles County. In these illustrations, Dammers depicts the last instar larvae of *E. phaeton* with large lateral black spots contiguous with the lighter spiracles on the abdomen from the fourth to tenth segment. While these spots are present in *E. euterpe*, they are greatly reduced in size and are remote from and not much larger than the black spiracle. Comparison between larvae of the Carrizo Plain *E. euterpe* population and *E. phaeton* shows this difference distinctly (Fig. 2). Fifth instar larvae of *E. p. phaeton* and *E. p. mojave* have two color morphs (green or pink). The black lateral spot on each segment is embedded in pink and/or green ground color. Additionally, *E. euterpe* has a prominent brown pattern on the dorsal and lateral surfaces.

Surveys and Distribution

PMJ conducted extensive surveys for adult moths at locations around the Carrizo Plain during the spring of 2003. The species was located along sandy washes in 2002, consistent with the habitat of the species at its previously known locality in Kern County. Survey sites for 2003 therefore were located by mapping gently sloping, sandy drainages within the Carrizo Plain National Monument with existing georeferenced data. From January through March, 20 potential sites were visited and surveyed at a slow pace to detect adult moths. These surveys produced three confirmed sites (two from 2002 and one new), two unconfirmed sites where moths were observed but identities could not be determined conclusively, and a description of other potential sites based on habitat similarities to confirmed sites.

The confirmed sites are located on washes flowing north from the Caliente Range and along the Elkhorn Scarp (Fig. 3). At the unconfirmed sites possible *Euproserpinus euterpe* adults were observed but determination of species was not certain. Potential sites that warrant further investigation based on presence of foodplant, geomorphology, and soils include the washes found along the northeast slope of the Caliente Range from Padrones Road to KCL Campground and the washes on the southwest slope of the Elkhorn Scarp from Latitude 35.055°–35.246° N to the Panorama Hills. Other potential sites are located outside the Carrizo Plain National Monument. The area to the northwest of the Monument was not explored.

We found potential sites that have been so degraded by agricultural use that the habitat cannot support the moth. Such sites include the washes flowing out of the Caliente Range into the Cuyama Valley. On many of the washes, the alluvial fans that would be prime habitat for the moth have been disked over and planted in various crops. Potential habitat has been replaced by agricultural uses in the washes flowing out of the hills east of Highway 33 between Highway 166 to just beyond the Ventura County line. (NB: The foodplant *Camissonia campestris* does not grow commonly south of this point and is replaced by a different *Camissonia* species.) These alluvial fans have been converted to agricultural use, but it is possible that a population of the moth could exist on a few of the lesser-used fans such as those around Ballinger Canyon Wash.

We identified sites that would be unlikely to support a population of *Euproserpinus euterpe* because of soil, geomorphology, or lack of host plants. These include the washes coming out of the northeast slopes of the Temblor Range, washes southeast of the Carrizo Plain National Monument that flow into the San Joaquin Valley, and washes surrounding the Elkhorn Plain, especially at the southeast sink.

FIG. 2. Euproserpinus larvae (length). Row 1: First instar *E. euterpe* (5 mm), third instar *E. euterpe* (12 mm). Row 2: Fourth instar *E. euterpe* (27 mm), fifth instar *E. euterpe* lateral (36 mm). Row 3. Fifth instar *E. euterpe* ventral (36 mm), fifth instar *E. phaeton* (35 mm).

NATURAL HISTORY

Phenology and Abundance. At two of the known sites, transect walks were conducted regularly throughout the flight season to gather additional information about the abundance and adult phenology of the species. Transect walks are the most effective method to gather information about the flight season that does not involve handling individuals (Pollard 1977, Watt *et al*. 1977, Thomas 1983). Mark-release-recapture studies should be avoided for listed, small Lepidoptera that may be harmed by handling (Gall 1984, Murphy 1988). Surveys were conducted as Pollard Walks, with the observer (PMJ) walking at a slow pace and recording every moth observed within a 5-m-wide area projected ahead of the observer (Pollard 1977, Thomas 1983). Temperature and other weather conditions were noted for each survey, and the location of each moth was recorded with a handheld Geographic Positioning System (GPS). To gain the maximum information from transect counts in subsequent analyses, transects were

FIG. 3. Range of *Euproserpinus euterpe* at Carrizo Plain. Shaded habitat region contains potential habitat with foodplant along sandy washes. Potential habitat on the south washes of the Caliente Range may extend farther to the northwest.

surveyed from the first detection of adults until no more were seen (Mattoni *et al*. 2001).

We analyzed capture records and observations of *Euproserpinus euterpe* from Walker Basin (Tuskes and Emmel 1981, Osborne 1999b) to compare them with the survey results from the Carrizo Plain. Over 90% of capture records or observations at Walker Basin were between March 13 and April 1. Even if one looks at the number of successful collecting trips and not the number of individuals taken, 75% of the trips were during this period. The earliest and latest collections were February 26 and April 6. Collectors usually

attempt to find particular species in places and at times when they are reasonably confident that the species will be found (Dennis and Thomas 2000). These records, therefore, should not be taken to be a complete description of the species' phenology at Walker Basin. They do, however, provide sufficient basis for an initial comparison.

The flight season for *Euproserpinus euterpe* at the Carrizo Plain in 2003 reached its peak almost two months earlier than the average for Walker Basin records (Fig. 4). Ninety-seven percent of Carrizo Plain observations were between January 27 and February 25, essentially completing the flight season before the date of the first collection record from Walker Basin. We suggest two explanations for the difference in phenology between the two populations. First, temperatures in late 2002 and early 2003 were much higher than usual, leading to abnormally early development for both plants and insects. The long-term average flight period at Carrizo Plain is likely substantially later in the year than observed in 2003. Second, the Carrizo Plain sites are at a lower elevation (640–840 m) than Walker Basin (1,060–1,100 m) and therefore temperatures will be higher earlier in the year, leading to an earlier flight season.

Behavior. *Euproserpinus* moths thermoregulate by basking on open ground in sandy washes or any other cleared area, including squirrel burrows and dirt roads (Osborne 1999b). Osborne (1999b) suggested that this behavior results in significant mortality where roads are frequently traveled. On warm days, moths will perch in the sandy washes, or less commonly in other cleared areas. When flushed, or when chasing after a flying insect, a moth usually will fly in a large curve 0.3-1.0 m above the sand for 15 m or more and return to sitting on the open substrate. Moths were never observed alighting on surfaces other than sand or clearings.

Adult moths did not nectar at flowers during any of the 2003 observations. Few nectar-providing flowers were available early in the flight season, but several species matured later in the season. Females were observed ovipositing early in the flight season before nectar was available. Nectar is not necessary for moths to survive or to complete their life cycle. We presume that adults will nectar; nectaring may extend the adult lifespan and provide energy for additional activity in

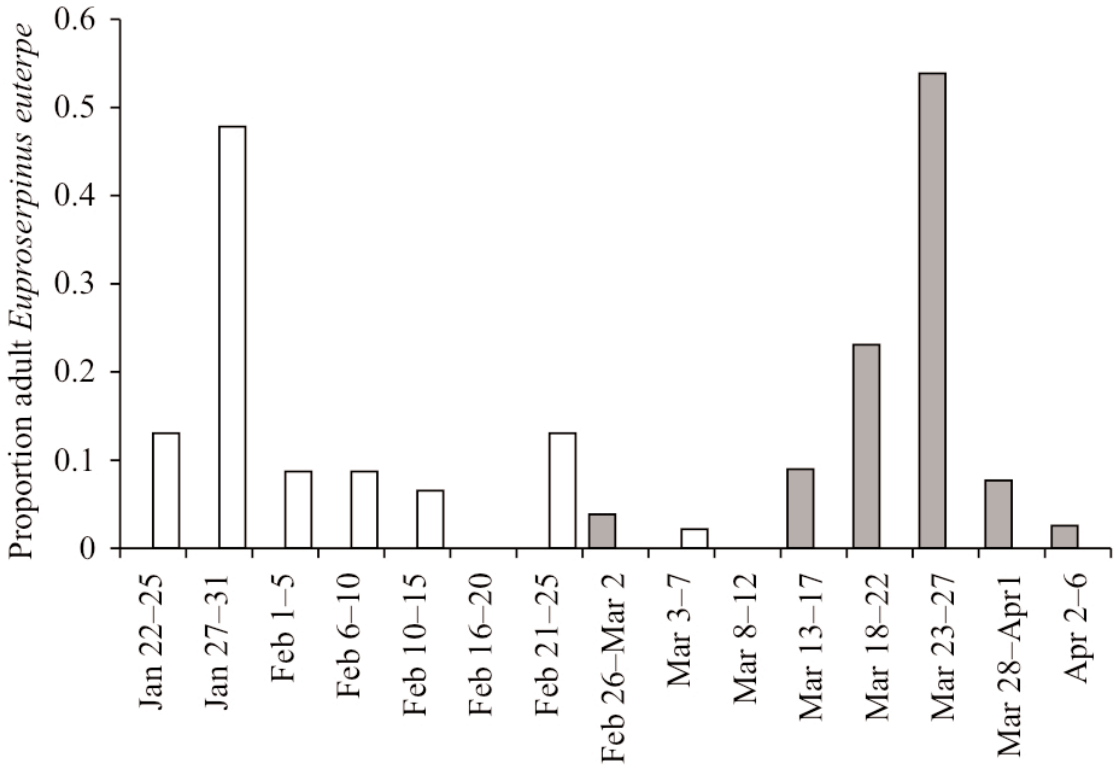

FIG. 4. Phenology of *Euproserpinus euterpe* at (a) Carrizo Plain (open bars) from observations in 2003 and at (b)Walker Basin (filled bars) from collections in 1974–1979 (Tuskes and Emmel 1981) and observations in 1999 (Osborne 1999b).

warmer weather, both of which increase opportunities for oviposition and thus may increase fecundity. *E. phaeton* commonly nectars on a variety of flowers (K. Osborne, pers. comm.) and P. Johnson (pers. comm.) documented *E. euterpe* nectaring at Walker Basin.

Reproduction and Larval Stages. Two female *Euproserpinus euterpe* were observed in egg laying behavior. One of the females laid one egg on a pebble and the second on a seedling (1 cm tall) of *Linanthus* sp. (Fig. 5). This egg was observed over several weeks, during which the plant dried up and finally blew away carrying the egg with it. To investigate oviposition and larval development, a single female was collected. This female was found with malformed forewings and was unable to fly. PMJ collected and placed her in a styrene box containing the host plant. Over the next several days she readily laid 75 to 100 eggs on facial tissue and less commonly on the host plant. This female is the source of the eggs and subsequently the larvae of this study.

On Carrizo Plain, larvae have been found feeding on *Camissonia campestris*, while larvae at Walker Basin are reported to feed on *Camissonia contorta epilobioides* (Tuskes and Emmel 1981), which is thought to be derived from a *Camissonia campestris* and *C. strigulosa* cross (Hickman 1993). *Camissonia contorta* is found at low density in the areas occupied by the moth at Carrizo Plain, mostly on the higher elevations of the washes, but it does not appear to be the primary foodplant. Other closely related sphingids use more than one species of Onagraceae as larval hosts (Osborne 1999a), so multiple hosts may be expected for *E. euterpe* as well.

First instar larvae exhibit the sclerotized thoracic shield and anal horn diagnostic of *E. euterpe*. Later instar larvae are brightly colored and patterned, which provides camouflage to blend in with surrounding plants, as suggested by McFarland (1966) and Osborne (1995). When feeding, later instar larvae exhibited a jerky side-to-side motion that resulted in the appearance of the foodplant and larvae being wind-blown (video available at http://www.urbanwildlands.org/kpsm.html).

Essential Habitat Elements. Sandy washes and other open soil are necessary for basking by adult moths on cool winter days. During 2002, over 40 specimens were flushed from sandy washes or lesser clearings such as those made by rodents, while no specimens were seen along dirt roads (primarily clay without sand) near or adjacent to washes. Day temperatures below 58° F

Fig. 5. Habitat of *Euproserpinus euterpe*. Row 1. Sandy washes showing cover of *Camissonia campestris* at Carrizo Plain, San Luis Obispo Co., CA. Row 2. Habitat at Walker Basin, Kern Co., CA (left), *Linanthus* sp. seedling at Carrizo Plain upon which *E. euterpe* egg was laid (right).

excluded any adult activity in 2003 observations. Between 58º F and 60º F, adults could be flushed from basking sites. Temperatures above 60º F were needed before "normal" activity occurred. On windy days these temperatures were slightly higher.

The foodplant *Camissonia campestris* appears to be essential for the Carrizo Plain population, although it is possible that other *Camissonia* species are used. *Camissonia campestris* is found abundantly throughout the Carrizo Plain but is somewhat restricted to sandy soils. Plants are most common within or on the banks of sandy washes where they can grow in monocultures of a square meter or more. Alluvial fans have been formed where washes flow out in the flatter plains. On these fans, *Camissonia* flourishes abundantly. These alluvial fans go through stages of succession gradually losing the sandy nature of the soil. On mature soils the *Camissonia* is less abundant than on immature sandy soils. Most of the patches of *Camissonia* do not appear to support populations of *Euproserpinus euterpe*, based on extensive surveys throughout the flight season. We presume that acceptable habitat is usually found along sandy washes with young alluvial sandy soils that support large patches of the foodplant. These conditions are often, but not always, found in washes with low or no banks. Despite many hours of searching, adults were never observed in the more mature soil types except in clearings caused by rodents despite many hours of searching in mature soils, but this does not rule out opportunistic use as basking sites of any small clearing near known localities. We also presume that the *Camissonia* must be sufficiently dense so that the plants are close enough for the newly emerged larvae to be able to locate seedlings and for larvae to locate additional plants when the original plant is consumed. Additional research is needed on this topic.

Sandy alluvial soils are necessary to provide sites for the mature larvae to burrow into the sand to pupate. We presume that if the soil is compacted the larvae may not be able to burrow. Older alluvial banks or fans are unsuitable for reproduction because the soil becomes too compact and loses the sandy consistency necessary for pupation. Indeed, Osborne (1995) found for the related species *Proserpinus clarkiae* that confined larvae would die without pupating if humid pupation sites were not provided. We presume that sandy alluvial soils located outside channels that are flooded yearly provide optimal habitat. This limitation in soil type would mean that most of the thousands of acres of *Camissonia* on the Carrizo Plain are unsuitable for the reproduction of the moth.

Predators and Parasites. No direct observations of predation or parasitism were made. Insectivorous birds, including horned larks (*Eremophila alpestris*), are common on the Carrizo Plain during the larval development period and may be predators. Predatory ground beetles (*Calosoma* sp.) also are present and active during the larval development period. The beetle is active on warm, sunny days, and hunts small soft-bodied insects. Several groups of wasps and flies that may be parasites of *Euproserpinus* are active during the early spring months. Predator ants of the genus *Formica* are common and active during the larval development period. Lizards may have an effect on the developing larvae but only *Uta stansburiana* was observed in the larval development areas.

DISCUSSION

The discovery of *Euproserpinus euterpe* at Carrizo Plain substantially extends the distribution of a species thought to be endemic to a narrow geographic range. Both populations share the morphological features that distinguish *E. euterpe* from *E. phaeton*. Future genetic analysis may provide greater understanding of the relationships between the populations of the two species.

Habitat conditions at Carrizo Plain are substantially similar to those at Walker Basin. At both localities, the moth uses annual *Camissonia* species as larval foodplant. Different foodplant species are apparently more important at the two locations — *Camissonia campestris* at Carrizo Plain and *Camissonia contorta* at Walker Basin. Current research is, however, inadequate to determine the use of additional *Camissonia* species at either location. Larvae from both the Carrizo Plain and the Walker Basin (Osborne 1999b) will eat other local *Camissonia* species if offered, without apparent ill effect. The moth lives in and around sandy washes with sandy alluvial soil at both localities. Both populations use plant-free areas for basking, including dirt roads at Walker Basin (Osborne 1999b). We made no observations of moths on roads at Carrizo Plain, although a road runs within 15–60 m of one site. This road is compacted smooth clay, while the roads at Walker Basin are sandy, so this difference is likely only one of substrate preference.

Disturbance and Dispersal. Little is known of the dispersal and colonization ability of *Euproserpinus euterpe*, nor the stability of populations over time. At the Carrizo Plain, one site seems not to have been plowed under for at least several decades, as suggested by the presence of mature *Ephedra* sp. bushes. In comparison, another occupied site was plowed under for many years before the early 1980s, which would have excluded the moth from the wash during that period. The near proximity of the disturbed site to the

undisturbed site leaves open the possibility that there has been recent emigration from one to the other. The soil conditions required by the species suggest an adaptation to movement into new habitats over the long term. We hypothesize that younger washes are necessary to provide appropriate soil conditions for the species, while older formations support consolidated soils and too few foodplants. It would be consistent with this habitat characteristic that the species is adapted to colonization of new habitats over the course of decades. This is a topic for future investigation.

More must be learned about the response of the moth to disturbance. Some disturbances, such as sheep grazing, are visibly deleterious to the species. Herds of sheep mechanically disturb soils and leave little forb cover, compared with the more solitary grazing behavior of cows. Grazing by sheep in arid landscapes increases soil compaction (Webb and Stielstra 1979), which is incompatible with maintenance of moth habitat. Sheep grazing suppresses biomass of native forbs, and excluding sheep grazing (along with excluding off-road vehicles) has shown to increase biomass of *Camissonia campestris* significantly (Brooks 2000). We observed washes in field surveys that had been grazed by sheep and turned into a muddy mess with little forb cover. It is not clear if this effect is permanent, but soil recovery from grazing is usually slow in arid environments.

Natural disturbances also affect moth habitat. For instance, following the 2003 field season, a freak summer storm flooded and silted in an occupied habitat. We have no knowledge of whether pupae are adapted to such events and emerge the following season, or whether they are adversely affected. Fires are highly unusual during the season of adult and larval activity. Clearing of vegetation by summer or fall fires would have an unknown effect. Based on behavior of captive larvae of *E. phaeton* (N. McFarland, pers. comm.), we believe that most pupation will occur deep in the soil. Tuskes and Emmel (1981) stated that *E. euterpe* larvae pupated near the surface but did not describe whether sand was provided for larvae to burrow deeper. Additional studies are necessary to determine how deep and where larvae pupate in nature. If pupation takes place near the surface, then summer and fall fires could be detrimental. This would probably only affect those larvae that migrate from washes and clearings into denser vegetation to pupate; by summer and fall, most *Camissonia* patches do not have sufficient fuels to maintain a fire.

***Erodium* and Larval Survival.** Tuskes and Emmel (1981) reported that female *Euproserpinus euterpe* frequently oviposit on the exotic annual *Erodium cicutarium*. Larvae they reared on *Erodium* in the laboratory did not feed and died within three days. Tuskes and Emmel (1981) hypothesized that because first instar larvae are "rather sessile" those larvae hatching on *Erodium* in the field are likely to die. This assertion has been widely repeated and forms the basis for the conservation strategy articulated for the species (U.S. Fish and Wildlife Service 1984). We (Longcore and Rich 2002) suggested that the first instar larvae are sufficiently mobile in the field to seek out palatable foodplant if plants are sufficiently closely spaced, which seemed possible because first instar larvae already move from oviposition sites on leaves and stems to flowerheads where they prefer to feed (Tuskes and Emmel 1981). In captive rearing, PMJ observed first instar larvae to move from plant to plant, suggesting that this also would be possible in the field. First instar larvae of many Lepidoptera species are capable of moving significant distances, and this ability is not proportional to body size (Reavey 1992). In an investigation of 42 Lepidoptera species, first instar larvae could live 1–20 days without food, with movement ability ranging 0.7–267.8 cm/hour (Reavey 1992). If suitable host plant is nearby, movement of first instar *Euproserpinus euterpe* larvae from nonpalatable plants to host plants is highly likely.

Some Lepidoptera, typically those with common host plants and those that diapause as eggs, do not lay their eggs directly on the host plant (Wiklund 1984). The effort to locate and oviposit on a common foodplant is wasted, while species with rare foodplants must locate eggs on them. In years with sufficient rainfall, *Camissonia campestris* is common, forming continuous beds in appropriate habitats at Carrizo Plain (Fig. 5; Row 1). The female moths we observed laid eggs on a pebble and a non-foodplant, showing no strong preference in oviposition choice at the fine scale. If eggs are laid on inanimate objects, it is unlikely that oviposition on nonpalatable plants is a maladaptive behavior. Females do not need to lay eggs directly on a common foodplant because neonate larvae hatched from eggs laid in the vicinity will have a high probability of encountering a foodplant.

We conclude that eggs laid on *Erodium* are not doomed, and that this exotic species does not present the negative population pressure once imagined. While we do not dispute that attempts to rear larvae on *Erodium* in the laboratory would fail, we discerned a greater ability of first instar larvae to move from plant to plant than previously observed (Tuskes and Emmel 1981). This revised interpretation is more consistent with current knowledge of the timing of *Erodium*

invasion in California. Research indicates that *Erodium cicutarium* invaded California from Baja California before the Mission period (that is, before 1769), and therefore invaded without disturbance from agricultural grazing (Mensing and Byrne 1998, Mensing 1998). *Euproserpinus* moths have persisted in landscapes with *Erodium cicutarium* for over 250 years and the introduction of this invasive species has likely reduced overall foodplant availability. This presumed reduction in *Camissonia* dominance seems the likely mechanism for any potential adverse effects on *E. euterpe*, not oviposition on *Erodium* itself as suggested by Tuskes and Emmel (1981).

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