

HYBRIDIZATION OF CHECKERSPOT BUTTERFLIES IN THE GREAT BASIN

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ABSTRACT. Two putative species of *Euphydryas* butterflies, *E. anicia* and *E. colon*, may be hybridizing in the north-central Great Basin after an extended period of geographic separation. Surveys were conducted throughout northern Nevada to estimate the distribution of each species and of apparent hybrids. More detailed mark-recapture studies were made at one site in the Pequop Mountains in order to examine ecological interactions between the species. The two are largely allopatric and readily separated by wing color and genital morphology. Although interbreeding was apparent from the occurrence of intermediate phenotypes and known mating attempts, the taxa are largely temporally segregated and prefer different larval hostplants. There is also a suggestion of an unbalanced sex ratio of phenotypically intermediate individuals. These *Euphydryas*, although closely related and not strict biological species, are undoubted historical entities and seem to be best treated as phylogenetic species.

Additional key words: distribution, *Euphydryas*, genitalia, hostplants, hybridization, Nevada, Nymphalidae, phenology, sex ratio.

Many taxa exist as intergrading populations in which individuals from neighboring populations are morphologically and ecologically similar, whereas individuals from distant populations are quite distinct. In some instances, however, phylogenetically distinct portions of a series of intergrading populations, or of two closely related species, may be sympatric. Such cases of “ring species” have been considered manifestations of allopatric speciation providing evidence of the differentiation of populations along environmental gradients (Irwin et al. 2001, Irwin & Irwin 2002). Interactions between contiguous or sympatric populations not only augment the understanding of speciation phenomena, but also potentially provide important information on several aspects of population biology (e.g., Endler 1977, Harrison 1993, Bull 1991, Futuyma & Shapiro 1995, Jiggins et al. 1996).

Hybrid zones have long intrigued biologists and an abundant literature speculating on the genetic, ecological, and evolutionary significance of interactions between closely related taxa in such areas has developed (e.g., Sibley 1961, Mayr 1963, Moore 1977, Grant & Grant 1992, Harrison 1993) including one for Lepidoptera (e.g., Remington 1968, Oliver 1979, Porter 1997, Sperling 1990, Scriber et al. 1995, Porter et al. 1995, 1997, Jiggins et al. 1996). More field research on the interactions between taxa in zones of overlap is needed; most investigations infer ecological interactions based on morphological and genetic data (but see Otte & Endler 1989, Lindroth et al. 1988a, b, Porter 1997, Mallet et al. 1998). Little attention has been paid

to the extent of interbreeding in these zones (e.g., Blair 1950, Ficken & Ficken 1968, Collins 1984, Johnson & Johnson 1985, Nichols & Hewitt 1988, Mallet et al. 1998, Benedict 1999). Ecological and demographic data from hybrid zones may, however, provide information crucial to reconstruction of paleoecological events, identification of biogeographic patterns, or prediction of future changes in closely related lineages (e.g., Hafner 1992, Scriber & Gage 1995, Benedict 1999). These data are particularly important since many interacting taxa do not readily fit into traditional taxonomic schemes (e.g., Cracraft 1989, Templeton 1989, Sperling 1990).

This work focuses on butterflies of the *Euphydryas chalcedona* (Doubleday) complex (Lepidoptera: Nymphalidae) in the north-central Great Basin, an area where two morphologically distinct forms of the group appear to hybridize. The objectives were to determine their geographical overlap in northern Nevada and the present extent and nature of interaction. To address these, populations of *Euphydryas* were placed into a broad biogeographic context by conducting regional surveys of wing color patterns and male genital morphology. To examine ecological interactions between forms in greater detail, concentrated investigations were conducted on a site in the Pequop Mountains (Elko County, Nevada) at which both forms were present. At this site, data were collected on wing phenotypes, genital morphology, and spatial and temporal distributions of the forms. Naturally occurring matings were quantified and oviposition hostplant preferences

were tested as an indicator of recent evolutionary history and potential overlap in hostplant utilization between the forms. In addition, the apparent sex ratio of the Pequop population was compared with sex ratios of allopatric populations to determine if this may be unbalanced in the Pequop Mountains (Haldane 1922). These data were supplemented with information from other sites where more than one form occurs.

STUDY SYSTEM

The taxa of the *Euphydryas chalcedona* complex are distributed across much of western North America, from Alaska to Mexico and east to the Great Plains (Scott 1986). The group consists of three nominally distinct species, *E. chalcedona*, *Euphydryas colon* (W. H. Edwards), and *Euphydryas anicia* (Doubleday & Hewitson) (Miller & Brown 1981). These species were defined primarily by the shape of the male genitalia and by wing shape and coloration (Gunder 1929, Bauer in Ehrlich & Ehrlich 1961). Within each of the three putative species, there is considerable between-population phenotypic variation in both wing color (Austin & Murphy 1998b) and male genital morphology (Scott 1978).

Largely in response to this phenotypic variation, nearly 80 names have been proposed for the various forms within the *E. chalcedona* group, many of which represent aberrations. At present, 11 subspecies are recognized for *E. chalcedona*, five for *E. colon*, and 22 for *E. anicia* (Miller & Brown 1981). Although Ferris (1989) synonymized *E. colon* with *E. chalcedona*, there is no consensus on their taxonomic status. Allozyme studies, however, suggested that variation in wing color and pattern was not accompanied by genetic differentiation to justify species-level characterization, and the three groups were tentatively lumped into one morphologically diverse species, *E. chalcedona* (Brussard et al. 1985, 1989, Scott 1986).

The "messy" systematic situation is compounded by the predominantly allopatric geographic distributions of the forms. Although distribution maps suggest broad sympatry in some areas of the western United States (Stanford & Opler 1993), the seemingly geographically sympatric taxa are usually ecologically allopatric, may have somewhat different flight seasons, and often have different larval hostplants. At most specific locations, therefore, only a single member of the complex is present. There are a few locations, however, at which two of the three named entities co-occur (Ehrlich & Murphy 1982, Austin & Murphy 1987, 1998b, Ferris 1988, Brussard et al. 1989). The phylogenetic history of each of the forms has not been fully clarified and it may be difficult to distinguish sec-

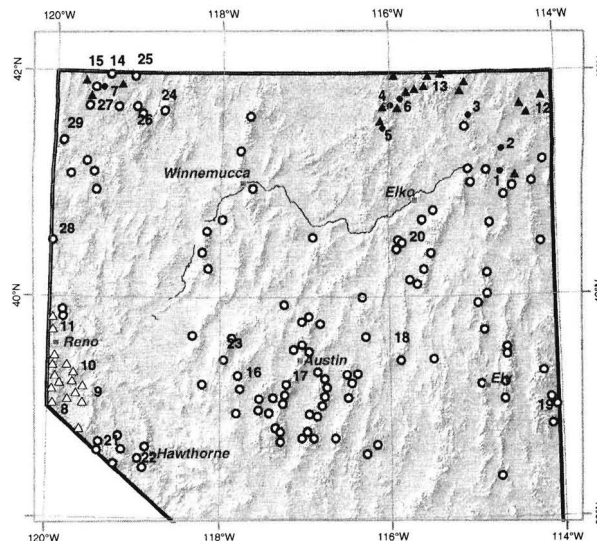


FIG. 1. Map of northern Nevada showing distributions of *Euphydryas anicia* (open circles), *E. colon* (closed triangles), and *E. chalcedona* (open triangles); closed circles indicate sites with more than one form. Irregular line passing through Elko and Winnemucca is the Humboldt River. Numbers refer to locations coded in Tables 1 and 3.

ondary from primary contact and/or intergradation (Mayr 1942, Endler 1977, but see Hammond 1990). Based, however, on the known paleoclimate and paleovegetation of western North America (Mifflin & Wheat 1979, Wells 1983, van Devender et al. 1987, Benson & Thompson 1987, Grayson 1993), allozyme data (Brussard et al. 1989), and present distributions, it appears that *E. chalcedona* and *E. colon* were southern and northern Pacific isolates, respectively, and that *E. anicia* was isolated somewhere between the Rocky Mountains and Sierra Nevada. It is probable that present distributions reflect post-Pleistocene dispersal and rejunction and not the result of a single rampantly differentiating lineage.

METHODS

Data on the distribution of butterflies of the *E. chalcedona* group in northern Nevada were collected as part of ongoing field studies throughout the region. These surveys, initiated in the mid-1970's, were expanded specifically to investigate the *E. chalcedona* complex during the late 1980's and early 1990's.

In order to further clarify the distribution of the three *E. chalcedona* group species, the genitalia of more than 800 male butterflies from 32 sites within Nevada (including one reported by Scott 1978) were scored according to Scott (1978). At seven of these sites, two forms or intermediates of the *Euphydryas chalcedona* complex have been recorded (Fig. 1). The remaining 25 sites supported only a single form.

TABLE 1. Number of individuals with each wing phenotype among museum specimens of the *Euphydryas chalcedona* complex from locations with sympatry or intermediates in Elko County, Nevada (location numbers refer to those in Fig. 1). R = red form ("pure" *E. anicia*), RI = intermediate phenotype (more similar to *E. anicia*), I = "true" intermediate, BI = intermediate phenotype (more similar to *E. colon*), B = black form ("pure" *E. colon*).

Location	Sex	Wing phenotype				
		B	BI	I	RI	R
1. Pequop Mountains	male	35	3	3	5	17
	female	8	1	0	1	3
2. Windemere Hills	male	42	0	1	0	1
	female	11	0	0	0	1
3. Snake Mountains	male	11	0	1	1	1
4. Independence Mts. (Maggie Summit)	male	16	1	0	2	0
	female	1	1	0	0	0
5. Independence Mts. (Jack Creek)	male	14	2	2	0	0
	female	2	0	0	0	0
6. Owyhee River Valley	male	32	2	0	0	0
	female	2	0	0	0	0

At a site in the Pequop Mountains, south of I-80 about two miles east of Pequop Summit at a mean elevation of approximately 2200 m (41°05'N 114°33'W; see Table 1, Fig. 1), comparatively detailed determinations of wing color were made during mark-release-recapture studies (MRR, techniques according to Ehrlich & Davidson 1961) over two seasons. The MRR studies were conducted along a dirt road in the bottom of a predominantly east-west oriented canyon. This canyon is surrounded by mixed riparian and canyon wash habitats with piñon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) on the surrounding hill-sides. From 20 May to 12 June 1989 and from 1 to 12 June 1990, 387 and 194 individual butterflies, respectively, were marked along this road. Upon initial capture, each butterfly was given a unique number and placed into one of five distinct categories based on wing coloration: red (R), red-intermediate (RI), intermediate (I), black-intermediate (BI), and black (B); voucher specimens from here and other sites are at the Nevada State Museum and Historical Society, Las Vegas. Categories R and B are here termed as "pure", RI, I, and BI as "intermediate", and I alone as "true intermediate." All butterflies were released in the center of the area in which they had been captured. Similar determinations of phenotype were made on museum specimens collected from several sites in northeastern Nevada.

Within field samples of butterflies, and accounting for developmental differences, males usually outnumber females, often by a broad margin (e.g., Ehrlich et al. 1984) due largely to behavioral differences between the sexes (e.g., Gall 1985). In general, with large samples taken throughout the flight season, it may be as-

sumed that an apparent sex ratio within a taxon should be correlative across populations using comparable collection techniques (Boyd et al. 1999). Accordingly, the sex ratios of museum specimens and individuals captured as part of the MRR studies were tabulated.

The MRR study in 1989 and 1990 also produced information on relative spatial and temporal distribution of red and black forms. In 1989, the site was divided into 36 areas of similar size. Thirty sites straddled the road and the remaining six were located adjacent to the road in the broadest area of the canyon. In 1990, only the 10 subsites that had the highest butterfly densities in 1989 were again sampled. For the purposes of this spatial and temporal delineation, R and RI individuals were considered "red", B and BI were considered "black", and the few true intermediates were omitted.

Probable differences in emergence timing between the two forms are indicated by differences in mean age of individuals. At each handling, all individuals were scored for wing wear, a common estimator of butterfly age (Orive & Baughman 1989). Butterflies were scored in 0.5 intervals from 0.5 (newly emerged) to 3.5 (worn, indicating extended flight).

To test whether individuals of different color forms at least attempt to interbreed, the genitalia of each male captured during the MRR studies was dipped in a powdered fluorescent dye upon initial capture and on each subsequent recapture. Some of this dye is typically transferred to a female during a subsequent mating, and mated females were examined under ultraviolet light for evidence of dye (Wheye & Ehrlich 1985, Fleishman et al. 1993). Use of this technique to investigate matings between members of different experimental classes assumes that dyed and undyed males are equally likely to achieve copulations, dyes of different colors are equally likely to be transferred during mating and retained by females after mating, and dye transfer occurs at consistent frequencies for successful and unsuccessful matings. The protocol does not assume that all matings are equally viable or are equivalent in an evolutionary sense. All R and RI males were dipped in pink dye, while B and BI males were dyed green.

Some mated females were retained during the MRR study to determine oviposition preference using techniques developed by Singer and co-workers (e.g., Singer 1986). Each female was sequentially offered each of three locally available potential oviposition hostplant species, *Castilleja angustifolia* (Nutt.) G. Don, *Penstemon speciosus* Dougl. ex Lindl. (both Scrophulariaceae), and *Symphoricarpos oreophilus* Gray (Caprifoliaceae) at five-minute intervals or at intervals permitted by weather conditions. A plant was

recorded as accepted if the female's abdomen was fully curled and the ovipositor extruded for at least three seconds. Actual oviposition was not permitted. A female was considered to have preferred plant species A over plant species B if a rejection of B was recorded after an acceptance of A (Singer 1982). If females were captured before 11:00, their preference-testing commenced on the day of capture. If they were captured after 11:00, testing commenced on the following day. In every case, plant species that were accepted on the first day of testing were recorded. In addition, examples of these plants were searched on two dates at the Pequop Mountains study area to determine the presence of egg masses.

Statistical significance (considered at $p < 0.05$ throughout) was determined using chi-square comparisons.

RESULTS

Distribution of *Euphydryas* in the northern Great Basin. Surveys in northern Nevada and adjacent areas revealed a fairly clear distribution of populations of the *E. chalcedona* group (Fig. 1). In the southern portion of the study area, the phenotypically red *Euphydryas anicia wheeleri* (Hy. Edwards) is widespread and often common. Across much of Nevada, this subspecies is associated principally with *Castilleja angustifolia*, but also with *Castilleja linariaefolia* Gray, *Pedicularis centranthera* Gray, and *Penstemon speciosus* (all Scrophulariaceae) (Murphy & Ehrlich 1983, GTA unpublished data). The presently known northern distributional limit of *E. anicia wheeleri* in Nevada occurs in the Toana Range, Windemere Hills, Snake Mountains, and Independence Mountains (all Elko County) westward generally south and east of the Humboldt River (Fig. 1).

In the northeastern portion of the study area, the phenotypically black *Euphydryas colon nevadensis* Bauer predominates and is relatively widespread across sagebrush-dominated (*Artemisia*) slopes and along riparian corridors (Fig. 1). Its known larval host-plants are *Symphoricarpos oreophilus* and possibly *Penstemon* (Bauer in Howe 1975, GTA unpublished data). The southern distributional limit of *E. colon nevadensis* in eastern Nevada is in the Pequop Mountains.

In the narrow geographic band of overlap between *E. anicia wheeleri* and *E. colon nevadensis*, three sites were found where black and red forms and intermediates fly together (northern end of the Pequop Mountains, Windemere Hills in the Thurston Spring area, Tabor Creek in the Snake Mountains) and an additional three sites with one form and intermediates (Wildhorse Crossing Campground in Owyhee River

TABLE 2. Wing phenotype of *Euphydryas chalcedona* complex individuals marked during the mark-recapture-release study in the Pequop Mountains (wing phenotype as in Table 1).

Category	1989			1990		
	Males	Females	Total	Males	Females	Total
R	61	27	88	29	9	38
RI	48	3	51	23	4	27
I	2	0	2	8	0	8
BI	64	5	69	35	3	38
B	165	12	177	75	8	83
Total	340	47	387	170	24	194

Valley, Jack Creek Campground and west of Maggie Summit in the Independence Mountains) (Fig. 1). The site in the Pequop Mountains supported large numbers of both red and black phenotypes during 1989 and 1990. Not surprisingly, the few locations of sympatry between red and black forms are topographically complex; these sites are canyons where sharply defined warm and cool slope exposures supporting distinctive plant communities are just meters apart.

In northwestern Nevada (and also adjacent north-eastern California and southern Oregon), populations of *E. colon* are all far north of the Humboldt River (Fig. 1). These largely black *Euphydryas colon wallacensis* Gunder are sympatric in some locales on the Sheldon National Wildlife Refuge (Humboldt County), but apparently do not hybridize, with the also largely black *Euphydryas anicia veazieae* Fender & Jewitt. The two phenotypes have partially overlapping flight seasons, but the details of their microsympatry require definition. In this region, *E. colon* is associated with *Symphoricarpos* while *E. anicia* apparently uses both *Penstemon* and *Castilleja* (Bauer in Howe 1975, Austin & Murphy 1998b). Just south and east of this area *E. anicia veazieae* intergrades broadly with the redder *Euphydryas anicia macyi* Fender & Jewitt.

Outside these two regions, only one form of the *E. chalcedona* complex is present at any given location in the Great Basin of Nevada, although in some areas their distributions approach (Fig. 1). The affinity of each population is unequivocal and individuals are readily identifiable by superficial characters that are consilient with genital morphology (see below).

Wing phenotypes. As noted, the broad scale surveys located sites in northeastern and northwestern Nevada where two *E. chalcedona* complex taxa were sympatric: the Pequop Mountains, the Windemere Hills, the Snake Mountains, and the Sheldon National Wildlife Refuge. The black form and intermediates were found in the Owyhee River Valley and at two sites in the Independence Mountains (Table 3, Fig. 1). Although at six of these seven sites (except in Hum-

TABLE 3. Genital type frequencies (scored after Scott 1978) of Great Basin *Euphydryas chalcedona* complex taxa (location numbers refer to those in Fig. 1; taxonomy after Miller & Brown 1981).

Location (all Nevada)	Year collected	Genitalia type						Phenotype	Taxonomy
		A	B	C	D	E	F		
ONE FORM PRESENT									
Newberry Mts, Clark Co.	1978	—	19	5	—	—	—	red	<i>E. chalcedona kingstonensis</i>
Carson Range, Douglas Co. (8)	1978–82, 84, 90	—	39	9	—	—	—	black	<i>E. chalcedona macglashanii</i>
Pine Nut Mts., Douglas/Lyon cos. (9)	1980–81, 84	2	18	4	—	—	—	black/orange	<i>E. chalcedona macglashanii</i>
Vicinity of Virginia City, Storey Co. (10)	1978, 80–81	2	13	1	—	—	—	black/orange	<i>E. chalcedona macglashanii</i>
Red Rock area, Washoe Co. (11)	1984	—	5	3	—	—	—	black	<i>E. chalcedona macglashanii</i>
Delano Mine, Elko Co. (12)	1990	1	19	8	1	—	—	black	<i>E. colon nevadensis</i>
Jarbidge Mts., Elko Co. (13)	1987, 90	—	7	1	—	—	—	black	<i>E. colon nevadensis</i>
Sheldon National Wildlife Refuge (Nv 34A, 1.8 mi. W Nv 8A), Humboldt Co. (14)	1987, 89	2	19	4	—	—	—	black	<i>E. colon wallacensis</i>
Sheldon National Wildlife Refuge (Nv 34A, 6.3 mi W Nv 8A), Humboldt Co. (15)	1987, 89–90	5	25	3	—	—	—	black	<i>E. colon wallacensis</i>
Virgin Mts., Clark Co.	1978–81, 88	—	—	—	—	5	19	red	<i>E. anicia hermosa</i>
Spring Mts. (Kyle Canyon), Clark Co.	1977–79	—	—	—	—	3	21	orange	<i>E. anicia morandi</i>
Desatoya Mts., Lander Co. (16)	1980	—	—	—	1	4	19	red	<i>E. anicia wheeleri</i>
Toiyabe Mts., Lander Co. (17)	1978, 80–81, 86, 91	—	—	—	—	8	16	red	<i>E. anicia wheeleri</i>
Roberts Mts., Eureka Co. (18)	1981	—	—	—	—	3	11	red	<i>E. anicia wheeleri</i>
Snake Range, White Pine Co. (19)	1984	—	—	—	—	—	19	red	<i>E. anicia wheeleri</i>
Cedar Ridge, Elko Co. (20)	1991	—	—	—	—	6	12	red	<i>E. anicia wheeleri</i>
Sweetwater Mts., Lyon/Douglas cos. (21)	1980–81, 84, 86	—	—	—	—	9	12	red/black	<i>E. anicia wheeleri</i>
Wassuk Mts., Mineral Co. (22)	1978, 80	—	—	—	—	5	14	red	<i>E. anicia wheeleri</i>
Clan Alpine Mts., Churchill Co. (23)	1978, 80–81	—	—	—	—	7	17	red	<i>E. anicia wheeleri</i>
Pine Forest Mts., Humboldt Co. (24)	1982, 84, 89	—	—	—	—	2	4	red	<i>E. anicia macyi</i>
West of Denio Junction, Humboldt Co. (25)	1984	—	—	—	—	7	5	red/black	<i>E. anicia veazieae-macyi</i>
Summit Lake, Humboldt Co. (26)	1981	—	—	—	11	8	5	red/black	<i>E. anicia veazieae-macyi</i>
Sheldon National Wildlife Refuge (Nv 8A, 5.7 mi. E Washoe Co. line) (27)	1984	—	—	—	13	18	4	black	<i>E. anicia veazieae</i>
Rush Creek, Washoe Co. (28) ¹	—	—	—	—	12	8	1	black	<i>E. anicia veazieae</i>
Granite Mts., Washoe Co. (29)	1980–81	—	—	—	13	28	11	black	<i>E. anicia veazieae</i>

TABLE 3. Continued.

Location (all Nevada)	Year collected	Genitalia type						Phenotype	Taxonomy
		A	B	C	D	E	F		
TWO FORMS AND/OR INTERMEDIATES PRESENT									
Pequop Mts., Elko Co. (1)	1980–82, 87, 90–92	—	26	8	—	—	—	black	<i>E. colon nevadensis</i>
		—	2	2	1	4	2	intermediate	hybrid ²
		—	—	—	—	12	5	red	<i>E. anicia wheeleri</i>
Windemere Hills, Elko Co. (2)	1991	—	31	11	—	—	—	black	<i>E. colon nevadensis</i>
		—	—	1	—	—	—	intermediate	hybrid ³
		—	—	—	—	—	1	red	<i>E. anicia wheeleri</i>
Snake Mts., Elko Co. (3)	1978, 80–81, 86	—	10	1	—	—	—	black	<i>E. colon nevadensis</i>
		—	1	—	—	1	—	intermediate	hybrid ⁴
		—	—	—	—	—	1	red	<i>E. anicia wheeleri</i>
Independence Mts. (Maggie Creek), Elko Co. (4)	1981, 87, 90	—	14	2	—	—	—	black	<i>E. colon nevadensis</i>
		—	1	—	—	2	—	intermediate	hybrid ⁶
Independence Mts. (Jack's Creek), Elko Co. (5)	1980–81	—	8	6	—	—	—	black	<i>E. colon nevadensis</i>
		—	3	1	—	—	—	intermediate	hybrid ⁷
Owyhee River Valley, Elko County (6)	1978, 80–81, 86	—	23	6	1	—	—	black	<i>E. colon nevadensis</i>
		—	—	1	1	—	—	intermediate	hybrid ⁵
Sheldon National Wildlife Refuge (Gooch Spring), Humboldt Co. (7)	1984, 89–90	2	8	4	—	—	—	black	<i>E. colon wallacensis</i>
		—	—	—	8	18	24	black	<i>E. anicia veazieae</i>

¹ Sample after Scott (1978).² BI phenotypes with genitalia B(n = 1), C(2); I phenotypes with genitalia B(1), E(1), and F(1), RI phenotypes with genitalia D(1), E(3), F(1).³ I phenotype with genitalia B(1).⁴ I phenotype with genitalia B(1), RI phenotype with genitalia E(1).⁵ BI phenotypes with genitalia C(1) and D(1).⁶ BI phenotype with genitalia B(1), RI phenotypes with genitalia E(2).⁷ BI phenotypes with genitalia B(2), I phenotypes with genitalia B(1) and C(1).

TABLE 4. Comparison of genital phenotypes of *Euphydryas chalcedona* complex taxa in Nevada (one taxon present in allopatric populations, two taxa present in sympatric populations).

Taxon	Genital phenotype						Mean ¹	Chi-square ²
	A	B	C	D	E	F		
<i>E. anicia wheeleri</i>								
allopatric	—	—	—	1	42	120	5.73	10.30
sympatric	—	—	—	—	12	7	5.36	
<i>E. anicia veazieae/macyi</i>								
allopatric	—	—	—	49	71	30	4.87	15.62
sympatric	—	—	—	8	18	24	5.32	
<i>E. colon nevadensis</i>								
allopatric	1	26	9	1	—	—	2.27	5.58
sympatric	—	112	34	1	—	—	2.24	
<i>E. colon wallacensis</i>								
allopatric	7	44	7	—	—	—	2.00	2.60
sympatric	2	8	4	—	—	—	2.14	
<i>E. chalcedona kingstonensis</i>								
so. Nevada	—	19	5	—	—	—	2.20	
<i>E. chalcedona macglashanii</i>								
western Nevada	4	75	17	—	—	—	2.14	
<i>E. anicia hermosa</i>								
so. Nevada	—	—	—	—	5	19	5.79	
<i>E. anicia morandi</i>								
so. Nevada	—	—	—	—	3	21	5.88	

¹ Derived by substituting 1–6 for genital types A–F, respectively (see text).

² Significant values in bold.

boldt County) intermediate phenotypes were present, no populations were composed primarily of intermediate butterflies.

Museum specimens from the six sites in Elko County with two forms and intermediates ($n = 222$), red and intermediate individuals were the smaller proportion of the populations, ranging from 5 to 43% of field caught samples (Table 1). No true intermediate females were found. The variation of *E. colon nevadensis* noted by Bauer (in Howe 1975) probably refers largely to intermediate phenotypes resulting from hybridization (e.g., see comment by Scott 1978).

In the Pequop Mountains, most butterflies (68% in 1989, 62% in 1990) were either red or black (Table 2) with essentially the same wing color patterns found on butterflies found at single-form sites. The remaining individuals had intermediate wing color (RI, I, BI). The number of black individuals probably was underestimated because surveys were terminated before the end of the flight season in both years. There were significant differences in phenotypic distributions for males and for the total sample for both years (chi-square = 10.55 and 10.87, respectively; $df = 4$), but not for females (chi-square = 3.79; $df = 3$). Most intermediates were either RI or BI; only a few, two in 1989 (out of 387 butterflies) and eight in 1990 (out of 194), were classified as true intermediates (overall <2% of

the total males, Table 2). Individuals of both the RI and BI classes, however, were sufficiently divergent from the pure phenotypes that they would have been considered outliers in single-form populations elsewhere in Nevada. The phenotypic distribution of females was significantly different from that of males (chi-square = 40.09; $df = 4$), due largely to proportionally fewer female intermediates (21%) than males (35%). This difference may have been even greater if sampling continued through the end of the flight season. No true intermediate females were found in either year.

Genital morphology. The distribution of male genital types followed generally accepted species classifications and biogeography as did wing phenotypes (Tables 3, 4). As previously indicated (Gunder 1929, Scott 1978), *E. chalcedona* and *E. colon* had genital morphology of types A, B, and C, whereas those of *E. anicia* were largely types D, E, and F. Some intrasub-specific variation was noted. Most notably, *E. anicia veazieae* and possibly *E. anicia macyi* had proportionally more D and E genital configurations than *E. anicia wheeleri*, *Euphydryas anicia morandi* Gunder, and *Euphydryas anicia hermosa* (W. G. Wright), all of which had mostly type F.

There were, however, some differences in the frequency of genitalia types between areas supporting one versus two members of the species group (Table

4). In northeastern Nevada, *E. anicia* from locations also inhabited by *E. colon* had significantly more type E and fewer type F genitalia than non-sympatric *E. anicia wheeleri*. On the Sheldon National Wildlife Refuge, where *E. anicia veazieae* flies with *E. colon*, the former had significantly fewer type D and E genitalia than in areas without *E. colon*. There was no overlap in the genital morphology of butterflies scored as pure for any area where two taxa were sympatric (Table 3).

Butterflies with intermediate wing color showed a range of genital types (Table 3). BI individuals had genital types B, C, and D and RI phenotypes had D, E, and F. True intermediates in wing color (I) exhibited genital types B, C, E, and F.

Sex ratio. Apparent male:female sex ratios among *Euphydryas* from the Great Basin ranged from 2.6:1 for *E. anicia* to just over 3:1 for *E. chalcedona* and *E. colon* (Table 5). Females represented just over 12% of the MRR sample from the Pequop Mountains and 13% of museum specimens from the sites with known hybridization (Table 5), these not statistically distinguishable (chi-square = 0.14; df = 1). The MRR sample, however, may be biased against females since, as noted above, the study was terminated before the end of the flight season. Both the sample from the Pequop Mountains and the museum sample from the hybrid zone have a significantly different sex ratio than samples from the remainder of the Great Basin (chi-square = 55.25, 20.12, respectively; df = 1). Further, within the Pequop sample itself, there is a significant difference between the sex ratio of individuals scored as pure (R and B) and all intermediates (chi-square = 5.61; df = 1, but note potential sampling problem), but not within the museum sample (chi-square = 0.03; df = 1). Even the sex ratio of individuals scored as pure was significantly different from other Great Basin *Euphydryas* (chi-square = 27.38 in the Pequops, 17.57 for museum sample, df = 1).

Spatial and temporal distributions. The spatial distributions of red and black butterflies in the Pequop Mountains did not appear to be distinct. In both 1989 and 1990, individuals of both forms were found in similar proportions in all subareas occupied. Virtually all of the *E. chalcedona* group butterflies were encountered along the lower half of the study area, being found throughout the wash (including areas along the dirt road and in areas of riparian vegetation). Given the topography of the site and the logistical limits imposed on the MRR efforts, it is doubtful that this study could have detected differences in distribution of the two forms that were less than several hundreds of meters. The males of both forms perch in and patrol along washes searching for females and would not be expected to exhibit perceptible habitat segregation.

TABLE 5. Numbers of males and females in samples of the *Euphydryas chalcedona* complex from the Great Basin.

Taxon or phenotype	Males	Females	% Females
Pequop Mountains (mark-release-recapture study)			
Pure	330	56	14.5
Intermediate	180	15	7.7
Total	510	71	12.2
Hybrid zone (museum specimens)			
Pure	169	26	13.3
Intermediate	23	3	11.5
Total	192	29	13.1
Other Great Basin (museum specimens)			
<i>E. colon</i>	233	77	24.8
<i>E. chalcedona</i>	180	54	23.1
<i>E. anicia</i>	1097	430	28.3
Total	1510	561	27.1

Distribution of females may reflect habitat preferences for oviposition, but this would be nearly impossible to determine in an area with an interdigitation or close proximity of contrasting vegetative associations as in the Pequops. Similar habitat preferences have been noted at other sites where both forms occur.

The temporal distribution of red and black individuals, however, was different. In 1989, 77% (n = 139) of red individuals were first captured on or before 1 June, but only 11% (n = 246) of black individuals were initially handled before that date. In 1990, the temporal subdivision was somewhat less pronounced, but still evident. In both years, the ratio of red to black individuals decreased steadily throughout the study period. Although both forms were present for most of each study period, substantial numbers of red and black individuals flew synchronously for less than a week during each year.

In both years, red individuals were consistently more worn than black butterflies captured on the same day. Based on these data and on correlation of wing wear to age, it is estimated that emergence of red individuals peaked two to three weeks before the peak emergence of black individuals. This is reinforced by the phenology seen generally over the broad expanse of the northern Great Basin in Nevada. Although these data were obtained over several decades and wide latitudinal and elevational ranges that tend to blur individual site and year patterns, they indicate a peak flight of *E. colon* occurring three weeks after that of *E. anicia* (Fig. 2).

During both 1989 and 1990, red individuals were much less numerous than black individuals. While the data do not permit exact population size estimates, in both years the number of black individuals appeared to be at least four times greater than the number of red individuals.

Mating within and between forms. The results of dye transfer experiments indicated that red and black individuals at least attempted to interbreed. In 1989, three of ten recorded matings (virgin females at time of first capture determined after Labine 1964, mated at time of recapture) appeared to have been red-black matings; no dye transfer was noted in 1990. Because of the small sample size, no estimate was made of the relative frequency of mating between individuals of different forms. The data indicate, however, that such matings (or attempts) do occur.

Hostplant utilization. First-day hostplant acceptance data for 25 red and 27 black females are summarized in Table 6. Red and black females showed notably different hostplant acceptance patterns. All red females accepted *Castilleja* as an oviposition hostplant. Twenty-two (88%) of these red females also accepted *Penstemon* as an oviposition hostplant. No red females accepted *Symphoricarpos*.

In contrast, black females exhibited a wider breadth of oviposition hostplant acceptance. Twenty-one of 27 (78%) black females accepted *Castilleja* during the first day of oviposition trials, 10 (37%) accepted *Penstemon*, and 24 (89%) accepted *Symphoricarpos*. There were statistically significant associations between phenotype and acceptance of *Symphoricarpos* and *Penstemon*, but not in acceptance of *Castilleja*. Red females accepted *Penstemon* significantly more often and *Symphoricarpos* significantly less often than did black females (Table 6).

DISCUSSION

Post-Pleistocene climatic vicissitudes in the Great Basin had a profound bearing on distributions of plants and animals (e.g., Wells 1983, van Devender et al. 1987, Harris 1990, Grayson 1993, Elias 1994, but see Riddle 1995). While extirpations undoubtedly occurred (e.g., Grayson 1987), distributional shifts were perhaps a more widespread response to climatic change (Reveal 1979, Harris 1990, Thompson 1990, Grayson 1993, Elias 1994), species adapted to more mesic habitats retreated, those adapted to more xeric environments extended their ranges, and all moved farther north, higher in elevation, or to cooler slope exposures (e.g., Bernabo & Webb 1977, Peters & Darling 1985). The time scale of distributional permutations varied among species (e.g., Webb 1986, Huntley 1991), but movements are thought to have been relatively rapid for insects (Elias 1994, Hewitt 1996). When closely related taxa enter into a changing biotic landscape, the potential consequences include not only the full gamut of interspecific interactions, but also a potential for genetic reorganization, the fusion of lineages,

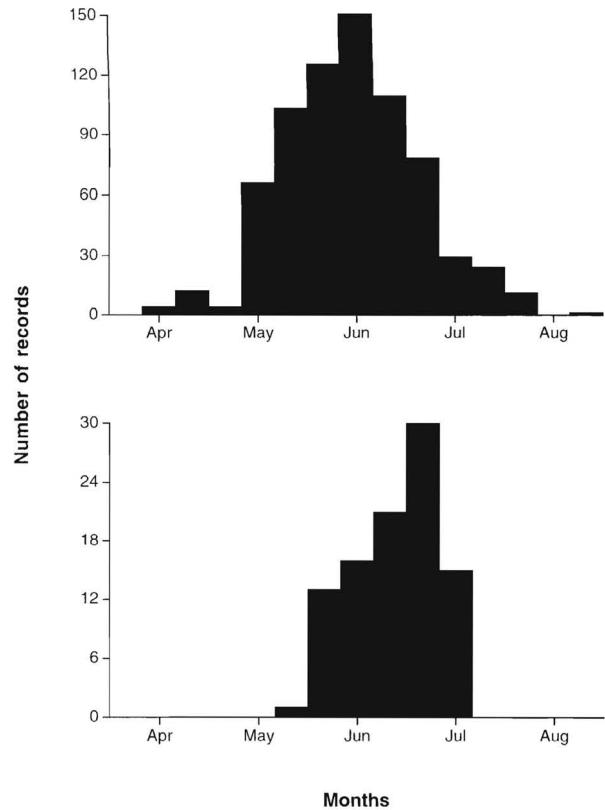


FIG. 2. Phenology of the *Euphydryas anicia* (*wheeleri*, *veazieae*, *macyi*; above) and *E. colon* (*nevadensis*, *wallacensis*; below) in northern Nevada. Records are divided into ten day intervals from April through August inclusively.

a decline of both taxa in zones of sympatry, and/or ecological and phenotypic character displacements.

***Euphydryas* hybridization.** Although there is considerable allopatry among the various phenotypes of the *E. chalcedona* complex in Nevada and elsewhere, large areas exist where they are potentially sympatric at the gross landscape level. Few instances, however, of actual sympatry have been identified (Dornfeld 1980, Ferris 1988, Austin & Murphy 1987, Guppy & Shepard 2001). At these locations, the interactions vary from no apparent intergradation to at least some hybridization (see also Scott 1978). Such variiform responses are not unique among hybridizing taxa (e.g., Short 1965, Rising 1983, Sperling 1987, 1990, Collins 1991).

The studies of the *E. chalcedona* complex in northeastern Nevada indicate existence of a narrow zone of sympatry between butterflies traditionally considered as the specific entities *E. anicia* and *E. colon*. Some hybridization occurs, although there is no evidence of introgression outside this zone. Several lines of evidence support this conclusion: (1) the presence of individuals with intermediate wing phenotype at sites of sympatry,

(2) a shift in male genital morphology across the hybrid zone, (3) an apparently skewed sex ratio, (4) direct evidence of mating between forms, and (5) the existence of different hostplant preferences. In addition, although there is an overlap in spatial distribution at sites of sympatry, these phenotypes are effectively disjoined from one another locally via phenological differences.

The observed level of phenotypically intermediate individuals in the Pequop Mountains implies a fair degree of hybridization between the two forms. This is what Short (1969) termed a "zone of overlap and hybridization" in which substantial numbers of pure phenotypes co-occur with hybrids leading to a bimodal pattern of genotypes and/or phenotypes (e.g., Jiggins & Mallet 2000). The data, however, do not indicate that the two *E. chalcedona* entities found in the Pequop Mountains will merge in the near future. In hybrid zones generally, fusion is a long-term process (Barton & Hewitt 1983, Zink & McKittrick 1995). While the separation between red and black forms is not complete as previously thought (Ehrlich & Murphy 1982, Austin & Murphy 1987, 1998b, Brussard et al. 1989), pure phenotypes outnumber intermediates and no populations dominated by hybrid swarms have been found. The partial temporal segregation of the red and black forms, reinforced by broad scale allopatry, has constrained the extent of hybridization.

Hybridization within *Euphydryas* is known to exist in only highly restricted areas despite considerable overlap in their overall distributions. Narrow hybrid zones are typical for many taxa and usually are maintained by some strong selective factor (Sibley 1961, Saino & Villa 1992, Scriber 1994, Scriber & Gage 1995, Jiggins et al. 1996, Harrison & Bogdanowicz 1997, Mallet et al. 1998). This is further curbed in the Great Basin by the highly insular nature of suitable habitat for *Euphydryas* enforced by a highly dissected topography. Among several models used to explain hybrid zones (Endler 1977, Moore 1977, Moore & Price 1993, van den Bussche et al. 1993), the best explanation for the hybridization of *Euphydryas* in northeastern Nevada appears to be the "tension-zone" or "dynamic equilibrium" model in which reduced fitness of hybrids is offset by continued introgression of parental genes (Bigelow 1965, Barton & Hewitt 1989, Barton & Gale 1993). The high relative abundance of pure phenotypes in the Pequop Mountains, an indicator of reproductive isolation and species-level differentiation (Patton 1973, Tucker & Schmidly 1981, Benedict 1999), may suggest that matings between phenotypically similar individuals are more frequent than between phenotypically dissimilar individuals. This may

TABLE 6. First day acceptance of three potential hostplants by black and red phenotypes of the *Euphydryas chalcedona* complex in northeastern Nevada.

Phenotype	Number accepting	Number rejecting	Chi-square ¹
<i>Castilleja linariaefolia</i>			
Black	21	6	4.3
Red	25	0	
<i>Penstemon speciosus</i>			
Black	10	17	12.1
Red	22	3	
<i>Symphoricarpos oreophilus</i>			
Black	24	3	38.7
Red	0	25	

¹ Significant chi-square values in bold.

be partially related to de facto assortative mating imposed by differences in phenology. Red populations in warmer and drier habitat to the south (or on south facing slopes) reach peak abundance considerably earlier than black populations in cooler and more mesic habitats farther north (Fig. 2). While climatic conditions are a primary determinant of developmental phenology of these butterflies, synchronization with primary larval hostplants is also a contributing factor (Mooney et al. 1980, 1981, Holdren & Ehrlich 1982). It seems likely that the difference in emergence times serves as the major barrier to matings between the two forms that might otherwise freely mate. It has been noted that hybridization often takes place when one taxon is considerably rarer than the other (e.g., Sibley & Short 1959, Ficken & Ficken 1968, Taylor 1973, Silberglied & Taylor 1978). It is of interest in this context that the phenologies are switched in central and northern Idaho with *E. colon* flying early and overlapping the later flying *E. anicia* (Ferris 1988).

Other instances of reported intergradation among *Euphydryas* in Nevada (Ehrlich & Murphy 1982, Murphy & Ehrlich 1983, Austin & Murphy 1987, 1998b, Brussard et al. 1989) now appear, with further data, to be only local variation. Variability within populations does not necessarily indicate hybrid origin (Brown & Wilson 1956, Sibley & West 1958, Schueler & Rising 1976).

Scott (1978, 1986) points to a gradual phenotypic change of *Euphydryas* occurring in some areas and an abrupt change in others. Species would be expected mostly to change abruptly whereas subspecies may either change abruptly or gradually, especially depending upon the absence or presence of past or present ecological or other barriers. Wing color and pattern appear to be evolutionarily labile among *Euphydryas* and potentially relate to thermoregulatory considera-

tions (e.g., Guppy 1986). Each nominal species, along with *Euphydryas editha* (Boisduval), has geographically convergent taxa while retaining its genital morphology and ecological integrity (e.g., Hovanitz 1941, Hovanitz & La Gare 1952, Austin & Murphy 1998a, b, see also Hammond 1990).

The significance of the differences in genital morphology in allopatry and sympatry is unclear. In north-eastern Nevada, type E genitalia were more common among *E. anicia wheeleri* that co-occur with *E. colon* than among allopatric *E. anicia wheeleri* (Table 4), but this may reflect either a small sample size or the effects of hybridization rather than ecologically meaningful differences. The genitalia of *E. colon nevadensis* are virtually identical at locales with and without *E. anicia*. In northwestern Nevada, the proportion of genital types of *E. anicia veazieae* and *E. anicia macyi* is different where they occur in sympatry with *E. colon* and allopatric sites (Table 4). Again, the genitalia of *E. colon* are not different in sites of allopatry and sympatry with *E. anicia*. Average genital scores (obtained by substituting numbers for letters) are virtually identical for allopatric-sympatric comparisons of *E. colon* in both the northeastern and northwestern Great Basin, exhibit an increase for *E. anicia veazieae* in sympatry with *E. colon*, and a decrease for *E. anicia wheeleri* in sympatry. Care, necessarily, must be taken in the interpretation of genitalia in an evolutionary context. Genitalia of butterflies are nearly always different between unambiguous species (e.g., Arnqvist 1998) and, although occasionally there is substantial intraspecific variation (Shapiro 1978, Burns 2000), they are invaluable taxonomically (e.g., Burns 1990, 1996). Their length, at least, is apparently under control of a single gene and they are not always indicative of lineage (Turner et al. 1961), nor do they serve as reproductive isolating mechanisms (Shapiro 1978, Porter & Shapiro 1990).

There are no data to determine the existence of negative ecological interactions concomitant with the sympatry of these *Euphydryas*. Differences in hostplant preference appear more than sufficient to preclude competition for this resource. Of note here is the broad sympatry of *E. anicia* and *E. editha* in much of the Great Basin with an apparent use of identical hostplants in several areas (Austin & Murphy 1998a, b). There is the possibility of mating interference since both *E. anicia* and *E. colon* mate largely along lineal topographic features (*E. editha* mates largely on hilltops in the Great Basin). Although the sympatry between these taxa is geographically narrow in northeastern Nevada, this does not appear to reflect competitive exclusion and they may segregate ecologically where topography is less severe (e.g., in northwestern

Nevada). The species do interact in some places to some degree, but their overall distributions most likely do not reflect interspecific interactions. Hostplant distributions, phenology, and climate are more likely to be limiting.

Our data do not directly address the possibility that hybrids have lower fitness (e.g., Moore & Koenig 1986, Alatalo et al. 1990, Saino & Villa 1992). The few intermediates and a possible deficiency of females suggests some genetic incompatibility (e.g., Jiggins et al. 2001) although there is no certainty that intermediate phenotypes refer to F_1 generations or backcrosses; reduced fitness may not be expressed until the F_2 generation (e.g., Johnson & Johnson 1985). Further study is warranted to determine whether there are temporal shifts in phenotypic frequencies; such instabilities are known among butterflies in the Great Basin (Boyd et al. 1999). Shifts would suggest fluctuations in relative fitness that would act as positive or negative selection forces on hybridization (Grant & Grant 1992, 1993, Bell 1997). Changes in abundance may result from local variations in microclimate; these are important in the early stage biology of *Euphydryas* (Weiss et al. 1988). Vacillations of year to year weather may affect distribution. Thus, sympatry may be fugitive at any of these "range edge" sites and dispersal in either direction may be hindered by unidentified physiological and/or ecological limitations (e.g., see Lederhouse et al. 1995, Shreeve & Smith 1992, Davison et al. 1999, Bryant et al. 2002, Scriber et al. 2002). Long-term climatic alterations may further affect the geographical boundaries of the zone of hybridization (e.g., Cook 1975, Scriber & Gage 1995).

Hostplant relationships. A number of *Euphydryas* subspecies have been described as "host races" (e.g., Murphy & Ehrlich 1980, 1983). Such superficial linkage between taxonomy and ovipositional behavior, however, can be misleading since shifts in hostplant use may occur over a comparatively small number of generations (Singer 1971, Thomas et al. 1987, Singer et al. 1993). Hostplant choice, therefore, may not be correlated with variation in morphology or genetics (Singer 1984, Baughman et al. 1990) and may be further confounded by the distribution of nectar sources (Murphy et al. 1984). Nevertheless, life cycles of local populations are often closely linked with variations in phenology of hostplants (Mooney et al. 1980, 1981, Holdren & Ehrlich 1982, but see Ehrlich et al. 1980) and ovipositional behavior does suggest recent ecological associations and, perhaps, reflect recent phylogenetic history (Brussard et al. 1989, Baughman et al. 1990).

The observed oviposition hostplant acceptance patterns by *Euphydryas* in the Pequop Mountains are

generally consistent with butterfly and plant phenology data. The early-flying red form appears to be limited to *Castilleja* and *Penstemon*, two plant species that are concentrated on warmer slopes. These two species are suitable (with fresh foliage) for larval consumption for a comparatively short portion of late spring and early summer. Early-flying black individuals may also use these two plant species as oviposition sites since no early-season egg masses were found on *Symphoricarpos*. Late-flying individuals seem to be constrained phenologically to *Symphoricarpos* for oviposition since both *Castilleja* and *Penstemon* senesce during the first few weeks of summer. *Symphoricarpos* is more common in cooler microclimates and is available as a potential larval food source well into summer. The distribution of egg masses in the field (Table 7) shifted from *Castilleja* and *Penstemon* early in the season to *Symphoricarpos* later reflecting the respective plant phenology.

Although the two forms of *Euphydryas* in north-eastern Nevada show differences in hostplant acceptances, they also exhibit overlap. The findings that substantial numbers of both accept *Castilleja* and that no early season egg masses were found on *Symphoricarpos* go far towards explaining the observed level of temporal overlap in flight periods. In the Pequop Mountains, the ability of early-season black females to use hostplants accepted by red females may encourage greater temporal overlap between the two forms or, conversely, may reinforce non-overlapping flight periods by early senescence of *Castilleja*. As yet, however, nothing is known of photoperiodic or climatic cues that may govern the dynamics of their diapause. The long-term implications of potential increased temporal synchronization are unclear. Given the apparent lack of premating isolating mechanisms between the two forms and that the two forms are probably at least partially interfertile, eventual complete blending may be a possibility in some locations, especially in the face of accelerated regional climate change if there are no genetic incompatibilities (e.g., Scriber & Gage 1995).

Black individuals are apparently less host-specific than red individuals (Table 6) and thus may be better able to track available plant resources. They use as a hostplant *Symphoricarpos*, a woody, drought-resistant species that is available long after alternative hostplants have senesced. The ability of black individuals to use hostplants common on both warm and cool slopes may allow for a comparatively longer and later flight period and greater abundance at the Pequop site. Occurrence of *Symphoricarpos* in the cooler habitats, and the tendency for *Euphydryas* larvae on woody perennial species to have slower growth rates (Williams et al. 1983a, b), undoubtedly contribute to the disparate mean emergence times of the two color

TABLE 7. Temporal shift in the distribution of *Euphydryas* egg masses in the Pequop Mountains (as number of plants with and without eggs).

Hostplant	11 June 1990		17 July 1990	
	With eggs	Without eggs	With eggs	Without eggs
<i>Castilleja</i>	7	306	0	302
<i>Penstemon</i>	14	315	0	310
<i>Symphoricarpos</i>	0	320	53	353

forms. This argument is weakened, however, since postdiapause larvae of *E. colon* may have access to *Castilleja* (and *Penstemon*); hostplant senescence is only a problem for prediapause larvae if this phenotype naturally uses hostplants other than *Symphoricarpos*.

Species limits and taxonomy. In passing, the data from this study contribute to the discordant views of species limits within the *E. chalcadon* complex. While *Euphydryas* are biologically among the best known butterflies (e.g., Murphy & Weiss 1988), there is no consensus on their taxonomy. There has been substantial disagreement about the taxonomic status of *E. chalcadon*, *E. anicia*, and *E. colon* and the extent and significance of gene flow between them. On one hand, overall similarity in wing color pattern, wing shape, and male genitalia (e.g., Scott 1978, 1986) buttressed by the low level of electrophoretically detectable differentiation between the groups (Brussard et al. 1989) and the existence of individuals of intermediate phenotypes suggest that they are well differentiated forms of a single polytypic species across a broad geographic area (but see e.g., Mensi et al. 1990, Nice & Shapiro 1999). On the other hand, nearly all individuals at a given location can easily be assigned to one of the three nominal species on the basis of one or more of those same phenotypic characteristics. This suggests that the three entities are largely reproductively isolated and are distinct, albeit closely related, evolutionary lineages warranting designation as species-level taxa (e.g., Ferris 1988). Further, although some workers have identified three species within the complex (Bauer in Ehrlich & Ehrlich 1961, Bauer in Howe 1975, dos Passos 1969, Miller & Brown 1981), most who have recognized more than one species retain *E. colon* taxa as subspecies of *E. chalcadon* (e.g., McDunnough 1927, Gunder 1929, dos Passos 1964, Dornfeld 1980, Ferris 1988, 1989, Guppy & Shepard 2001). Allozyme data, however, suggest that *E. colon* are more closely related to *E. anicia* than to *E. chalcadon* (Brussard et al. 1989); genetic distances between the putative taxa are within the range of sibling species (Brussard et al. 1985, 1989). Interfertility between taxa may be a retained ancestral trait (Cracraft

1989, Zink & McKittrick 1995) and hybridization is not necessarily between sister taxa (Omland et al. 1999).

Rationale at all levels are at times hampered by taxonomic misinterpretations and misidentifications, incorrect speculations, or, simply, incomplete data (e.g., Johnson 1994). *Euphydryas* suffer similarly as a brief review of the application of names will illustrate (Gunder 1929, dos Passos 1961, 1963, 1964, 1969, Bauer in Howe 1975, Miller & Brown 1981, Scott 1986, Brusard et al. 1989, Ferris 1989). The phenotype identified here as *E. colon wallacensis*, for example, may not be the same as that further north. Gunder (1928) noted that the genitalia of *E. colon wallacensis* approached those of *E. anicia* and suggested they represented a connecting link. Similarly, Scott (1978) showed variation in the genitalia of populations considered to be this taxon; in fact, populations in Montana had genitalia predominantly of intermediate configurations. No such intermediacy was seen among populations identified here as *E. colon wallacensis* (Table 3).

Euphydryas, therefore, are among those taxa that cannot be conveniently pigeon-holed taxonomically (Murphy & Ehrlich 1984), but have the potential to elucidate a spectrum of disciplines (Mayr 1963, Endler 1977, Collins et al. 1993, Barton & Gale 1993, Bossart & Scriber 1995, Jiggins et al. 1996, Gill 1997). These forms have not differentiated to the extent that their measured allozymes are notably distinct and may readily, but apparently not always, interbreed if environmental conditions act to decrease the difference in adult phenologies. Such conundrums have been attributed to recent gene flow (Arnold 1997) or recent speciation (Niegel & Advise 1986, Nice & Shapiro 1999) where disparate species exhibit assortative mating and potential hybrid inferiority without apparent genetic differences (Johnson & Zink 1983, Johnson & Johnson 1985, Cicero & Johnson 1995). The putative species of *Euphydryas*, while not strictly biological species (Bigelow 1965, Mayr 1982, Barton & Hewitt 1983, but see Johnson et al. 1999), have undoubtedly evolved with some independence over at least the course of the Pleistocene and Holocene and qualify as phylogenetic species (Craycraft 1989, Zink & McKittrick 1995). Genetic exchange may occur broadly without hybridizing taxa becoming panmictic (Grant & Grant 1992, Moore & Price 1993, Parsons et al. 1993, Bell 1996). Concluding conspecificity anticipates a fusion that may never occur (e.g., Patton & Dingman 1968, Zink & McKittrick 1995) and ignores the historical aspects of the hybridizing entities (Barton & Hewitt 1983). Gene flow, and not hybridization, may be the critical variable (Bigelow 1965, Ferguson 2002, but see Ehrlich &

Raven 1969) and Buth (1984) cautioned the use of allozyme data for interpreting phylogeny.

That the putative species remain identifiable and distinct despite areas of sympatry and some hybridization attests to their independence and justifiable species-level status. The absence of interaction in some areas of sympatry and the lack of apparent introgression (judged by phenotypic characters) at other locations contrasts with rather broad areas of introgression in Nevada between subspecies of the "traditional" *Euphydryas* species (e.g., between *E. anicia macyi* and *E. anicia veazieae*, *E. anicia wheeleri* and *E. anicia hermosa*, and *E. chalcedona kingstonensis* and *E. chalcedona klotsi*; see Austin & Murphy 1998b). It is clear, however, that the *E. chalcedona* complex is dynamic and lends a number of interesting interactive scenarios. Effort is warranted more in the location and investigation of these situations and placing them in an evolutionary and biogeographic context in conjunction with more recently developed genetic techniques rather than in arguing their place in an anthropic and thus artificial taxonomic scheme.

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