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EUPHILOTES ANCILLA (LYCAENIDAE) IN THE SPRING MOUNTAINS, NEVADA: MORE THAN ONE SPECIES?

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ABSTRACT. Two independent temporal cohorts of *Euphilotes ancilla* (Lepidoptera: Lycaenidae) with different larval host plants occur sympatrically in portions of the Spring Mountains of southern Nevada. Their diapause intensities (as determined in the laboratory) and flight seasons exhibit little or no overlap, but phenotypes of the cohorts appear identical. It is speculated that they arose from changes in the relative phenology of their larval host plants in response to climatic alterations subsequent to the Pleistocene. Although these *Euphilotes* seem to behave as separate biological entities, their taxonomic level remains equivocal. Until more information is forthcoming, they are recognized as separate subspecies: *E. ancilla purpura* and *E. ancilla cryptica* **n. ssp**.

Additional key words: conservation, new subspecies, Polyommatinae, sympatric divergence.

Euphilotes Mattoni, 1978, a genus of polyommatine Lycaenidae, exhibits an often baffling array of taxa at both specific and infraspecific levels. Not only has their genus-level nomenclature experienced numerous upheavals over the years, but their species-level taxonomy has suffered through chaos dating nearly to their initial discovery. This taxonomy arguably has had less historical consensus than that of any other North American genus of butterflies, with three to as many as eleven species recognized in myriad combinations (Barnes & McDunnough 1917; McDunnough 1938; Mattoni 1954a, 1954b, 1965, 1977, 1988; Downey 1961; dos Passos 1964; Shields 1974; Langston 1975; Miller & Brown 1981; Scott 1986; Pratt 1988, 1994; Shields & Reveal 1988; Pratt & Emmel 1998; Opler & Warren 2002; Warren 2005). This confusion originates from very similar superficial appearances of the numerous taxa; knowledge of larval morphology and host plants, adult genitalia, and geographical and temporal distributions are often necessary for identification.

The life cycles of *Euphilotes* are closely coordinated with those of their larval host plants, *Eriogonum* (Polygonaceae)(Langston 1963; Langston & Comstock 1966; Shields 1975, 1977; Arnold 1983a, b; Pratt & Ballmer 1986, 1993; Arnold & Goins 1987; Pratt 1988, 1994; Mattoni 1990; Peterson 1997). That species-rich genus of plants, including spatially and/or temporally separated varieties, is widespread in and nearly entirely confined to western North America (Reveal 1969, 1978). More than one taxon of *Euphilotes* may co-occur, either synchronously or not, but most co-occurring species use different host plants (Pratt & Ballmer 1986; Ballmer & Pratt 1988; Shields & Reveal 1988). Although there are exceptions, a single taxon of *Euphilotes* uses but one species of larval host plant at any one site (Pratt & Ballmer 1986, Shields & Reveal 1988). Their eclosion is closely consilient with flowering phenology of larval host plants, and nearly all populations are univoltine (Pratt & Ballmer 1986, 1993; but see Newcomer 1964; Langston 1974; Shields 1975, 1977; Pratt & Ballmer 1986; Pratt 1988, 1994; Pratt & Emmel 1998; Davenport 2003). Pupae of some can extend diapause (holdover) through more than one winter (Pratt & Balmer 1986). Phenologies of butterflies may respond to elevational and latitudinal gradients tracking seasonal progression of larval host plants (Peterson 1997; Pratt & Ballmer 1993). Local populations fly for no more than 4–8 weeks annually (e.g., Langston & Comstock 1966; Arnold 1983a, b; Arnold & Goins 1987; Peterson 1995b; Mattoni *et al*. 2001).

The generalities of the life history of *Euphilotes* obscure its complexity wherein members of the genus exploit nearly all possible combinations of spatial, temporal, and larval host plant use patterns (Pratt 1988). These encompass a variety of seasonal, elevational, and

latitudinal replacements, irregular bivoltinism, and co-occurring overlaps in use of larval host plants. Numerous instances exist where two or more taxa are more or less sympatric (either synchronic or allochronic), but these usually use different larval host plants, and are distinguishable morphologically (Pratt & Ballmer 1986, 1993; Pratt 1988, 1994; Pratt & Emmel 1998; fide G. Pratt). Others have spatially approximate and apparently consubspecific populations using different larval host plants that temporally overlap for a minority of their collective flight season (Arnold 1983a). These situations suggest incipient speciation (Arnold 1983a; but see Pratt & Emmel 1998). Genetic exchange was found between phenologically disjoined populations in Washington (Peterson 1995b, 1996). Those populations using the same larval host plant and having overlapping diapause intensities, however, are not sympatric, but elevationally disjunct, and gene flow is thought to be in a stepping-stone fashion along an elevational gradient tracking the phenology of larval host plants (Peterson 1995b).

During more than four decades of investigations of the butterfly fauna of southern Nevada, observations were made on the endemic *Euphilotes ancilla* that occurs as several apparently distinct populations at middle elevations of the Spring Mountains (Clark and Nye counties). This *Euphilotes*, referred to as near both *Euphilotes enoptes enoptes* (Boisduval, 1852) and *Euphilotes ancilla ancilla* (Barnes & McDunnough, 1918), as a subspecies of *E. enoptes*, by Shields (1977), was considered as an undescribed endemic subspecies (Austin & Austin 1980; Austin 1981, 1985). A revision of *Euphilotes* proposed recognition of several species within the *E. enoptes* group, the Spring Mountains' populations became a subspecies of *E. ancilla* (Pratt & Emmel 1998), and this phenotype was subsequently described as *Euphilotes ancilla purpura* by Austin (1998). Its populations are located at the southern extent of the distribution of *E. ancilla* and their flight period extends to the latest reported date for the species.

The first known records of *Euphilotes ancilla* in the Spring Mountains are represented by material at the American Museum of Natural History taken in July 1928. Subsequently, there had been few reports (single records in 1936, 1959, 1966, and 1972) until the late 1970s when it was found to be locally common on occasion, flying from early June to mid-August at elevations between 1860 and 2190m (Austin & Austin 1980). Later, Weiss *et al*. (1997) had records for 11 sites between 1800 and 2500m with an overall flight season from mid-May through mid-August. The majority of records was from early June to early August with no notable peak.

The tendency of males of *Euphilotes ancilla* in the Spring Mountains to congregate on stream banks and at seeps from late May to mid-June undoubtedly biased early accounts of distribution. The known and assumed only larval host plant (and principal adult nectar source), *Eriogonum umbellatum* Torrey var. *subaridum* S. Stokes, is widespread in these mountains, but is often locally sparse. No butterflies were found at stands of this plant during May and June, since flowers had yet to appear. Prior to 1998, females had not been found until late July when the then known host plant came into bloom. These records unfoundedly suggested that males emerged a month or more before females and often occurred at mud in large numbers early in their flight season. Males were infrequently seen at mud after late June, although this resource is continually available.

Original observations on phenology of *Euphilotes ancilla* in the Spring Mountains were paradoxical for several reasons. *Euphilotes* was not known to emerge several weeks before host plants reach early bloom (Langston 1963; Pratt & Ballmer 1986). Extreme protandry was unknown among *Euphilotes*; the lag of female emergence had not been found to exceed eight days (Arnold 1983a; Peterson 1995b). Males of a short-lived butterfly with residence times of two to nine days (Arnold 1983a, b) would not be expected to eclose more than a month before the first females emerge. It was fortuitously discovered during 1999 that two varieties of *Eriogonum umbellatum* serve as larval host plants for *Euphilotes* in the Spring Mountains: an early-flowering *Eriogonum umbellatum* Torrey var. *juniporinum* Reveal and a late-flowering *Eriogonum umbellatum* var. *subaridum*. This suggested that perhaps this *Euphilotes* exhibited a simple bivoltine life history with seasonal replacement of larval host plants, a strategy not unusual among multivoltine butterflies. Since, however, bivoltinism and seasonally alternate larval host plants are not common among members of *Euphilotes*, investigations reported here were focused towards a fuller understanding of the distribution and biology of these butterflies.

Materials and Methods

Distribution and phenology. Spatial and temporal distributions of *Euphilotes ancilla* were determined from specimens, published accounts, field notes, and more recent surveys. These latter were facilitated by historical records of and searches for larval host plants, and observations at water sources where males are encountered at mud. Surveys along roads and trails in the Spring Mountains were undertaken from late April through September 1998–2003 including the west slope

of the range from Wheeler Pass southeastward to Potosi Mountain and the Red Rock area and the east slope from Big Timber Spring to Harris Mountain (Fig. 1).

To further quantify phenology of *Euphilotes ancilla* and its larval host plants, five transects were established near Willow and Cold creeks during spring 2002. Three were within stands of *Eriogonum umbellatum* var. *juniporinum* (two on a hillside above Willow Creek, 1825m and 1850m in elevation, and one on a flat along the road from Willow Creek to Cold Creek, 1775m) and two in stands of *E. umbellatum* var. *subaridum* (one at Cold Creek, 1825m, and the other adjacent to a seep between Willow and Cold creeks, 1775m). These transects were walked at 7–13 day intervals during 2002 and 8–11 day intervals during 2004 encompassing nearly the entire flowering season of *Eriogonum*. Stage of flower development was recorded for the first 100 plants encountered as none, early bud, late bud, flower (at least one per inflorescence), and senescent (e.g., see Peterson 1995b). The proportion of plants producing flowers was the maximum in bud or flower, or that had senesced on any one visit (Fig. 2 shows only those that were in flower). The presence of *Euphilotes* was also recorded.

Diapause intensity. Methods for determining intensity of diapause followed those of Pratt & Ballmer (1993). This, the mean number of days between removal from refrigeration and eclosion, is a standard indicator of flight season in *Euphilotes*; its caveats were discussed by Pratt & Balmer (1993). Using these data, the occurrence and intensity of diapause in different populations may be compared. If two populations are distinct, they will have different emergence patterns that, in the field, should correlate with flowering phenologies of their respective larval host plants.

Larvae of *Euphilotes ancilla* were obtained by examining larval host plants, with special attention to parts of plants with ants (see also Arnold 1983a). These parts and those on which larvae were found were clipped and transported in plastic containers to the laboratory in Henderson, Nevada. In the Willow and Cold creeks area (1775–1825m in elevation; hereafter referred to as Willow Creek), 86 larvae were collected between 3 and 23 June 2000 from *Eriogonum umbellatum* var. *juniporinum*; eight were collected in early August 2000, and 31 were collected between 3 and 22 August 2001 from *E. umbellatum* var. *subaridum*. Searches for larvae elsewhere in the Spring Mountains proved fruitless during 2000 and 2001, since host plants had apparently been negatively impacted by continuing drought.

Once at the laboratory, larvae from all samples were individually separated into small plastic cups covered with elastic nylon. Flowers of appropriate host plants were maintained in each cup in a plastic bud vial provided with water that kept flowers fresh and potentially more hydrated than under field conditions. Larvae were kept at room temperature (*ca*. 21°C) and ambient light. Containers and vials were cleaned daily and provided with fresh host plant as needed. Excess host plant was refrigerated at 4°C and replaced by new stock from the field every 3–5 days. Larvae were so maintained until they pupated. Pupae were placed on a bed of sterilized crushed limestone (collected from the same location as the larvae) in a ventilated plastic container, separated by date of pupation, and stored at room temperature and light regimens. On 1 October of each year, all pupae were refrigerated at 4°C. Their container was covered with paper towels (not touching the pupae) that were lightly misted every 7–10 days to prevent desiccation. Pupae were removed from the refrigerator the following 1 February and maintained again at a room temperature of about 21°C. These were monitored daily until pupae eclosed, died, or failed to break diapause. These latter were then again subjected to the refrigeration protocol as above.

RESULTS AND DISCUSSION

General biology. Larvae of *Euphilotes* feed on reproductive parts of *Eriogonum*, including sepals, flowers, pollen, and young seeds (Arnold 1983a; Pratt 1988, 1994; Mattoni 1990; Pratt & Ballmer 1993; Peterson 1997). Those from the Spring Mountains are typical, feeding largely on developing fruit, although one was recorded feeding on pollen. They remained concealed within inflorescences throughout development. No larval nests were constructed, although they are in some populations of *Euphilotes* (Pratt & Ballmer 1986). Pupation by *Euphilotes* is usually in the soil or among debris at the base of the larval host plant, but may occur in flower heads or near bases of leaf axils (Arnold 1983a, Arnold & Goins 1987). Since all pupae in this study were on the floors of larval containers, these populations are assumed to pupate in litter or soil.

Many larvae in third and fourth instars during 2000 were attended by ants. These attendant ants included five species, four associated with larvae from the first flight and two with the second; one of these occurred during both flights (Table 1). Data for associations of ants for the second flight may have been biased by the few larvae encountered. In contrast, no ants were seen attending larvae during 2001. All species of ants were, as expected, those of the secretion-nectar feeding guild (e.g., Hölldobler & Wilson 1990). Associations of ants with larval *Euphilotes* are facultative and seemingly

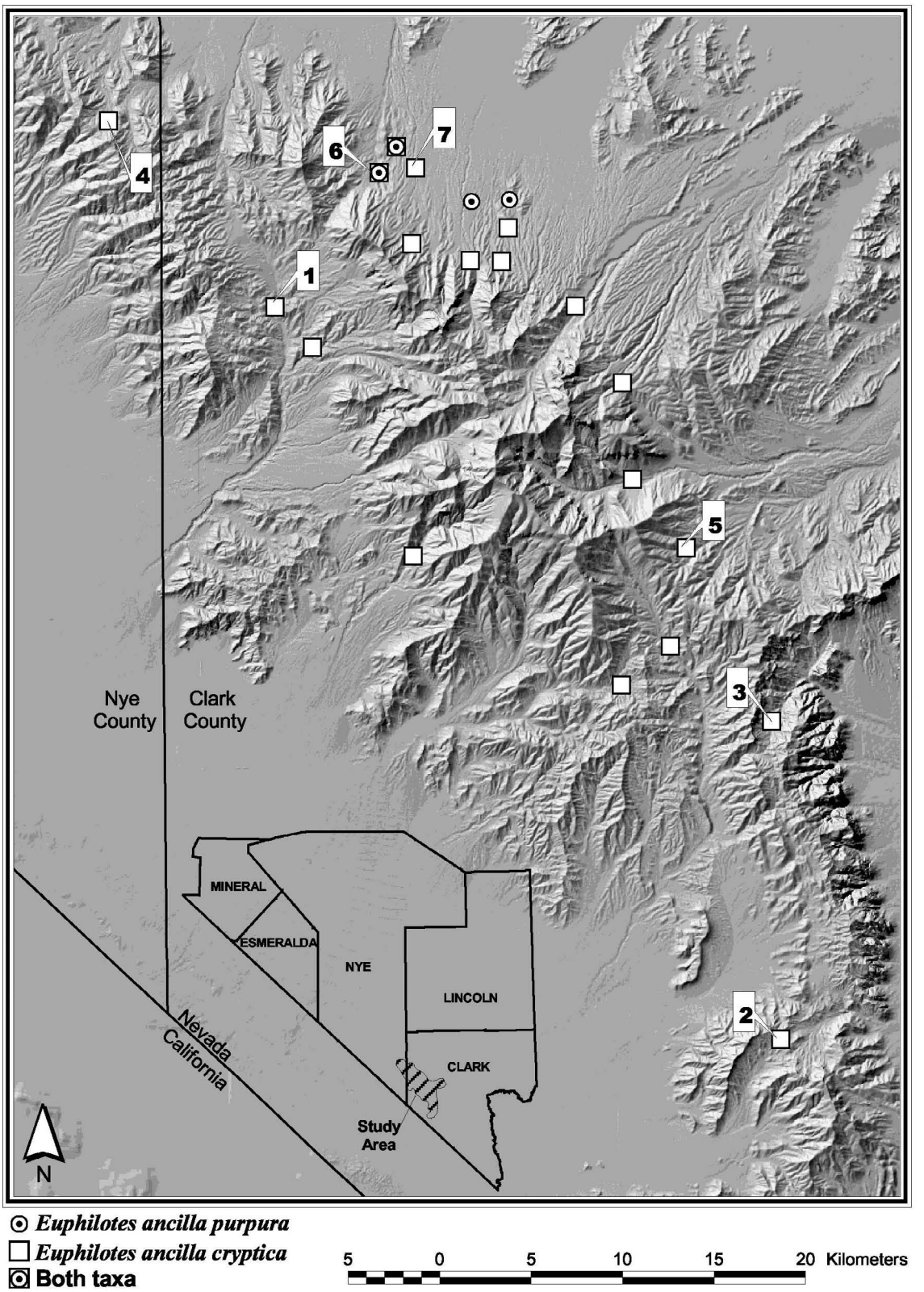

FIG. 1. Distributions of *Euphilotes ancilla* in the Spring Mountains, Nevada. Identified sites are (1) Wheeler Pass, (2) Potosi Mountain, (3) Switchback Spring, (4) Big Timber Spring, (5) Harris Mountain Road, (6) Willow Creek, and (7) Cold Creek.

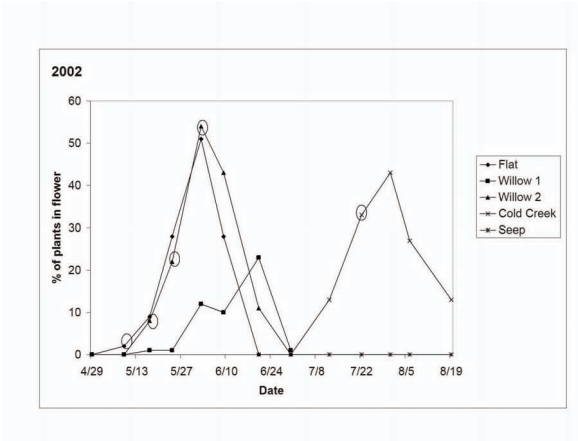

FIG. 2a. Phenology of *Eriogonum umbellatum* near Willow Creek, Spring Mountains, Nevada during 2002 (encircled datapoints indicate presence of adult *Euphilotes*; see text for locations of transects).

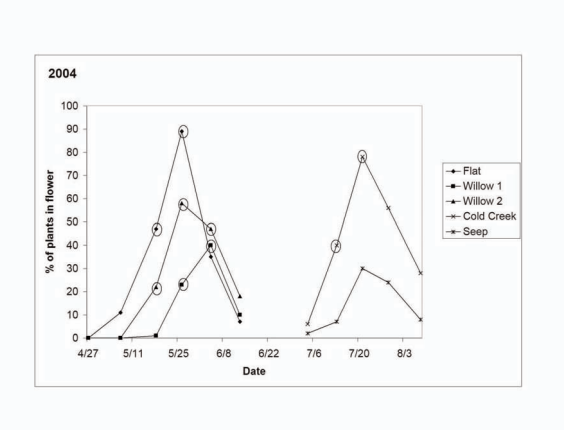

FIG. 2b. Phenology of *Eriogonum umbellatum* near Willow Creek, Spring Mountains, Nevada during 2004 (encircled datapoints indicate presence of adult *Euphilotes*: see text for locations of transects).

unpredictable (Ballmer & Pratt 1991, Peterson 1995a; see also Shields 1973); it is therefore not surprising that none was found during 2001. These data on attendance by ants, although likely incomplete, represent the first reports for these populations.

Of the 86 larvae collected in June 2000, 81 pupated between 8 June and 1 July, the eight collected in August 2000 pupated between 14 and 24 August, and 30 of the 31 collected in August 2001 pupated between 11 August and 3 September. Larvae from *Eriogonum umbellatum* var. *juniporinum* pupated over a period of 24 days at an average of 12.8 days (SEM = + 0.55, variance = 38.6%) after the first pupation; those on *E. umbellatum* var. *subaridum* also pupated over a 24 day period at an average of 16.6 days (SEM = ±0.84, variance 6.3%). These means are significantly different (t = 1.982, df=109).

Of the 125 immatures collected, one died in the larval stage and five died as pupae, all of unknown causes, and five larvae were intentionally sacrificed for preservation. None was parasitized. The absence of parasitism was unexpected, although Shields (1973) also reported no instances of parasitism. High incidences of parasitism by tachnids (Diptera)(42–60%) and braconids (Hymenoptera)(20%), however, were recorded among *Euphilotes* in California (Arnold 1983a; Mattoni 1990); likewise, parasitism by Hymenoptera and Diptera approaching 60% occurred in Washington (Peterson 1997).

The reared sample from the Spring Mountains was female biased (43:65, 39.8% males), although this is not a significant deviation from equality (chi square = 1.871). In two species of *Euphilotes* reared from Californian populations, the sex ratio was nearly 1:1 with males slightly outnumbering females (52.3%; Arnold 1983a); Shields (1975) also found equal numbers of males and females.

Distribution and phenology of larval host plants. *Eriogonum umbellatum* var. *juniporinum* was encountered in the Spring Mountains only in the northeastern portion of the range at elevations of 1775 to 1950m. At these sites, its dispersion is patchy on dry slopes in sparse piñon-juniper woodland and in areas of disturbance (especially old burns), with loose soils of high limestone content. It blooms from late April to late June. This phenotype of *Eriogonum umbellatum*, with cream-colored flowers and a rather prostrate growth form, was described relatively recently and reported from White Pine and Lincoln counties of Nevada (Reveal 1985a, b). In the Spring Mountains, this is apparently the plant previously identified as *Eriogonum umbellatum* var. *versicolor* S. Stokes (Beatley 1976; Kartesz 1987). That plant has also been recorded in upper Clark Canyon (Beatley 1976), but that record was

TABLE 1. Ants associated with larvae of *Euphilotes ancilla* in the Spring Mountains, Nevada during 2000.

Species	Number	Date
MYRMICINAE		
Crematogaster mormonum Emery	14	3, 8, 9, 17 June; 3 August
Monomorium minimum (Buckley)	9	3 August
DOLICHODERINAE		
Forelius pruinosum (Roger)	3	3, 8, 9 June
FORMICIMAE		
Camponotus hyatti Emery	13	3, 8, 9 June
Formica laeviceps Creighton	6	3, 8, 9 June

not reverified since parts of Clark Canyon are privately owned and inaccessible. Most *Eriogonum umbellatum* var. *juniporinum* had one to several flower heads during 2000. It was in flower (10–20% of the plants) on the first visit to Willow Creek on 20 May, with bloom continuing through 28 June; these largely appeared to produce seeds. During 2001, the majority of plants again had one to several flower heads and also largely appeared to produce seeds. The flowering season extended from 9 May through 30 June 2002 (Fig. 2a); senescence was rapid after mid-June. Plants at two of the three transect sites flowered more or less synchronously peaking in early June; those at the remaining site exhibited a peak in mid-June (Fig. 2a). The proportion of plants producing flowers differed between sites with maxima of 38 to 64%. In 2004, the plants were in flower from 7 May to after 13 June. Those at two sites again peaked simultaneously, but in late May, and the other peaked in early June (Fig. 2b). The proportion of plants that produced flowers (63–90%) exceeded that in 2002.

The distribution of the more apparent, brightly yellow-flowered, and erect *Eriogonum umbellatum* var. *subaridum* in the Spring Mountains has been better documented both historically (Clokey 1951; Beatley 1976) and through more recent surveys. It occurs as scattered populations across much of the range on both slopes between about 1800 and 3000m and flowers from July through September. Throughout the Spring Mountains, *Eriogonum umbellatum* var. *subaridum* had a poor flowering year in 2002 with only 5–10% producing flowers, these mostly in shaded situations. Many of the flowers dried before they produced seeds and, at Willow Creek, were heavily grazed by ungulates, severely reducing the number of flowers available to any *Euphilotes* present. It was first seen in bloom in early July and had essentially senesced by the end of August. The plant flowered profusely in 2004 when a large percentage produced flowers and seeds. It was first seen in bloom during early July and flowered at some sites into early September. On two transects studied in 2002, the plant exhibited distinctly contrasting flowering patterns. No plants produced inflorescences at one site, while 58% of those at the other did. These latter bloomed from mid-July to beyond mid-August, with a peak in late July (Fig. 2a). In 2004, both populations produced flowers (33–86% of the plants) between early July and early August with a peak in late July (Fig. 2b).

Distribution and phenology of *Euphilotes*. Surveys since 1998 indicated a broader spatial distribution of *Euphilotes ancilla* in the Spring Mountains than previously known and clarified knowledge of its temporal distribution. *Euphilotes ancilla* is now known from a number of sites distributed across much of the range on both slopes from Big Timber Spring to Switchback Spring in the Red Rock Canyon area and on Potosi Mountain between 1775 and 2750m (Fig. 1). Its spatial and temporal distributions are a subset of those of *Eriogonum umbellatum*. Since all species of *Euphilotes* fly only during the flowering period of their host plants and do not occur far from them, the perceived distributions of butterfly and plant reflect reality, at least in the more readily accessible portions of the Spring Mountains. No butterflies, however, have been found at numerous other sites that support larval host plants. At some of those localities, *Eriogonum umbellatum* var. *subaridum* seems too sparse to support *Euphilotes*; dense and apparent populations of *Eriogonum* are preferred (Shields & Reveal 1988). Other sites appear suitable and may well support the butterfly, but will require visits over several years to confirm recorded absences (e.g., see Shapiro 2006). Adults in populations of *Euphilotes*, including in the Spring Mountains, appear absent or very rare during dry years suggesting holdover pupae (e.g., Pratt & Balmer 1986; Shields & Reveal 1988). Their absence

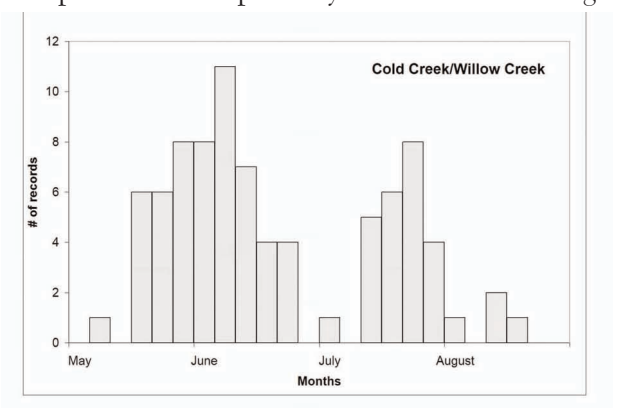

Fig. 3a. Phenology of *Euphilotes ancilla* in the Willow Creek area, Spring Mountains, Nevada.

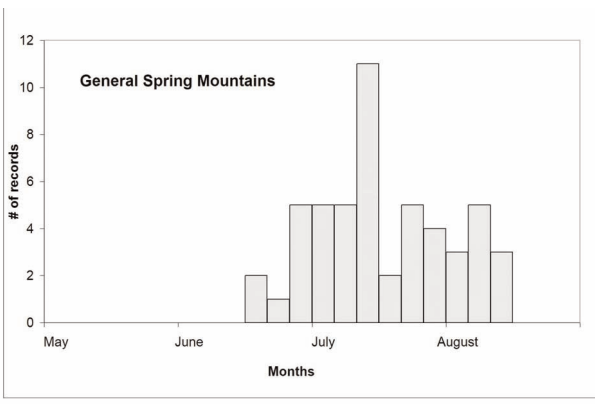

Fig. 3b. Phenology of *Euphilotes ancilla* in the Spring Mountains, Nevada, away from the Willow Creek area.

from a population of *Eriogonum*, therefore, may be more indicative of that year's local weather than the absence of the butterfly. Flowering by *Eriogonum* is related to age of the plant (Arnold & Goins 1987; Arnold 1990) and thus age structure must also be accounted for in considering distributions of *Euphilotes*.

Historical and recent phenological data from Willow Creek reveal two flight periods that could be interpreted as indicating allochronic sympatry. This discovery of two cohorts of *Euphilotes* separated in time and with distinct larval host plants having disparate flowering seasons solved the originally perceived enigma. Cumulative records of adults for this site extend from 9 May to 25 June and from 11 July to 19 August indicating peak flights in early and mid-June and in mid- and late July, with a single record on 3 July (Fig. 3a). These temporal data from a period of 31 years do not account for annual variation in weather, overestimating season length that may occur in any individual year, and underestimating intervals between flight periods. For *Euphilotes*, initiation, peak, and apparent length of flight seasons can vary annually up to about three weeks, but dispersion of emergence times shows little variability (Mattoni *et al*. 2001). In addition, prolonged rainy periods and high soil moisture may extend flowering times of *Eriogonum* and drought may curtail them; both have consequent impact on the eclosion of *Euphilotes* (Pratt & Ballmer 1986; Shields & Reveal 1988; see also Langston 1974). The virtual absence of records at Willow Creek during late June and early July (the three records between 25 June and 11 July were in one year, 1995) is clarified when data from individual years are considered when the two flight periods are separated by more than four to perhaps as many as seven weeks. Thus, no *Euphilotes* were seen at Willow Creek for 31 days between 24 June and 25 July 1998, 35 days from 16 June to 21 July 1999, 45 days from 3 June to 18 July 2000, 45 days from 27 May to 11 July 2001, 49 days from 24 May to 12 July 2002, and 46 days between 29 May and 14 July 2003, and 39 days between 4 June and 13 July 2004. Counts of *Euphilotes* along transects during 2002 and 2004 were, at best, marginally successful probably due to an extended drought. In all instances, however, adults were observed during the early or peak stages of flowering when inflorescences were often still largely in bud (Fig. 2, see also Peterson 1997). It is of interest that the early-flying cohort seems more abundant at mud than the late-flying cohort; water sources are often spatially closer to the larval host plant used later in the season than to that used earlier.

Away from Willow Creek, populations of *Euphilotes* associated with *Eriogonum umbellatum* var. *subaridum* appear to be chronically small, and adults are often not detected during some years. Records for these populations extend from 18 June to 14 August and suggest a single flight peaking in early and mid-July that corresponds largely with the late-flying cohort at Willow Creek (Fig. 3b). These records, however, not only span 85 years, but are from a variety of elevations and slope exposures that, when combined, obscure local phenological patterns. Adults were frequently seen during 1998 and 1999 along Harris Mountain Road, in lower Kyle Canyon, and in the vicinity of Deer Creek. Along Harris Mountain Road, few adults (1–4 individuals) were seen between 19 June and 13 July 2000. Neither adults nor larvae were encountered at known sites in lower Kyle Canyon from 12 July to 30 August 2000, or at Deer Creek from 29 June to 13 August. During July 2001, adults were encountered in fair numbers in the Wheeler Pass area, but none was encountered further south in the Spring Mountains.

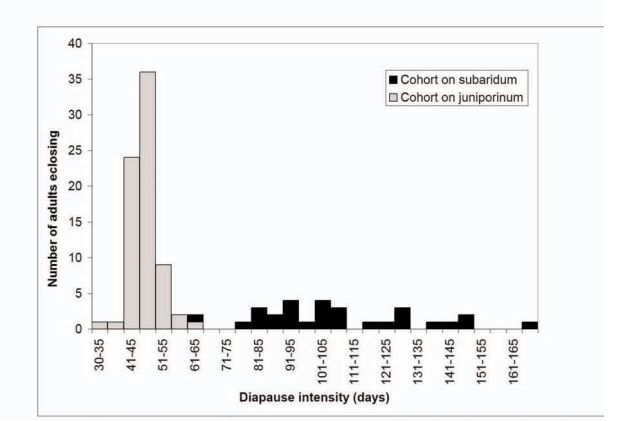

FIG. 4. Diapause intensity of *Euphilotes ancilla* from the Spring Mountains, Nevada.

Diapause intensity. Of the 81 pupae from larvae collected on *Eriogonum umbellatum* var. *juniporinum*, five (6.8%; 1 male, 4 females) emerged without apparent diapause between 26 June and 26 September after an average pupal period of 47.8 days (range 14–106 days, SEM = +18.09). The remaining pupae were refrigerated. One died before and one died during refrigeration. The 74 viable pupae (28 males, 46 females) emerged between 2 March and 6 April 2001 at an average of 46.9 days after removal from refrigeration (range 30–65 days, SEM = +0.54; Fig. 4). Of the eight pupae from larvae on *Eriogonum umbellatum* var. *subaridum* in 2000, seven (4 males, 3 females) emerged between 13 May and 29 June 2001 (one remained as a viable pupa), an average of 116.9 days after removal from refrigeration (range 102–149 days, SEM = +6.25; Fig. 4). Of 31 larvae collected from that plant in 2001,

one was preserved. The remaining larvae pupated and were refrigerated, along with the holdover pupa from 2000. Of these 31 pupae, two died, one disappeared, and 15 from larvae collected in 2001 (7 males, 8 females) eclosed between 3 April and 17 June 2002 at an average of 96.8 days after removal from refrigeration (range 62–136 days, SEM = ± 5.14; Fig. 4); the holdover from 2000, a female, emerged on day 90. The remaining 12 pupae continued in diapause and were again refrigerated for four months. One died, six (3 males, 3 females) eclosed between 28 April and 19 July 2003 at an average of 132.2 days after their return to room temperature (range 87–169, SEM = ±10.58; Fig. 4). The remainder, still viable, was again refrigerated. Two of these died in 2004 after removal from refrigeration and one eclosed after 76 days. The remaining two pupae remain viable through the end of 2005. The eclosion of all 30 pupae from the second flight averaged 109.0 days after removal from refrigeration (SEM = ±4.59). The mean diapause intensities of pupae from the first and second flights and emerging after one year of overwintering were significantly different (t = 19.61, df=87).

Emergence of pupae from the first flight (excluding those that did not enter diapause) extended over 26 days with a variance of 10%, and over 75 days with a significantly different variance of 21% ($F_{15, 74}$ = 18.35) for the sample from the late flight collected during 2001 that emerged without holding over (Table 2). The diapause intensities of males and females were identical for first flight individuals, but second flight males preceded females by an average of eight days (combined 2000 and 2001 individuals that emerged the first year after pupation, Table 2). The differences between the sexes in their time of emergence are within the range of reported lag times for *Euphilotes* (Arnold 1983a; Peterson 1995b).

The diapause responses of these *Euphilotes* serve to elaborate the existence of two cohorts. The difference in mean diapause intensity of 62 days is essentially the same as the differences between first dates that adults have been recorded (63 days; 9 May, 11 July) and between the median date that adults of each flight have been seen in the field (55 days; 6 June, 31 July). Also, and perhaps not coincidently, the differences in first emergence dates of the two cohorts from pupae that entered diapause (32 days) and in the median dates of emergence for each cohort (52 days) are nearly encompassed by the number of days the species was not seen at Willow Creek in each of several years (31–49 days; see above). The variance in diapause intensity of individuals of the second flight (21%) was greater than that of the first (10%) and that of holdover pupae was similar, but yet slightly higher (24%). Variance of the emergence dates for the few pupae without apparent diapause was extreme (89%), perhaps suggesting that this is an abnormal response. The lack of diapause is likely an artifact of experimental protocol (*fide* G. Ballmer) and not an indication of bivoltinism.

The seemingly longer flight period of the early-flying cohort may be a function of accumulation of degree days that vary annually and with microhabitats of individual pupae since, under controlled conditions, there was little variance in diapause intensity (82% eclosed within a ten day period); this agrees with a seemingly longer overall flowering period of *Eriogonum umbellatum* var. *juniporinum* (see Table 2). The extended length of the emergence period of the late-flying cohort, with its higher variance, may reflect adaptation to a potentially irregular flowering of the larval host plant due to annual variability in timing and amount of summer precipitation and its effects on soil moisture. Holdover pupae may act as a hedge against drought (e.g., Nakamura & Ae 1977; Waldbauer 1978; Shapiro 1980; Sims 1983). Pratt's (1988) data also indicated a greater spread of emergence dates for *Euphilotes* eclosing late in the season, but perhaps no significant seasonal trend in its variance.

Taxonomic considerations. The revelation of two cohorts of *Euphilotes* in the Spring Mountains spawns uncertainties on their conspecificity. As noted above, nearly all *Euphilotes* are univoltine; bivoltinism occurs in few populations and not in all years (Langston 1974; Pratt & Ballmer 1986). The existence of two ostensibly obligate and site-specific strategies of voltinism within one gene pool seems unlikely. Despite low average vagility of *Euphilotes*, individual dispersal may exceed 1000m (Arnold 1983a; Peterson 1997). Consequently, there is no reason to consider that spatially separated populations in the Spring Mountains exist as closed gene pools (see also Peterson 1995b, 1996). Some other butterflies, however, exhibit life histories with split generations, where some individuals develop directly and others of the same generation enter diapause or develop more slowly, in part as a function of host plant quality or temperature (e.g., Lees & Archer 1980; Wiklund *et al*. 1983; Nylin *et al*. 1989; Nylin 1992; Wedell *et al*. 1997; Schönrogge *et al*. 2000; Fischer & Fiedler 2001). Genetic discontinuity of the Spring Mountains' *Euphilotes* is more likely along a temporal axis.

The origin of and selective agents leading to two cohorts of *Euphilotes ancilla* in the Spring Mountains are at best conjectural. These *Euphilotes* have likely been isolated from populations elsewhere since at least the termination of the Pleistocene as probably have

other taxa of butterflies there (e.g., Emmel & Austin 1998). Their constancy in phenotype and genital morphology across space and time suggests a single origin. During the Pleistocene and perhaps early Holocene, they may have used one or both varieties of *Eriogonum umbellatum*, although earlier flowering taxa seem usual within the *Euphilotes enoptes* species group (Pratt & Ballmer 1986; Pratt & Emmel 1998). These *Eriogonum* likely had overlapping or completely synchronous flowering periods (see arguments by Pratt & Ballmer 1993; Pratt 1994) constrained by a cooler climate (e.g., Spalding & Graumlich 1986; Van Devender *et al*. 1987; Wharton *et al*. 1990). It follows that the butterfly had a single flight throughout the region as is presently usual among *Euphilotes ancilla* elsewhere. With subsequent climatic warming (Van Devender & Spaulding 1979; Van Devender *et al*. 1987), it is feasible that flowering seasons of the two taxa of *Eriogonum* diverged, each blooming at a more favorable season for its respective development (e.g., Pratt & Ballmer 1993; see also Shields & Reveal 1988). This in turn allowed divergence of the butterfly into two cohorts having somewhat different diapause intensities with a selection against genetic configurations outside the optimum imposed by the phenologies of their larval host plants. The warm and dry altithermal (7000–4500 BP)(Antevs 1938, 1948; Baumhoff & Heizer 1965), may well have been the *coup de grâce* for totally allochronic flowering periods of *Eriogonum* and forced the selection for two seasonal cohorts of *Euphilotes*.

The presumptive seasonal isolation of and perhaps absent genetic continuity between these cohorts of

TABLE 2. Comparison of the seasonal cohorts of *Euphilotes ancilla* at Willow and Cold creeks, Spring Mountains, Nevada.

trait	early season cohort	late season cohort
PLANT		
larval host plant	*Eriogonum umbellatum* var. *juniporinum*	*Eriogonum umbellatum* var. *subaridum*
flowering period	late April-late June	mid-July-early September
BUTTERFLY		
flight season1	early May-early July	mid-July-mid-August
length of flight season[1]	55 days	39 days
visitation to mud	common to abundant	infrequent
length of pupation period[2]	24 days (n=81)	24 days (n=30)[3]
mean length of pupation period	12.8 days	16.6 days
variance of pupation date	38.6%	6.3%
diapause intensity	46.9 days (range 39-65)	109.0 days (range 62-169)[4]
variance of diapause intensity	9.9%	22.7%
emergence span	26 days (n=74)[5]	75 days (n=15)[6]
mean length of emergence period[7]	16.9 days	35.3 days
emergence time lag (male-female)[8]	-0.3 days (n=28 m, 46 f)	8.0 days (n=11 m, 11 f)
non-diapause pupae	5 (n=81)	0 (n=38)
holdover pupae	0 (n=79)	13 (n=35)

[1] overall from many seasons
[2] time from first to last larva to pupate
[3] from larvae collected in 2001; those collected in 2000 pupated over a 10 day period (n=8)
[4] includes holdover pupae; this was 96.8 days for those emerging the first year after pupation (range 62-149 days, n=22) and 132.2 days after holding over for one year (range 87-169 days, n=6)
[5] only those pupae of larvae collected in 2001 that emerged the first year after pupation; emergence span was 47 days for those collected in 2000 and not holding over (n=7) and 82 days for pupae holding over for one year (n=6)
[6] mean of summation of emergence days after first adult eclosed
[7] non-holdover pupae only
[8] only those pupae that entered diapause; apparent non-diapause pupae had an emergence span of 92 days (n=5)

Euphilotes tempt the consideration of two taxa (the holotype of *E. ancilla purpura* is from the first flight), yet the conundrum of taxonomic level appears. They may be adjudged as host plant and temporal subspecies separated by those and other biological divergences (Table 2, see below). These differences in sympatry, however, are potentially effective isolating mechanisms that could well describe sibling species, despite identical phenotypes. Arguments for two species allied to *E. ancilla* in the Spring Mountains appear most likely (Table 2), yet potential for gene flow exists via the few early flight individuals that may not enter diapause (but see caveat above) and through the overlap (by one individual) in diapause intensity. Low levels of gene flow, however, do not discount species-level differentiation (e.g., Sperling 1993). A continuum of differentiation exists among taxa and, although some may not necessarily possess the range of criteria to consider them full species, they exhibit sufficient differentiation that does not permit inclusion within a single species (e.g., Martin *et al*. 2002). Mallet's (1995, see also Sperling 2003) proposal that evaluation of discontinuities in any of many genetic, ecological, behavioral, and morphological traits to provide useful templates for taxon-level inquiries has merit among these *Euphilotes*. Species-level recognition, however, imposes more questions (e.g., which, if either, is *Euphilotes ancilla*) and requires information on gene flow and genetic distance.

The system, whatever it may be in the Spring Mountains, strongly supports the evolutionary scenario proposed by Pratt & Ballmer (1993) and Pratt (1994) whereby speciation processes in *Euphilotes* are propelled by opportunistic colonizations of alternately available and seasonally disjunct larval host plants concomitant with modification of diapause intensities. These differentiations were probably effected in many instances by climatic perturbations during the Pleistocene and Holocene modifying distributions and phenologies of larval host plants (see also Shields & Reveal 1988; Scriber & Ording 2005). The uses of alternative host plants, often with temporal variables, appear as key events leading to divergence, potentially in sympatry, not only for *Euphilotes* (Pratt 1988, 1994) and other butterflies (e.g., Brown & Heineman 1961; Cardé *et al*. 1970; Pratt & Ballmer 1991; Scott 1998), but also among other insects (e.g., Tauber & Tauber 1978; Smith 1988; Bush 1994; Feder 1998; Abrahamson *et al*. 2001; Emelianov *et al*. 2001; Berlocher & Feder 2002; see also Kankare *et al*. 2005). Differentiation through allochronic isolation may be rapid on the order of a few centuries in some Lepidoptera (Groman & Pellmyr 2000; Thomas *et al*. 2003). The nature of *Eriogonum* facilitates this phenomenon through its species richness and biological diversity, where any one site may be inhabited by several taxa with an array of actual or potential phenological specializations.

As noted above, the use of a seasonal progression of larval host plants is not unusual among multivoltine butterflies. In the Spring Mountains, the two ostensibly phenotypically identical cohorts of *Euphilotes* using different seasonally available larval host plants appear superficially to use a simple and comparatively uninteresting bivoltine strategy. It would, however, be unusual in that *Euphilotes* are not usually bivoltine, and it is apparently unique in that the earlier-flying "generation" does not give rise to the later-flying one. Whatever the level of differentiation between these cohorts, the *Euphilotes* in the Spring Mountains represent a heretofore unknown step within the evolutionary sequence proposed for the genus. The question posed in the title of this paper, however, yet remains with an equivocal answer.

SUBSPECIES DESCRIPTION

Since the two cohorts of the *Euphilotes* in the Spring Mountains are obviously different taxa feeding on different taxa of plants, they at least qualify as host plant races. Only one of these, that flying in May and June (as noted above), has been named. The later-flying cohort is here named and described.

Euphilotes ancilla cryptica Austin & Boyd, new subspecies

Diagnosis. *Euphilotes ancilla cryptica* is distinguished from *E. ancilla purpura* by several biological traits (see above, Table 2) including larvae feeding on *Eriogonum umbellatum* var. *subaridum* (vs. *E. umbellatum* var. *juniporinum*), flight season in July and August (vs. May and June), and diapause intensity of 109 days (vs. 47 days).

Description. Size, wing pattern, and genital morphology apparently identical with *E. ancilla purpura* (see Austin 1998), but with different biological characteristics (Table 2). *Euphilotes ancilla cryptica* is distinguished from other taxa of *E. ancilla* by the same characters as is *E. ancilla purpura* (see Austin 1998).

Types. *Holotype: Male* – NEVADA: Clark Co.; Spring Mts., Cold Creek, 20 July 1978, *leg.* G. T. Austin. Allotype: *Female* – same data as holotype. *Paratypes:* (all NEVADA: Clark Co.; Spring Mountains, *leg.* G. T. Austin, including some paratypes of *E. ancilla purpura*) - same data as holotype (10m, 2f); same location as holotype, 28 July 1977 (5m, 1f), 19 August 1977 (1f); Willow Creek, 20 July 1977 (1 m), 20 July 1978 (7m). Types are all deposited at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida.

Type locality. NEVADA: Clark County; Spring Mountains, Cold Creek, 1825m in elevation, towards the northern end of these mountains.

Distribution. The taxon is known from several sites

on both slopes of the Spring Mountains in Nye and Clark counties, Nevada (Fig. 1).

Etymology. This cryptic taxon has been included within *E. ancilla purpura*, since the latter was recognized as different from other phenotypes of the *Euphilotes enoptes* complex.

Discussion. The conspecificity of *Euphilotes* flying early and late in the season in the Spring Mountains is unknown at present, although field and laboratory observations indicate that they are discrete biological entities with little or no overlap of several biological traits. Their sympatry suggests species-level status. Molecular data may yield insights into their relationships, although their divergence may be too recent to give meaningful resolution of their phylogeny and affinities (Peterson 1995b; Nice & Shapiro 1999; Shapiro & Forister 2005). For now, the conservative approach of subspecific-level taxonomy is adopted (see taxonomic considerations above).

Conservation. *Euphilotes ancilla* in the Spring Mountains was considered a species of conservation concern (Anonymous 1998; RECON 2000). With the recognition of two taxonomic entities, management must be focused on each separately. *Euphilotes ancilla purpura* is currently known only from the east slope of the Spring Mountains within relatively small stands of *Eriogonum umbellatum* var. *juniporum* between Willow Creek and West Mud Spring and lower Macks Canyon near the northern end of the Spring Mountains in Clark County (Fig. 1). This taxon, however, is often abundant at those sites. Perhaps its larval host plant is more predictable due to its flowering in the spring when there is potentially more soil moisture than later in the year. The plant's occurrence beneath junipers and pinõns may also provide a moister environment and, along with a relatively unapparent aspect, protect it from grazing.

Euphilotes ancilla cryptica, by contrast, is more widespread as is its larval host plant, *Eriogonum umbellatum* var. *subaridum*. The butterfly occurs in scattered populations from Big Timber Spring to Potosi Mountain (Fig. 1) and in smaller numbers. The host plant sparingly produces flowers in some years, possibly due to drought, and appears subject to greater grazing pressures by ungulates.

The known center of abundance of both taxa of butterflies, in the Cold and Willow creeks area, is faced with considerable disturbance from development and recreation. These, but especially *Euphilotes ancilla purpura*, are at risk with the threat of wildfire exacerbated by invasive weeds and habitat degradation due to unrestricted camping, noncompliant off-road vehicles, equestrian pollution, and feral and introduced ungulates.

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