

HYBRIDIZATION OF *LIMENITIS* IN THE WESTERN GREAT BASIN (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT.— The distribution and nature of sympatry and interaction of *Limenitis weidemeyerii*, *Limenitis lorquini*, and their "fridayi" hybrid were investigated in the southwestern Great Basin during 1996-1998. *L. weidemeyerii* is univoltine, *L. lorquini* is at least bivoltine, and "fridayi" showed a peak flight corresponding to the peak flight of *L. weidemeyerii* and the first brood of *L. lorquini*. This "Mono" hybrid zone extends from the Wassuk Range in western Nevada to several canyons on the east slope of the Sierra Nevada (Devils Gate Summit to Lee Vining Creek) in eastern California where these *Limenitis* inhabit streamside willow associations. *L. weidemeyerii* occurs as pure populations to the east and *L. lorquini* occurs to the north, west, and south of the hybrid zone. The hybrid zone has a general east to west gradient of decreasing proportions of *L. weidemeyerii* and increasing proportions of *L. lorquini*; hybrids are most common at intermediate locations. The trend varies somewhat, in part due to the convoluted axis of the hybrid zone with several subaxes and the geographical proximity of populations of one or the other parentals. Both parental phenotypes span the width of the hybrid zone and represent 28-90% of populations sampled within the hybrid zone. "Fridayi" is intermediate in size to *L. weidemeyerii* and *L. lorquini* and exhibits a range of superficial and genital phenotypes between the parental species. Field caught samples of "fridayi" are female deficient compared to field caught samples of non-hybrid *Limenitis*. The Mono hybrid zone appears to be maintained by hybrid inferiority balanced by continued dispersal of parentals into the zone. A shift in phenotypic proportions at some sites within the Mono hybrid zone has been apparent during the last 20 years.

Another hybrid zone, the "Humboldt" hybrid zone, is known in northern Nevada in the Santa Rosa and Pine Forest ranges. This zone has not been well-studied, but appears phenotypically more stable than the Mono hybrid zone. Hybrids far outnumber parentals, and no sex-ratio skew is apparent. This zone, unlike the Mono hybrid zone, may be maintained by hybrid superiority with little or no dispersal into the zone by parentals.

Due to the apparent stability of the Mono hybrid zone, an apparent reduction of gene flow through the hybrid zone, and at least some genetic incompatibility, *L. lorquini* and *L. weidemeyerii* are considered separate species.

KEY WORDS: Arizona, *Basilarchia*, biogeography, California, distribution, genetics, genitalia, habitat, hostplants, hybrids, Limenitidini, Nearctic, Nevada, North America, phenology, sex ratio, taxonomy, Utah.

The existence of hybrid or introgressive individuals within some populations of *Limenitis* Fabricius, 1807 (Nymphalidae: Limenitidinae) near Mono Lake, California, in the western Great Basin of the United States has been known since Gunder (1932) described *Basilarchia lorquini* form *fridayi* (hereafter referred to as "fridayi"). In the Walker River drainage and adjacent areas of western Nevada and eastern California in 1996, 1997, and 1998, we took the opportunity to sample many populations that included "fridayi" intermediates and those of their parental taxa, *Limenitis lorquini* Boisduval, 1852, and *Limenitis weidemeyerii* W. H. Edwards, 1861. Here we report our information on the distribution and phenotypes of these *Limenitis* in this region, document their relative abundances, evaluate them in light of previously known distributions, and provide a baseline for future investigations on their dynamics. Brief notes are also made on another, but less well-studied, hybrid zone in northern Nevada.

METHODS

Samples of *Limenitis* were initially taken in 1996 to document their phenotypic occurrence at various locales in the western Great Basin. Later in 1996 and especially in 1997 and 1998, when hybridization was encountered over a rather wide area, systematic samples were taken of all individuals encountered. We also examined series in the collection at the Nevada State Museum and in various private collections; additional data were provided by other museums.

Phenological and distributional records for *L. weidemeyerii* and *L. lorquini* are from Austin's Nevada database, including records from

throughout the state and information gathered as part of this study. Nevada records for "fridayi" are from this same database; California data for "fridayi" are from this study, museum specimens, and the literature.

Limenitis specimens were scored on various phenotypic traits, modifying and expanding the criteria used by Porter (1990). Forewing length was measured from its base to the furthest extent of the apex. Wings were scored for 17 characters often used to distinguish the two species including those noted during this study. Four characters of the male genitalia were based upon the right valva. The character states are detailed in Table 1 (see also Fig. 1). Each specimen was scored individually for each character ("0" for a *L. weidemeyerii*-like trait, "1" for an intermediate trait, "2" for a *L. lorquini*-like trait). The computed wing character score for each specimen ranged from 0 for a pure *L. weidemeyerii* to 34 for a pure *L. lorquini*. Scores for male genitalia ranged from 0 (*L. weidemeyerii*) to 8 (*L. lorquini*). There were too few definitive characters noted for female genitalia for meaningful comparisons. The presence or absence of a series of red macules on the dorsal hindwing to the pale median band (Fig. 4, 6, 8, 10, 13-14, 16, 19, 38-41, 63, 65-66; the "eavesi" macules, see below) was also noted. Specimens from outside the area of interaction in the Great Basin of Nevada and eastern California were scored similarly to provide reference samples to assess the variation expected within allopatric populations of *L. weidemeyerii* and *L. lorquini*. The scores for these specimens, and criteria for defining hybrids, are given below in the results. Historical specimens from other collectors and museums were likewise scored, but, except for

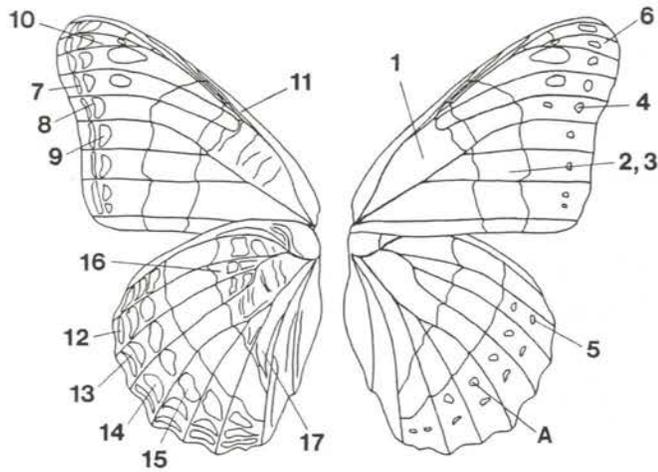


Fig. 1. Wing characters scored on Great Basin *Limenitis*; numbers refer to characters as described in Table 1: 1. dorsal ground color, 2. median band width, 3. median band color, 4. DFW submarginal macules, 5. DHW submarginal macules, 6. DFW apex, 7. VFW marginal line, 8. VFW submarginal line, 9. VFW submarginal macules, 10. VFW apex, 11. central VFW costa, 12. VHW submarginal macules, 13. VHW submarginal line, 14. VHW submarginal macules, 15. VHW postmedian band, 16. VHW basad to median band, 17. VHW cell CuA_2 . "A" represents an "eavesi" macule.

series collected by the authors, these are potentially biased towards obvious hybrids.

Sample locations, years, and sizes are given in Table 2. Voucher specimens are deposited at the Nevada State Museum and Historical Society, Las Vegas; at the Nevada State Museum, Carson City; in the Boyd collection; and in the collections of the individuals and institutions noted in the acknowledgements.

Comparisons of frequency distributions were made using chi-square analyses, differences between means were calculated using the *t*-test, and differences in variances were calculated with the variance ratio test (*F*) (Zar, 1974). Most pertinent statistical values are given in Appendix I; a few are within the text or on figures. Statistical significance is at the 0.05 level throughout.

THE TAXA

The wings of *L. weidemeyerii* and *L. lorquini* differ considerably in their color and markings. *L. weidemeyerii* (Fig. 2, 20, 38, 44) is the larger of the two species, black in color with white and often broad bands across the forewing and hindwing, and with little red-brown color. *L. lorquini* (Fig. 19, 37, 43, 49) is smaller, browner with pale cream-colored and usually narrow bands, and with orange-brown to red-brown on the dorsal forewing apex and, especially, on the venter. The pale bands of *L. weidemeyerii* strongly reflect ultraviolet light whereas those of *L. lorquini* reflect it slightly (Scott, 1974).

TABLE 1. Character traits of western Great Basin populations of *Limenitis* (see Fig. 1) Characters were scored "0" for *L. weidemeyerii* state, "1" for intermediate state, and "2" for *L. lorquini* state.

TRAIT	"WEIDEMEYERII" STATE	INTERMEDIATE STATE	"LORQUINI" STATE
Dorsum			
1. ground color	black	intermediate	brown
2. median band width	broad	intermediate	narrow
3. median band color	white	intermediate	cream
4. FW submarginal macules	prominently present	vaguely present	absent
5. HW submarginal macules	prominently present	vaguely present	absent
6. FW apex	black	narrow red-brown, variously mixed with black	broadly red-brown
Venter			
7. FW marginal line	distinctly blue-gray	intermediate	absent/indistinct, cream
8. FW submarginal line	black	mixed red-brown and black	red-brown
9. FW submarginal macules	white	intermediate	cream
10. FW subapex	black (excludes red-brown along veins on some individuals)	intermediate	red-brown
11. central FW costa	black	intermediate	red-brown
12. HW marginal line	broad and distinct	intermediate	narrow and indistinct
13. HW submarginal line	black	mixed red-brown and black	red-brown
14. HW submarginal macules	blue	intermediate	lavender
15. HW postmedian band	narrow and dull red	intermediate	broad and red-brown
16. HW basad to median band	largely gray	intermediate	largely red-brown
17. HW cell CuA_2	all gray	intermediate	1/3 to 1/2 red-brown
Genitalia (right valva)			
18. harpe length	long	intermediate	short
19. harpe breadth	broad	intermediate	narrow
20. basal valva breadth	narrow	intermediate	broad
21. terminal spines	several short	one long, several short	one long (occasionally one or two short)

TABLE 2. Sample sites and sizes for scored Great Basin populations of *Limnitis* (# refers to location number in Fig. 75-76), m = male, f = female.

#	LOCALITY	YEAR	N
<i>Limnitis weidemeyerii</i> (non-hybrid zone)			
1	NV: Elko Co.; Jarbidge Mts, various locations	various	40m10f
2	NV: Elko Co.; Spruce Mt.	various	1m1f
3	NV: Elko Co.; Pequop Mts., 1.9 mi. W of Pequop Summit	various	4m
4	NV: Elko Co.; E Humboldt Range, various locations	various	1m1f
5	NV: Elko Co.; Ruby Mts., various locations	1984	1m1f
6	NV: Elko Co.; Independence Mts., various locations	various	28m2f
7	NV: Elko Co.; Ruby Valley	1975	2m
8	NV: White Pine Co.; Schell Creek Range, various locations	various	7m2f
9	NV: Eureka Co.; Roberts Mts., various locations	1981	3m
10	NV: Lander/Nye cos.; Toquima Range, various locations	various	25m4f
11	NV: Nye Co.; Big Smoky Valley, Little Smoky	1984	4m1f
12	NV: Lander/Nye cos.; Toiyabe Range, various locations	various	39m10f
13	NV: Lander Co.; Desotoya Mts., Carroll Summit	1983	1m
14	NV: Churchill Co.; Clan Alpine Mts., various locations	various	9m6f
15	NV: Pershing Co.; Humboldt Range, various locations	various	25m1f
16	NV: Mineral Co.; Pilot Mts., Dunlap Canyon	various	2m
<i>Limnitis lorquini</i> (non-hybrid zone)			
17	NV: Esmeralda Co.; White Mts., Trail Canyon	1980	1m
18	CA: Mono Co.; Lower Rock Creek	various	10m5f
19	CA: Mono Co.; Sonora Pass Road, various locations	1996	28m1f
20	CA: Mono Co.; Antelope Valley, various locations	1996	14m2f
21	CA: Mono Co.; Mill Creek/Little Antelope Valley	1996-97	34m3f
22	NV: Lyon Co.; Smith Valley	1996-97	2m
23	NV: Lyon Co.; N end Sweetwater Mts., Garden Canyon	1967, 80	2m
24	NV: Lyon Co.; lower East Walker River, from the "Elbow" to junction with the West Walker River	1996-97	8m
25	NV: Lyon Co.; Mason Valley, various locations	1996-97	20m9f
26	NV: Douglas Co.; Pine Nut Mts., various locations	1972	3m
27	NV: Douglas Co.; Carson Valley, various locations	various	31m12f
28	NV: Carson City/Douglas/Washoe cos.; Carson Range, various locations	various	30m11f
29	NV: Storey Co.; Virginia City area	various	4m
30	NV: Washoe Co.; Peavine Peak Road	various	14m1f
31	NV: Lyon Co.; Fernley, various locations	various	27m9f
32	NV: Lyon Co.; Fallon, various locations	various	8m3f
33	NV: Churchill Co.; Ft. Churchill	1966	2m
"fridayi" populations (Mono hybrid zone)			
34	CA: Mono Co.; Lee Vining Creek	1997	15m3f
35	CA: Mono Co.; Mono Lake	1979	4m2f
36	CA: Mono Co.; Sierra Nevada, Virginia Lakes Rd.	1996	2m
37	CA: Mono Co.; Sierra Nevada, Green Creek	1996-97	18m2f
38	CA: Mono Co.; Sierra Nevada, Summers Creek	1996-97	26m2f
39	CA: Mono Co.; Sierra Nevada, Robinson Creek	1996	2m
40	CA: Mono Co.; Sierra Nevada, Buckeye Creek	1996	1m
41	CA: Mono Co.; Sierra Nevada, By Day Creek	1997	13m
42	CA: Mono Co.; US 395, vic. Devil's Gate Pass	1997	1m
43	CA: Mono Co.; Bodie Hills, Aurora Canyon	1996-97	18m1f
44	NV: Mineral Co./CA: Mono Co.; Bodie Hills, Bodie Creek	1997	15m2f
45	CA: Mono Co.; Bodie Hills, Bridgeport Canyon	1998	38m2f
46	CA: Mono Co.; Sweetwater Mts., Silverado Canyon	1996	3m
47	NV: Lyon Co.; Sweetwater Mts., Sweetwater Canyon	1997	24m1f
48	NV: Lyon/Douglas cos.; Sweetwater Mts., Desert Creek	1980s	8m4f
		1996-97	54m8f
49	CA: Mono Co.; upper East Walker River, from Bridgeport Reservoir to Nevada line	1980s	11m
		1991	1m
		1996-97	35m6f
50	NV: Lyon Co.; middle East Walker River, from California state line to "Elbow"	1970-80s	10m4f
		1996-97	13m1f
51	NV: Mineral Co.; Wassuk Range, Powell Canyon	1996	4m
52	NV: Mineral Co.; Wassuk Range, Corey Peak Road	1970-80s	24m4f
		1996-97	46m6f
53	NV: Mineral Co.; Wassuk Range, Cottowood Canyon	1996-97	50m3f
"fridayi" populations (Humboldt hybrid zone)			
54	NV: Humboldt Co.; Pine Forest Range, Blue Lake Road	1970s	21m7f
		1980s	19m3f
55	NV: Humboldt Co.; Santa Rosa Range, various locations	1980s	22m7f

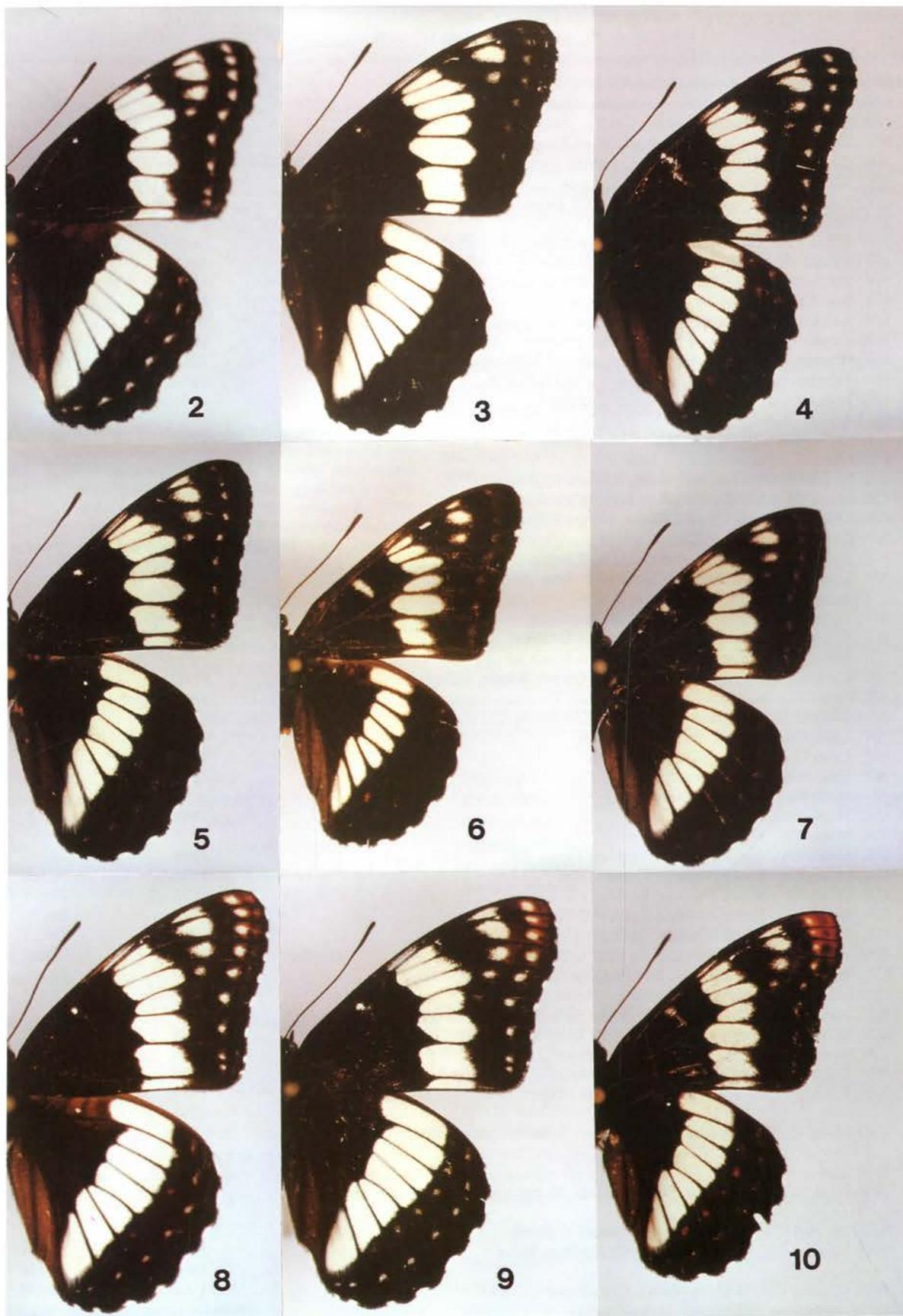


Fig. 2-10. Male *Limenitis* from the western Great Basin, dorsal surface. 2. non-hybrid zone *L. weidemeyeri*, NV: White Pine Co.; Schell Creek Range, Cleve Creek, 3-10. Mono hybrid zone *Limenitis*, 3. CA: Mono Co.; East Walker River, 4. CA: Mono Co.; Sierra Nevada, Virginia Creek, 5. NV: Lyon Co.; East Walker River, 6. CA: Mono Co.; Sierra Nevada, By Day Creek, 7. CA: Mono Co.; Sierra Nevada, Summers Creek, 8-10. NV: Mineral Co.; Wassuk Range, Corey Peak Road.

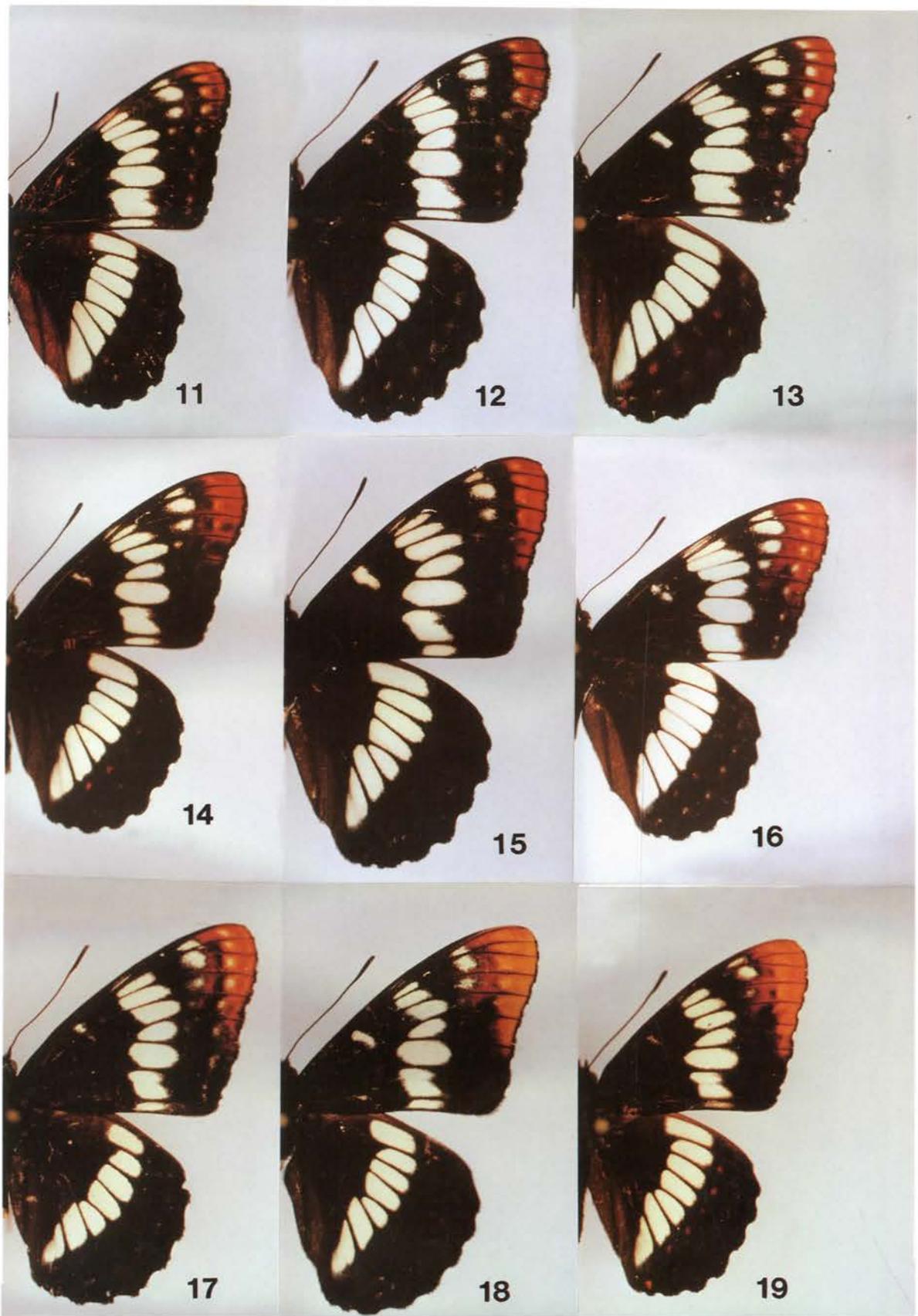


Fig. 11-19. Male *Limnitis* from the western Great Basin, dorsal surface. 11-18. Mono hybrid zone *Limnitis*, 11. CA: Mono Co.; Sierra Nevada, Summers Creek, 12. CA: Mono Co.; Sweetwater Mountains, Sweetwater Canyon, 13. CA: Mono Co.; Sierra Nevada, Summers Creek, 14. CA: Mono Co.; Bodie Hills, Bridgeport Canyon, 15. CA: Mono Co.; East Walker River, 16. NV: Mineral Co.; Wassuk Range, Corey Peak Road, 17. CA: Mono Co.; Sweetwater Mts., Sweetwater Canyon, 18. NV: Mineral Co.; Wassuk Range, Corey Peak Road, 19. non-hybrid zone *L. lorquini*, NV: Washoe Co.; Pyramid Lake.

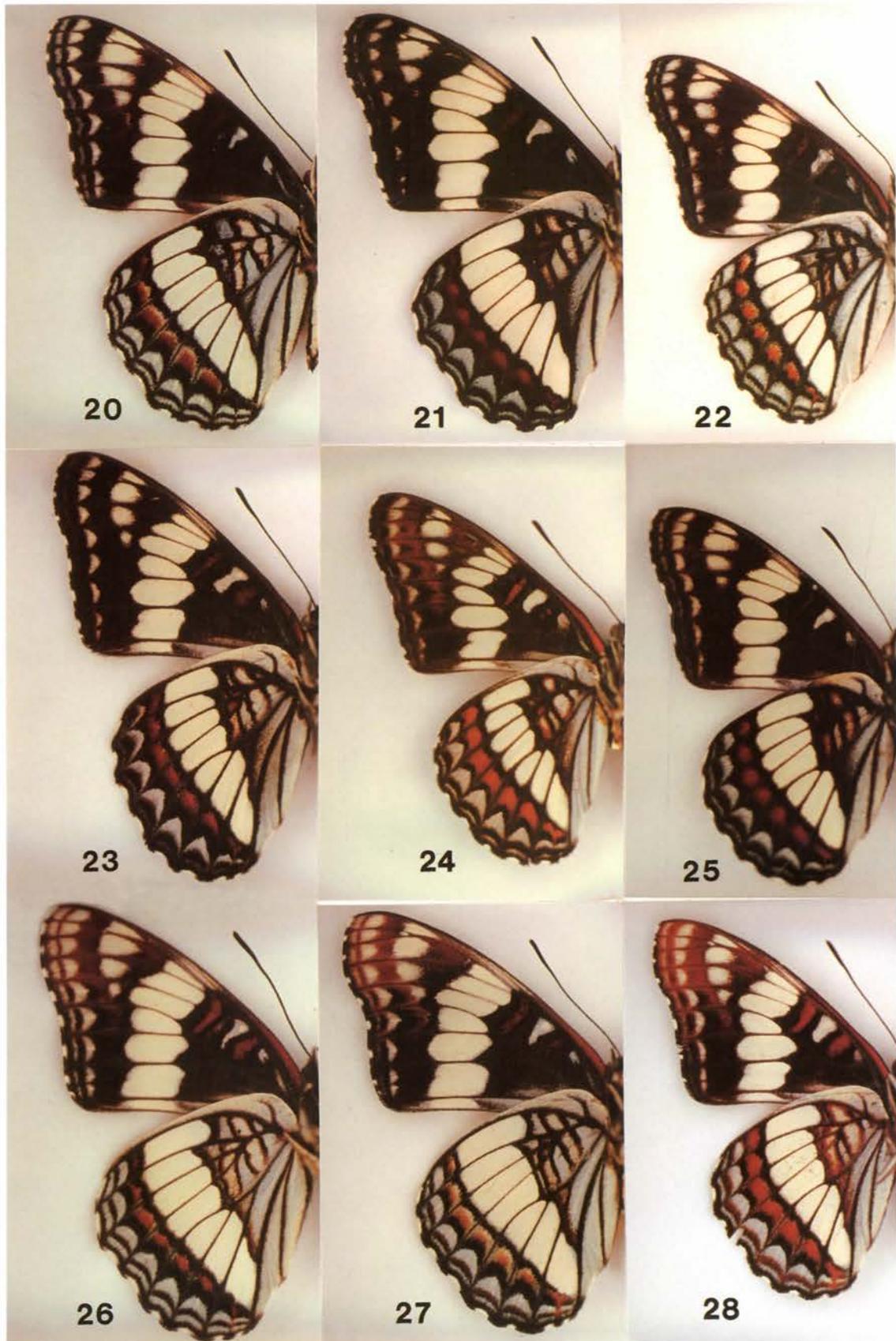


Fig. 20-28. Male *Limnitis* from the western Great Basin, ventral surface. Same specimens as Fig. 2-10.

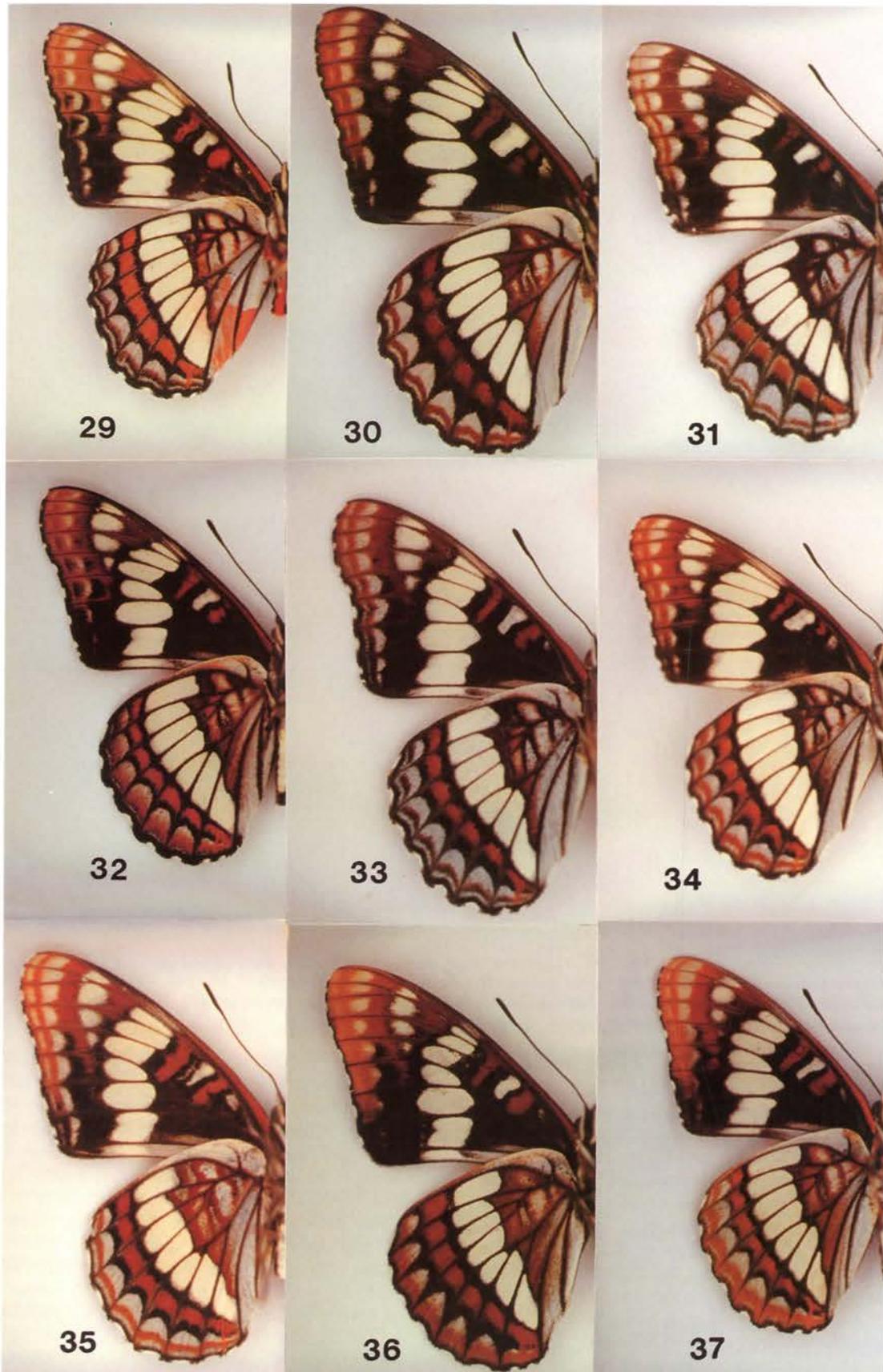


Fig. 29-37. Male *Limenitis* from the western Great Basin, ventral surface. Same specimens as Fig. 11-19.

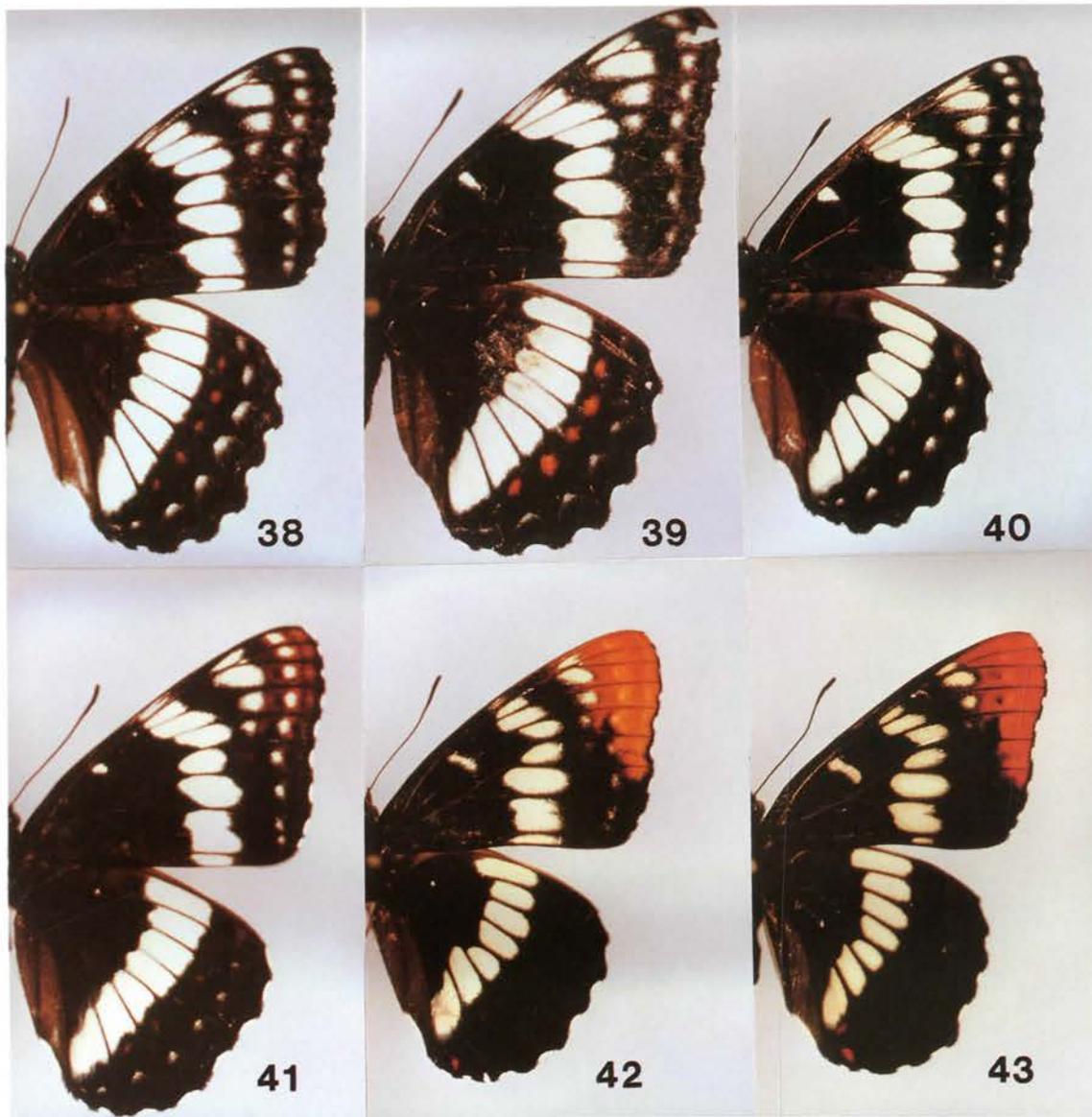


Fig. 38-43. Female *Limenitis* from the western Great Basin, dorsal surface. 38. non-hybrid zone *L. weidemeyerii*, NV: Nye Co.; Toiyabe Mts., Ophir Canyon, 39. non-hybrid zone *L. weidemeyerii*, NV: Elko Co.; Jarbidge Mts., Jarbidge Canyon, 40-42. Mono hybrid zone *Limenitis*, 40-41. NV: Mineral Co.; Wassuk Range. Corey Peak Road, 42. CA: Mono Co.; Sweetwater Mts., Sweetwater Canyon, 43. non-hybrid zone *L. lorquini*, NV: Pershing Co.; Selenite Range, Limbo Range Road.

The male genitalia of *L. weidemeyerii* and *L. lorquini* are different in the morphology of their valvae (Nakahara, 1924; Chermock, 1950; Platt *et al.*, 1970), these differing in overall shape and especially in the spination of the caudal end (Fig. 74; note that the valva of the "*L. weidemeyerii*" illustrated by Carpenter and Hobby (1944) does not resemble that of any individual we examined and is undoubtedly misidentified). The valva of *L. weidemeyerii* is robust, has a long and broad caudal end, and has several relatively short, often hook-like, terminal spines (an average of nearly 7; Platt *et al.*, 1970) and that of *L. lorquini* is less robust, has a shorter and more slender caudal end, and has a single long and often a few shorter terminal spines (an average of 2.5; Platt *et al.*, 1970). Platt *et al.* (1970) found that the valvae of the two taxa (*L. weidemeyerii* from Wyoming; *L. lorquini* from Montana and Idaho) occupy different regions in a three dimensional canonical matrix. There are no data on the genitalia of more southern populations of these *Limenitis* or for "fridayi" populations. Female genitalia of *Limenitis* have not been described.

L. lorquini occurs from northern Baja California, Mexico, northward through much of California, Oregon, and Washington, through southwestern Canada (southern British Columbia and southwestern Alberta and Saskatchewan), and east to northwestern Nevada, eastern Idaho, the western third of Montana, and southwestern Alberta (Comstock, 1927; Jones, 1951; Austin, 1985a; Brown *et al.*, 1992; Dornfeld, 1980; Emmel and Emmel, 1973; Kohler, 1980; Ferris and Brown, 1981; Garth and Tilden, 1986; Scott, 1986; Stanford and Opler, 1993; Bird *et al.*, 1995; Layberry *et al.*, 1998). The species is bivoltine or more in its range southward and possibly single-brooded northward (e.g., Scott, 1986). Larvae of *L. lorquini* feed principally on various species of *Salix* and *Populus* (Salicaceae), but are also known to feed on *Prunus*, *Cotoneaster*, *Holodiscus*, *Spiraea*, and *Malus* (Rosaceae), and *Ceanothus* (Rhamnaceae) (Scott, 1986). Oviposition in the western Great Basin has been noted on *Salix exigua* Nutt. and *Populus fremontii* Wats., two previously unreported hostplant species (Austin, unpubl. data).

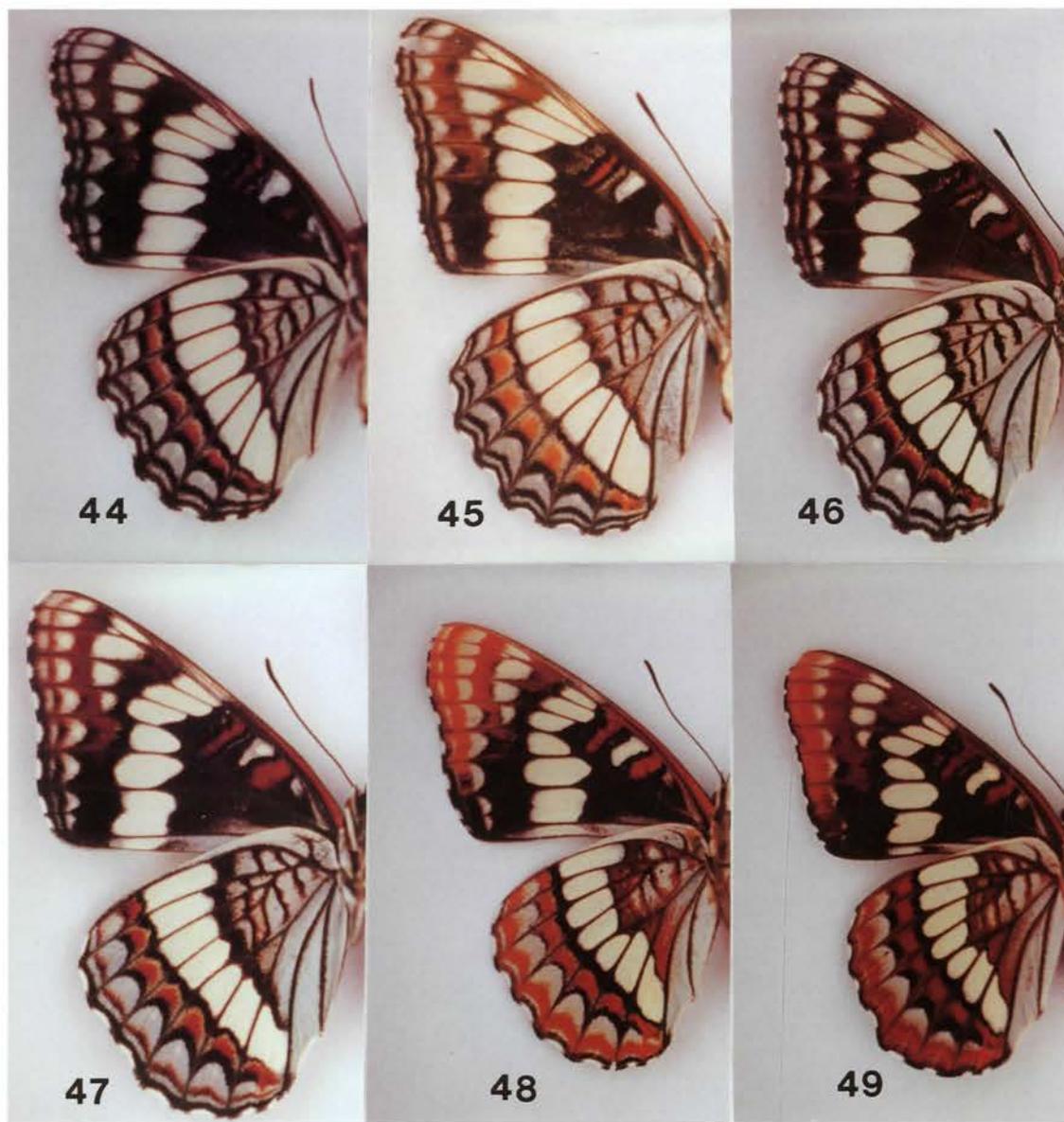


Fig. 44-49. Female *Limenitis* from the western Great Basin, ventral surface. Same specimens as Fig. 38-43.

The taxonomy of *L. lorquini* was reviewed by Perkins and Perkins (1966) and generally two subspecies have been recognized: *L. l. lorquini* in the southern part of the species' distribution, with its type locality restricted to Hwy. 70 at Soda Creek, E. Branch North Fork Feather River Canyon, 2500' elev., Plumas County, California (Emmel *et al.*, 1998) and *Limenitis lorquini burrissoni* Maynard, 1852, described from Landsdowne, British Columbia, from the northern part of the species' range. Austin and Emmel (1998; see also Brown, 1934) recognized that the southern California phenotype was separable from that at the type locality of the species and that the populations in the White Mountains (western Nevada/eastern California) were phenotypically different from other populations.

It has been suggested (Poulton, 1909; Orsak, 1977; Platt, 1983; Garth and Tilden, 1986; Scott, 1986; Porter, 1988) that, with its red-brown forewing apices, *L. lorquini* may be mimetic with the often sympatric *Adelpha bredowii* Geyer, [1837], or with *Doxocopa* Hübner, [1819], but the reality of this has yet to be demonstrated.

L. weidemeyerii ranges throughout much of the Great Basin and Rocky Mountains regions from southern New Mexico, southeastern Arizona, and extreme east-central California, through most of

Nevada, Utah, Colorado, Wyoming, and Montana, southwestern Oregon, southern Idaho, southeastern Alberta, and east to the western Dakotas and western Nebraska (Johnson, 1973; Toliver and Holland, 1977; Thormin *et al.*, 1980; Dornfeld, 1980; Kohler, 1980; Ferris and Brown, 1981; Austin, 1985a; Garth and Tilden, 1986; Scott, 1986; Royer, 1988; Bailowitz and Brock, 1991; Stanford and Opler, 1993; Bird *et al.*, 1995; Layberry *et al.*, 1998). The species appears to be univoltine in most of its range, although it may have two broods at some southern and low elevation sites (e.g., Scott, 1986; but see Bailowitz and Brock, 1991). Larvae of *L. weidemeyerii* feed principally on various *Salix* and *Populus* (Salicaceae), but also feed on *Prunus*, *Amelanchier*, and *Holodiscus* (Rosaceae) (Scott, 1986). Known hostplants in the Great Basin are *Salix exigua*, *Populus angustifolia* James, *P. fremontii* (a previously unreported hostplant species), *Populus tremuloides* Michx., *Amelanchier utahensis* Koehne, and *Holodiscus boursieri* (Carr.) Rehd. in Bailey (Emmel *et al.*, 1970; Austin, unpubl. data).

L. weidemeyerii was reviewed by Perkins and Perkins (1967) who recognized five subspecies; an additional subspecies was subsequently described by Austin and Mullins (1983) from southeastern

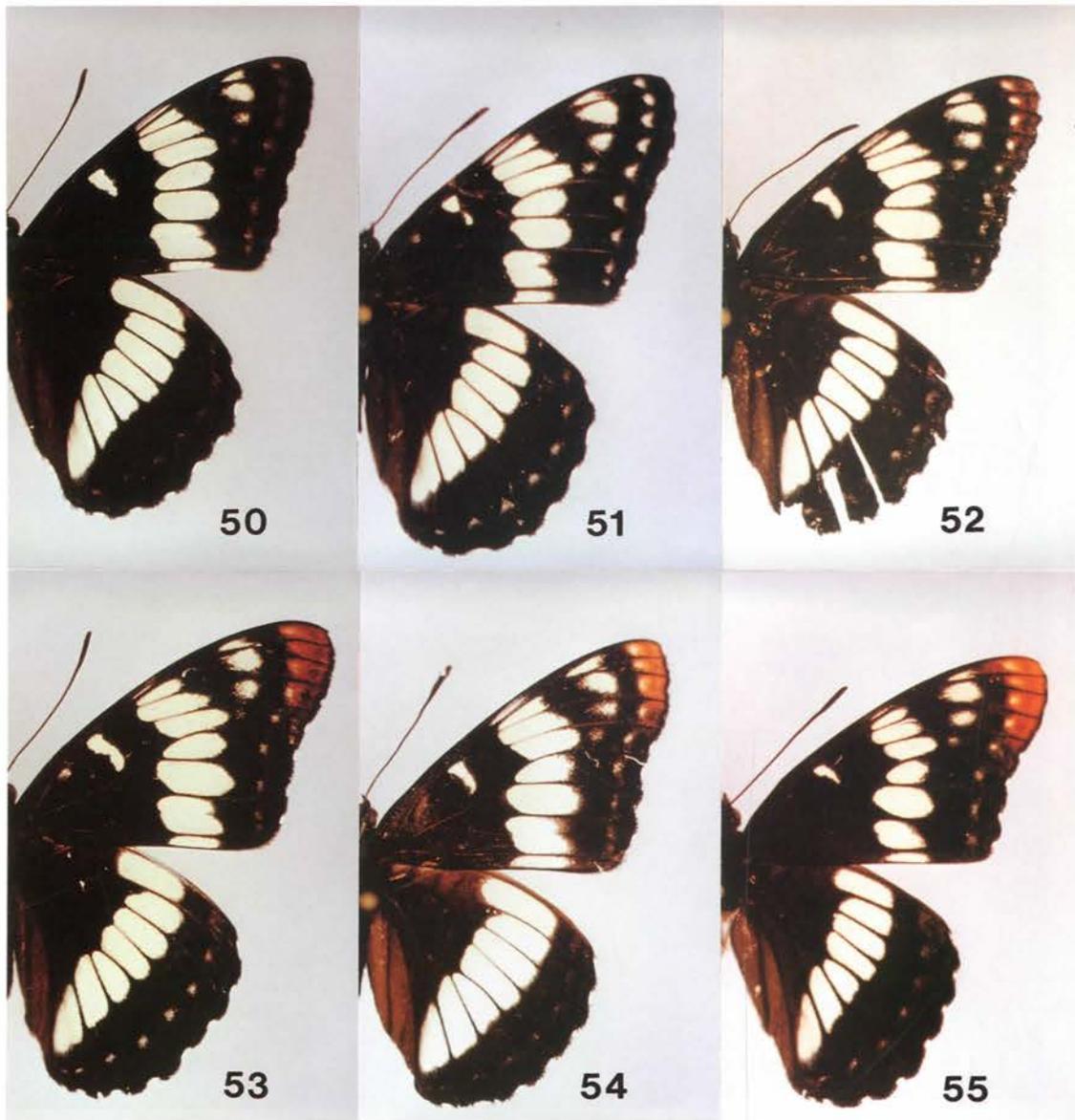


Fig. 50-55. Male *Limnitis* from the western Great Basin, Humboldt hybrid zone, dorsal surface. All from NV: Humboldt Co.; Pine Forest Range, Blue Lake Road.

Arizona. *Limnitis weidemeyerii latifascia* Perkins & Perkins, 1967, occupies most of the western portion of the species' range and is the subspecies (wholly or principally) in contact with *L. lorquini*.

Since its description (Gunder, 1932), the form "fridayi" "Öi" generally been considered a hybrid between two widely recognized species, *L. lorquini* and *L. weidemeyerii*. Gunder (1932) described the "fridayi" phenotype based on a holotype female from "Leevining Creek, near Mono Lake, Mono County, Calif." He noted that this represented "the connecting link between *lorquini* Bdv. and *nevadae* B. & Benj." and was "hybridical in appearance, combining characters of each." Brown (1934) found the Mono Lake population to be composed of about 70% *L. weidemeyerii*, a few *L. lorquini*, and the balance exhibiting the "fridayi" phenotype. McDunnough (1938) and dos Passos (1964) included "hyb. (hybrid) *fridayi*" as a synonym of *Limnitis weidemeyerii nevadae* (Barnes and Benjamin, 1924). Hovanitz (1949) noted apparent hybridization along the Sierra Nevada and in the northern Rocky Mountains. Shields (1963) found *L. weidemeyerii* and "fridayi" during 1961 at Lee Vining and Mono Lake. Garth and Tilden (1963) considered "fridayi" to be a hybrid

(between *L. w. nevadae* and *L. l. lorquini*) "since the blend is an even one, in which the characteristics of neither species predominate." Perkins and Perkins (1967) concurred, described *L. w. latifascia* as the subspecies involved in the interaction, and listed hybrid "fridayi" in synonymy with that subspecies. They further noted that "fridayi" "generally exhibits a prominent, white submarginal ocellation dorsally" (a character also noted by Gunder, 1932) and that "all *fridayi* specimens examined (including those in which the orange of the apices was lacking) possessed *one* distinction" from *L. weidemeyerii*, "an orange replacement of black" in "the area medial to the submarginal lunules" on the ventral hindwing.

Remington (1968) reported that *L. weidemeyerii* and *L. lorquini* "hybridize freely" . . . everywhere that they meet . . . at Mono Lake and Bridgeport, California, in border ranges just northward in Nevada, and probably in every major pass across the Continental Divide in Montana and just north of the Canadian border." Platt *et al.* (1970) noted apparent hybridization between contiguous or overlapping combinations of *Limnitis arthemis* (Drury, [1773]), *L. lorquini*, and *L. weidemeyerii* "in several restricted localities of

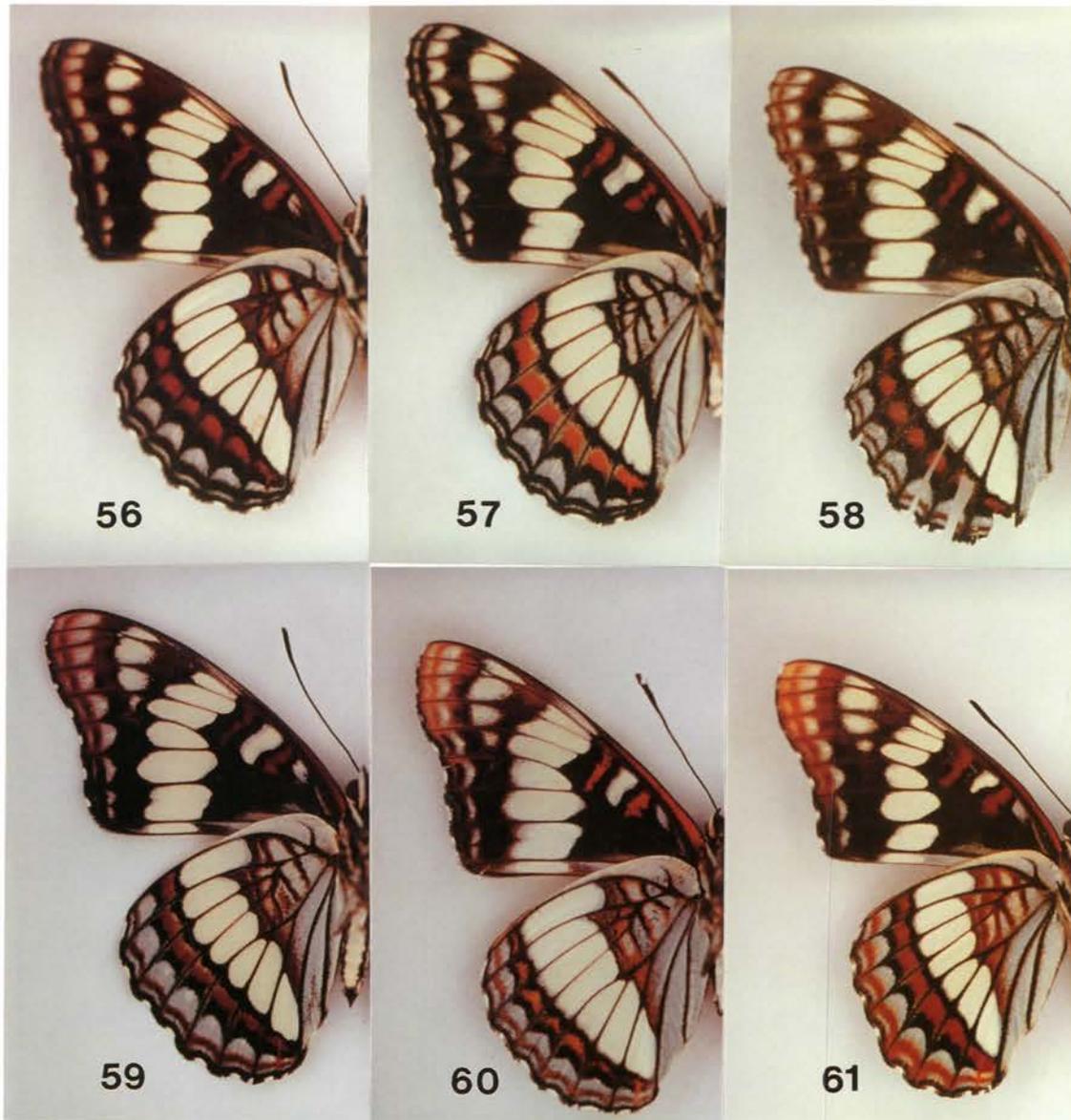


Fig. 56-61. Male *Limenitis* from the western Great Basin, Humboldt hybrid zone, ventral surface. Same specimens as Fig. 50-55.

British Columbia, northern Idaho, western Montana, and California." Perkins and Perkins (*in* Howe, 1975) wrote of "considerable" hybridization between *Limenitis* species and mentioned hybrids (one illustrated) from Mono Lake. Dornfeld (1980) noted that *L. weidemeyerii* and *L. lorquini* hybridize in the Mono Basin of California and that "some Oregon specimens also show traces of this cross." Miller and Brown (1981) reported "fridayi" as a hybrid between *L. w. nevadae* and *L. l. lorquini*. Austin (1981) pointed out that the correct *L. weidemeyerii* subspecies for this was *L. w. latifascia*. Pyle (1981) generally stated that in areas where the species of *Limenitis* "meet, a measure of hybridism often takes place." Ferris and Brown (1981) noted "fridayi" as a hybrid "which looks like *L. weidemeyerii* with a slight rusty red DFW apical patch" which is known "where their [*L. lorquini* and *L. weidemeyerii*] ranges overlap or meet." Garth and Tilden (1986) stated that a "hybrid" looking like *L. weidemeyerii*, but with "a suggestion of the red tips and the brown UN markings" of *L. lorquini* "is found in the vicinity of Mono Lake, where these two species meet." Tilden and Smith (1986) noted hybridization between the two species "notably near Mono Lake . . . where their ranges

meet, resulting in Friday's Admiral" which was "similar" to *L. weidemeyerii*, "but has a small brown patch at FW apex."

Scott (1986) described these hybrids under *L. weidemeyerii* as having "the fw tip slightly orange and with a red line between the rows of blue un marginal crescents" and said that they "may be recent hybrids with *L. lorquini*, but most are probably due to introgression (transfer of genes owing to past hybridization) because *L. lorquini* is rare or absent" in most areas where the "fridayi" phenotype is found. He recorded its distribution from Mono County, California, to central and northern Nevada, eastern Idaho, and western Montana. Austin and Murphy (1987, 1988) noted several populations exhibiting intermediacy in the western Great Basin. The most extensive study of the interactions between these taxa was by Porter (1990). He found that several wing pattern characters showed intermediacy between *L. weidemeyerii* and *L. lorquini*, a steep cline in wing pattern traits in eastern California and western Nevada, and a significant sharing of gene pools with apparent substantial gene flow across the cline indicating conspecificity of *L. weidemeyerii* with *L. lorquini*. Porter and Shapiro (1991) briefly noted hybridiza-



Fig. 62-67. Female *Limenitis* from the western Great Basin, Humboldt hybrid zone, dorsal surface. 62. NV: Humboldt Co.; Santa Rosa Range, 3.1 mi. S Hinkey Summit, 63. NV: Humboldt Co.; Santa Rosa Range, Lye Creek, 64. NV: Humboldt Co.; Santa Rosa Range, Buckskin Mountain, 65. NV: Humboldt Co.; Santa Rosa Range, Lye Creek, 66-67. NV: Humboldt Co.; Pine Forest Range, Blue Lake Road.

tion in the Mono Lake area and the presence of hybrids and "pure" *L. weidemeyerii* "near Sonora Pass" (but see below).

As noted, both *L. weidemeyerii* and *L. lorquini* interact variably with other species of *Limenitis* where their distributions are contiguous or overlap. Thus *L. lorquini* hybridizes with *Limenitis arthemis rubrofasciata* (Barnes & McDunnough, 1916) in British Columbia, Alberta, and Montana (Remington, 1968; Bird *et al.*, 1995; Layberry *et al.*, 1998), and *L. weidemeyerii* interbreeds with this same taxon in British Columbia, Alberta, and Montana (Remington, 1968; Pinel and Kondla, 1985; Bird *et al.*, 1995) and with *Limenitis arthemis arizonensis* W. H. Edwards, 1882, in Arizona (Bauer, 1954; Remington, 1958, 1968; Perkins and Garth, 1972; but see Porter, 1989). Both species are also known to hybridize rarely with *Limenitis archippus* (Cramer, [1776]) (Cross, 1937; Gage, 1970; Perkins and Gage, 1970; Simpson and Pettus, 1976; Platt *et al.*, 1978; Platt and Maudsley, 1994).

That the distributions and interactions of *L. weidemeyerii* and *L.*

lorquini remain dynamic was demonstrated during surveys of the butterfly fauna of the Walker River drainage in Mono County, California, and Douglas, Lyon, and Mineral counties, Nevada, during 1996 when *L. weidemeyerii* and "fridayi" were encountered in areas where they had not previously been reported (see below). Despite an ongoing interest in "fridayi" by both biogeographers and collectors, specific localities of its occurrence are generally lacking in the literature, which mostly cites the "classic" locality at Mono Lake. Aside from Porter (1990), there are similarly no data on specific locales for *L. lorquini* and *L. weidemeyerii* in regions where their distributions approach nor is there information on proportions of the "parental" phenotypes and intermediates in zones of contact and sympatry.

Remington (1968) noted that the hybridization of *L. lorquini* and *L. weidemeyerii* was "intense" and, at a number of locales in Montana, there was evidence that this extended "many miles" east (but not to the west) of the Continental Divide. Elsewhere ("Califor-

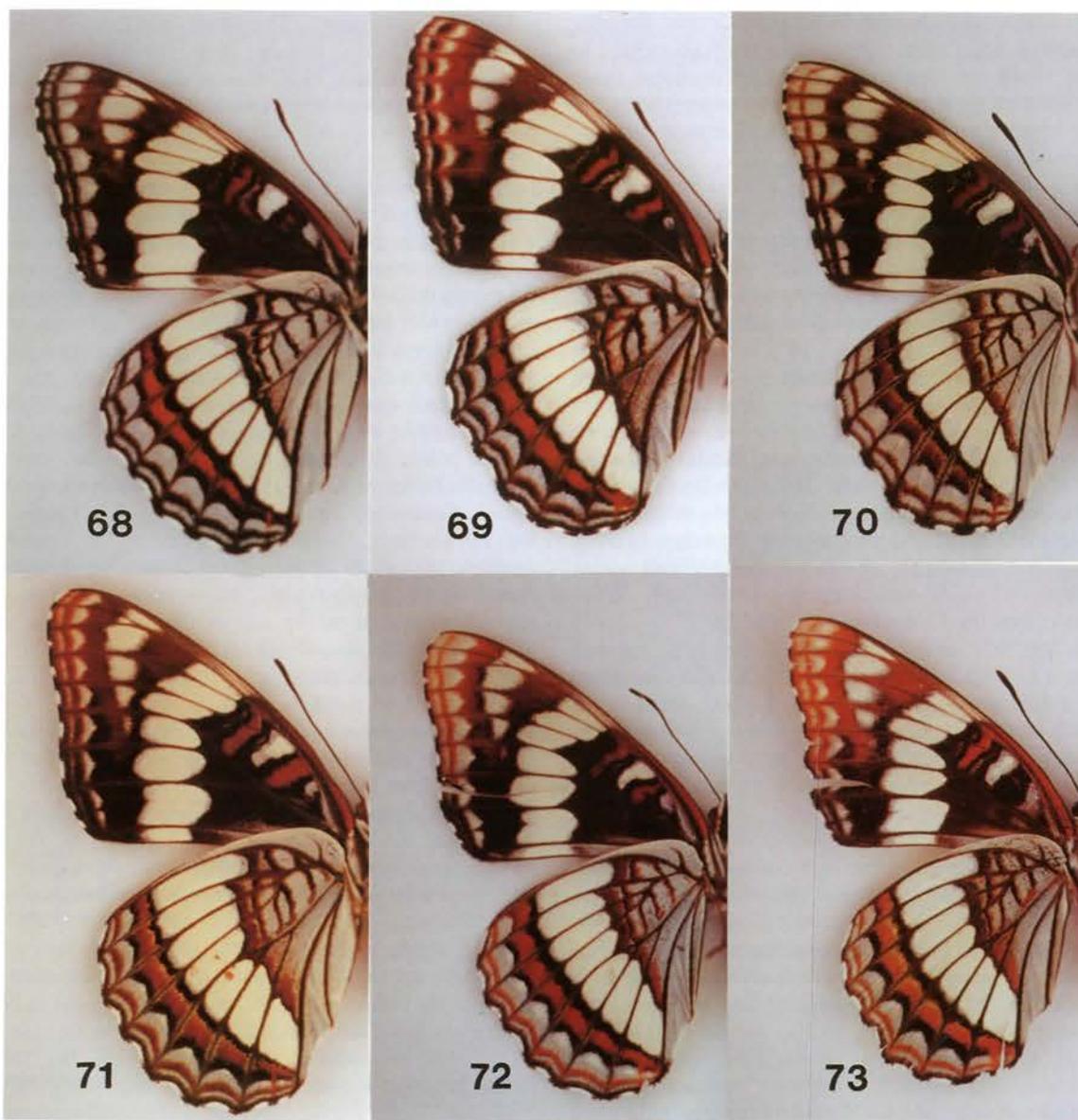


Fig. 68-73. Female *Limenitis* from the western Great Basin, Humboldt hybrid zone, ventral surface. Same specimens as Fig. 62-67.

nia, most of Montana"), the zone was stated to be narrow (Remington, 1968). Subsequent investigations have shown this to be about 75km wide in the southern Great Basin, from the canyons west of Bridgeport, California, to just west of Hawthorne, Nevada (the "Mono" hybrid zone), although apparently "pure" populations of *L. lorquini* occur in the intervening valley of the lower East Walker River in the south. Another hybrid zone, nearly 100km wide, is known in the northern Great Basin, from the Pine Forest Range to the Santa Rosa Range, Humboldt County, Nevada (the "Humboldt" hybrid zone) (Austin and Murphy, 1987; Porter, 1990; this study). It is generally assumed that these zones of hybridization have been the result of *L. lorquini* spreading eastward into populations of *L. weidemeyerii* (Platt, 1983; Porter, 1990). It should be noted that the distribution of *L. weidemeyerii* does not extend west of the Continental Divide in the north into northern Idaho or Washington, but extends increasingly westward in the south to reach the east slope of the Sierra Nevada in Mono County, California. Conversely, *L. lorquini* barely enters the western Great Basin, but northward it occurs considerably eastward into eastern Idaho and the western third

of Montana (e.g., Stanford and Opler, 1993).

RESULTS

Non-hybrid Populations

Distribution and ecology. In the Great Basin, *Limenitis weidemeyerii* is largely a montane species and occurs in most of the major mountain ranges. It is commonly found along willow (*Salix* spp.) and cottonwood (*Populus angustifolia*) lined stream courses, but it also occurs in aspen (*Populus tremuloides*) groves, on relatively dry hillsides, and in some riparian situations in the valleys of central and northern Nevada (Fig. 75-76). *L. weidemeyerii* is unknown in western Nevada between the Spring Mountains and the southern end of the Wassuk Range and in California south of Mono Lake or north of Devil's Gate Pass. *L. lorquini* occupies an essentially complementary distribution in the extreme western Great Basin (Fig. 75-76) where it occurs mostly in willow (*Salix*) dominated riparian areas along montane and lowland river and stream courses on the east slope of the Sierra Nevada. It extends eastward into Nevada along the entire

courses of the Walker, Carson, and Truckee rivers (e.g., Austin 1985b). Note that the record of *L. lorquini* for Elko County, Nevada, indicated by Stanford and Opler (1993; see also Scott, 1986) is unverified as are those for Nye and White Pine counties; these records may be based on apparent variant *L. weidemeyerii* (e.g., see Fig. 39, 45). *L. lorquini* does not range into drier canyons and flats as does *L. weidemeyerii*.

Phenotypes. Size.— Female *L. lorquini* and *L. weidemeyerii* are significantly larger than their males (Table 3). Both sexes of *L. lorquini* are significantly smaller than the corresponding sex of *L. weidemeyerii*. Females exhibit more variance in forewing length than males; this is significant for both *L. weidemeyerii* and *L. lorquini*. Sex for sex, *L. lorquini* and *L. weidemeyerii* are not significantly different in their variance.

Wing characters.— All 296 *L. lorquini* scored from non-hybrid populations have cumulative wing character scores of 28-34 and 228 of 231 *L. weidemeyerii* have scores of 0-6. The three *L. weidemeyerii* scoring higher are a male and a female from Pershing County, Nevada (scores of 8 and 7, respectively) and a female from Elko County, Nevada (score of 10). Males are somewhat less variable than females in both species. Based on scores of wing characters of these reference samples, five phenotypic classes are distinguished within hybrid populations: "1" — *L. weidemeyerii* (scores 0-6); "2" — intermediate, but closest to *L. weidemeyerii* (7-13); "3" — clearly intermediate (14-20); "4" — intermediate, but closest to *L. lorquini* (21-27); and "5" — *L. lorquini* (28-34). Classes 2-4 are considered "fridayi" within hybrid zones. Some "pure" individuals (with scores of 0-6 and 28-34) within hybrid zones actually may include backcrossed individuals (e.g., otherwise typical *L. weidemeyerii* with red-brown apices), but these categories appear close to reality and facilitate discussion.

L. lorquini and *L. weidemeyerii* may be readily distinguished by most of the characters examined in this study, although one or both species exhibit some variability in many of the characters examined. Thus, *L. lorquini* nearly invariably has a brown ground color; narrow and cream-colored bands; no pale submarginal macules on the dorsal hindwing; a red-brown forewing apex on both surfaces; a vague or absent marginal line, a red-brown submarginal line, cream-colored submarginal macules, and red-brown on the central costa of the ventral forewing; and a red-brown submarginal line, lavender submarginal macules, a prominent red-brown postmedian band, red-brown proximad to the pale band, and prominent red-brown scaling in cell CuA₂ on the ventral hindwing. In contrast, *L. weidemeyerii* has a black ground color; white bands; a black forewing apex on both surfaces; a black submarginal line and white submarginal macules on the ventral forewing; and a broad and distinct marginal line, a black submarginal line, blue submarginal macules, and an all gray cell CuA₂ on the ventral hindwing. *L. weidemeyerii* shows variation in the width of the wing bands, the presence of the submarginal macules on the dorsal hindwing, the development of the marginal line and the color of the central costa on the ventral forewing, and the development of the red-brown postmedian band and the color proximad of the pale band on the ventral hindwing. *L. lorquini* is variable in the development of the marginal line on the ventral hindwing. Both species are variable in the development of the forewing submarginal macules although these are present on all *L. weidemeyerii* and usually absent on *L. lorquini*. The phenotype of *L. lorquini* with red macules distad of the pale band on the dorsal hindwing (form "eavesi" Hy. Edwards, 1877) includes 8% of males and 30% of females; a similar form of *L. weidemeyerii* includes 13% of males and 75% of females (Table 4). The differences between the sexes in the occurrence of these macules are significant as is the difference between females, but not the

males, of the two species.

Genital characters.— The male genitalia of Great Basin *L. weidemeyerii* and *L. lorquini* (Fig. 74) resemble those previously illustrated (Nakahara, 1924; Platt *et al.*, 1970). Scores of genitalia for non-hybrid populations of *L. weidemeyerii* range from 0 to 2 (mean = 0.34, variance = 0.40) and of *L. lorquini* range from 6 to 8 (mean 7.60, variance = 0.35).

Female genitalia of both of these species of *Limenitis* exhibit a flaring sterigma with a finely folded and weakly sclerotized central area leading to the ostium bursae. The seventh sternite is fused with the lamella antevaginalis and usually cannot be removed without damaging the latter. The antrum is sclerotized ventrally and laterally and leads to a membranous ductus bursae (on some individuals this has a lightly sclerotized area at about its midpoint) which expands gradually to a bulbous corpus bursae. This latter has a parallel pair of signa, each composed of finely sclerotized horizontal and zigzagged lines extending from its middle to the cephalad end. Attached to the corpus bursae is a more or less globular sac, equivalent to the appendix bursae of Klots (1956). These structures are very similar on both *L. weidemeyerii* and *L. lorquini* (Fig. 77). The trough leading to the antrum on *L. weidemeyerii* tends to be broader than on *L. lorquini*, the mouth of the antrum is less broad, and the appendix bursae usually originates near the cephalad end of the corpus bursae (usually originates on the side of the corpus bursae of *L. lorquini* about 1/3 the distance to the caudal end).

Sex ratio. Field caught samples of *L. weidemeyerii* and *L. lorquini* from non-hybrid populations in the Great Basin include 79% and 78% males, respectively (Table 5); these proportions are not significantly different from each other or from that of field caught *L. archippus* from the Great Basin.

Phenology. In the Great Basin, *L. lorquini* is at least bivoltine with records for Nevada extending from late May to mid October (Fig. 78) and apparent peaks in mid-July and mid-August; data accumulated over a 30 year period suggest that the broods overlap. Data for individual years are insufficient to indicate the reality or not of this overlap. Fresh individuals from some areas into late September suggest the presence of at least a partial third brood towards the end of the flight season. Records for *L. weidemeyerii* in Nevada extend from early June (late May in Clark County) to early September (Fig. 78). Based on samples from many years, the species appears univoltine with a peak flight in mid-July (early July in southern Nevada).

Mono Hybrid Zone

Distribution and ecology. Numerous *Limenitis* populations were encountered in the southwestern Great Basin region during 1996, 1997, and 1998. This area includes a zone of hybridization extending from the Wassuk Range, southwest to the Sweetwater Mountains and Bodie Hills, along the middle and upper East Walker River and its various tributaries on the east slope of the Sierra Nevada, north to Devil's Gate Pass, and south to Mono Lake and a major tributary, Lee Vining Creek (Fig. 75-76). Porter and Shapiro (1991) mentioned the occurrence of "fridayi" and *L. weidemeyerii* phenotypes "near Sonora Pass." We found no evidence of these in the West Walker River drainage of California, including several sites in the vicinity of Sonora Pass; all *Limenitis* encountered were *L. lorquini*. Within the Mono hybrid zone, the several populations exhibited various proportions of *L. weidemeyerii*, *L. lorquini*, and "fridayi" (Fig. 76). Historical information indicated that these proportions have changed in at least some of these populations over the last 20 years (Fig. 79). The population at Corey Peak Road has increased its proportion of *L. weidemeyerii*, *L. weidemeyerii* has appeared and/or "fridayi" has become more prominent along the middle and upper East Walker

TABLE 3. Forewing length of Great Basin *Limenitis* (in mm, mean \pm SE, with range and n in parentheses; *t* and F values are for differences between the sexes; numbers in bold are significant; for *t* and F values for differences between the phenotypic classes, see Appendices Ia and Ib).

Taxon and population	males	females	<i>t</i>	F
<i>L. lorquini</i> (non-hybrid zone)	29.9 \pm 0.11 (25.8-34.0, n = 165)	34.2 \pm 0.24 (29.9-38.0, n = 54)	35.59	1.75
<i>L. lorquini</i> (Mono hybrid zone)	30.3 \pm 0.12 (27.2-34.0, n = 131)	34.8 \pm 0.36 (31.1-38.3, n = 25)	14.46	1.87
"fridayi" (Mono hybrid zone)	32.0 \pm 0.16 (28.0-37.3, n = 120)	36.8 \pm 0.76 (32.8-39.3, n = 8)	7.43	1.51
"fridayi" (Humboldt hybrid zone)	33.2 \pm 0.22 (30.1-36.2, n = 47)	37.5 \pm 0.17 (33.3-41.0, n = 14)	8.73	1.69
<i>L. weidemeyerii</i> (Mono hybrid zone)	33.3 \pm 0.13 (29.3-36.8, n = 115)	38.1 \pm 0.38 (35.1-41.4, n = 14)	12.48	1.12
<i>L. weidemeyerii</i> (Humboldt hybrid zone)	33.3 \pm 0.17 (31.4-36.3, n = 11)	--	--	--
<i>L. weidemeyerii</i> (non-hybrid zone)	33.8 \pm 0.11 (29.9-37.3, n = 183)	38.8 \pm 0.32 (34.1-43.7, n = 40)	20.69	1.95

TABLE 4. Frequency (%) of form "eavesi" among Great Basin *Limenitis* (chi-square values are for differences between the sexes; all are significant; for chi-square values for differences between the various phenotypic classes, see Appendix Id).

Taxon and population	males	females	chi-square
<i>L. lorquini</i> (non-hybrid zone)	8.3 (n = 168)	29.6 (n = 54)	15.86
<i>L. lorquini</i> (Mono hybrid zone)	11.4 (n = 140)	26.9 (n = 26)	4.41
"fridayi" (Mono hybrid zone)	14.2 (n = 134)	66.7 (n = 9)	16.11
<i>L. weidemeyerii</i> (Mono hybrid zone)	18.8 (n = 133)	66.7 (n = 15)	17.11
<i>L. weidemeyerii</i> (non-hybrid zone)	13.1 (n = 190)	75.0 (n = 40)	69.46
<i>L. lorquini</i> (Humboldt hybrid zone)	--	100.0 (n = 1)	--
"fridayi" (Humboldt hybrid zone)	17.6 (n = 51)	64.3 (n = 14)	11.93
<i>L. weidemeyerii</i> (Humboldt hybrid zone)	0.0 (n = 11)	50.0 (n = 2)	--

TABLE 5. Sex ratios of field collected Great Basin *Limenitis* (for chi-square comparisons between the phenotypic classes, see Appendix Ie).

Taxon and population	males	females	% females
<i>L. archippus</i> (Nevada)	260	69	21.0
<i>L. weidemeyerii</i> (Nevada)	503	131	20.7
<i>L. lorquini</i> (western Nevada-eastern California)	318	91	22.2
<i>L. weidemeyerii</i> + <i>L. lorquini</i> (Mono hybrid zone)	286	55	16.1
"fridayi" (Mono hybrid zone)	158	9	5.4
<i>L. weidemeyerii</i> + <i>L. lorquini</i> (Humboldt hybrid zone)	11	3	21.4
"fridayi" (Humboldt hybrid zone)	51	14	21.5

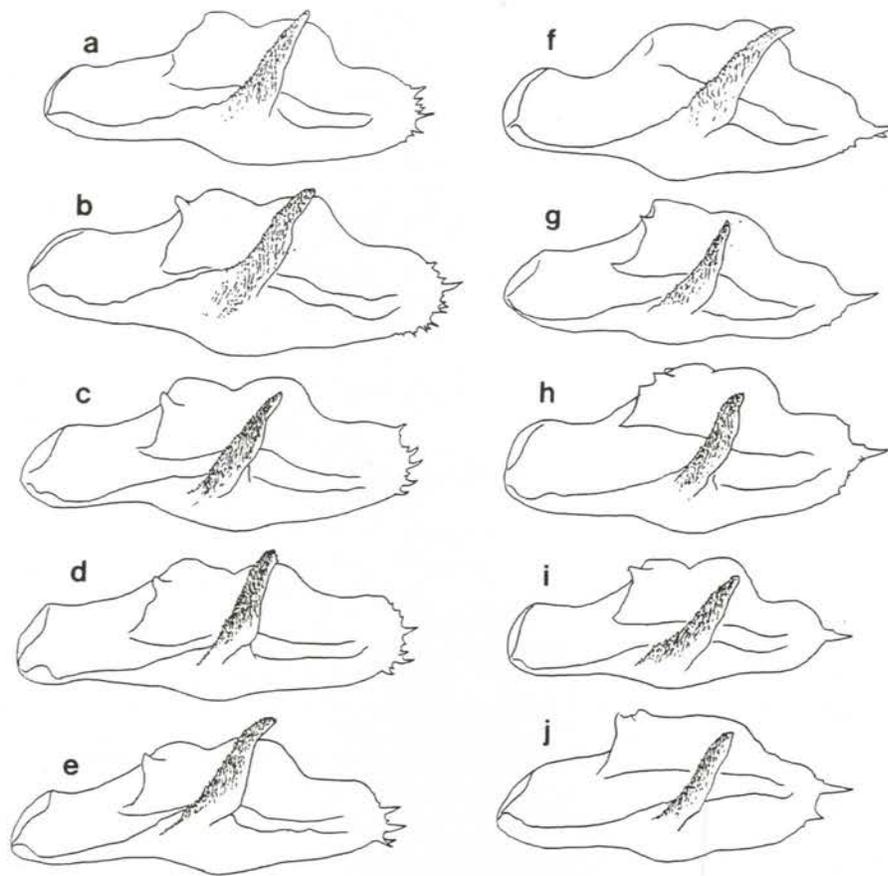


Fig. 74. Internal view of left valvae of Great Basin non-hybrid zone *Limenitis* (all from Nevada): a-e. *L. weidemeyerii* – a-b. Elko Co. (GTA #7704, #7705); c-e. Nye Co. (GTA #7692, #7688, #7693); f-j. *L. lorquini* – f. Carson City (GTA #7698); g-j. Lyon Co. (GTA #7842, 7872, 7839, 7834).

River and at Desert Creek, and *L. lorquini* has become more abundant in Bridgeport Canyon.

Peripheral to this area of overlap are apparently pure populations of *L. lorquini* westward on the west slope of the Sierra Nevada; to the south on the east slope of the Sierra Nevada (e.g., Rock Creek) and in the White Mountains; and to the north along the entire length of the West Walker River, the lower East Walker River, and the Walker River below the juncture of its two forks to at least Schurz. Note, however, that a male *L. lorquini* with "melanic apices" from Coleville, Mono County, California, was illustrated by Perkins and Perkins (1967). East of the hybrid zone, populations of *L. weidemeyerii* are known in the Pilot Mountains (apparently non-hybrid, based upon a very small sample), Desatoya Mountains, Clan Alpine Mountains, and widely into central and northern Nevada (Fig. 75).

Populations of *Limenitis* in the southwestern Great Basin which include the "fridayi" phenotype occur exclusively in riparian habitats dominated by willows, generally along streams and rivers (Fig. 80). The population at Summers Creek was associated with streamside willows within a large grove of aspen on which all three phenotypes perched. Aspens also occurred adjacent to populations at By Day Creek, Green Creek, and along the Virginia Lakes Road. In Aurora Canyon, *Holodiscus* was common on hillsides adjacent to dense willow stands along the creek.

Phenotypes. *Size.*— *L. weidemeyerii* and *L. lorquini* which score as "pure" (scores of 0-6 and 28-34, respectively) from the hybrid zone are smaller and larger, respectively, than those from outside this area (Table 3). "Fridayi" are intermediate in size between *L. lorquini* and *L. weidemeyerii* (contra Brown, 1934, who stated that "fridayi" was

like *L. weidemeyerii* "in its greater wing expanse"). For both sexes there is a gradient of increasing size, from *L. lorquini* away from the hybrid zone to *L. lorquini* within the hybrid zone, "fridayi", *L. weidemeyerii* within the hybrid zone, and *L. weidemeyerii* outside the hybrid zone (Fig. 81). Among males, the differences in size are all significant. The "pure" female phenotypes of each of the species from outside and inside the hybrid zone are not different in size, but both inside and outside the hybrid zone *L. lorquini* and *L. weidemeyerii* are significantly different in size from the "fridayi" phenotype.

Although females of "fridayi" and hybrid zone *L. weidemeyerii* show more variance in size than males, this is not significant (as it was for the parental species from outside of the hybrid zone). Variance in female *L. lorquini* from the hybrid zone, however, is significantly different from that of hybrid zone males. Males and females of "fridayi" show more variance in size than "pure" phenotypes from both inside and outside of the hybrid zone, but this pattern is significant only for males.

Wing characters.— A total of 487 *Limenitis* were scored from the Mono hybrid zone and exhibit a range of variation from "pure" *L. weidemeyerii* to "pure" *L. lorquini* (Fig. 3-18, 21-36, 40-42, 46-48). *L. weidemeyerii* from this hybrid zone resemble those from non-hybrid populations, but, for nearly every character, there is a greater proportion of intermediate individuals especially for band width, band color, and the condition of the ventral forewing marginal line and ventral hindwing postmedian band. Similarly, *L. lorquini* from the hybrid zone exhibits more intermediacy than those from non-hybrid populations especially in ground color, the presence of forewing sub-

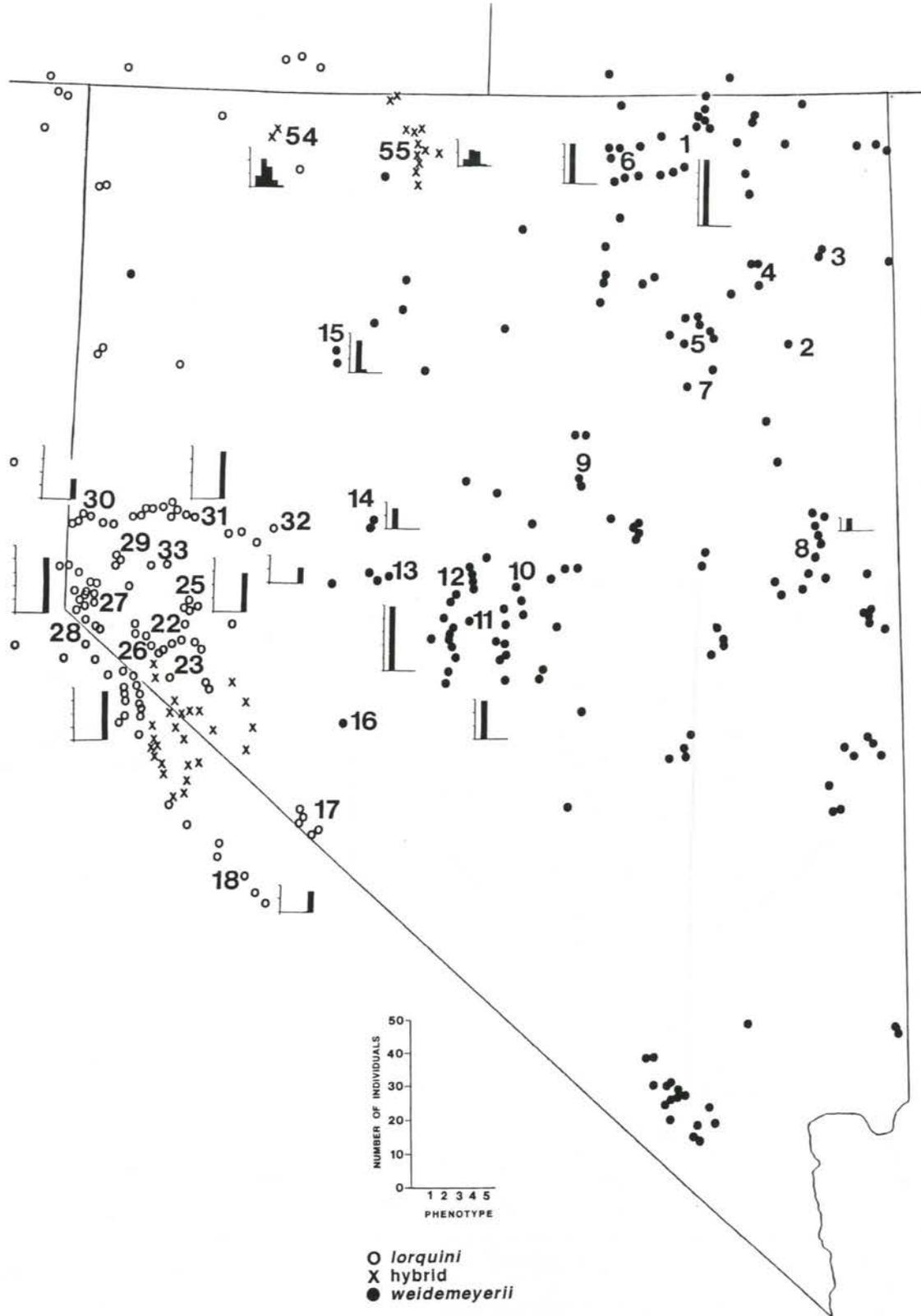


Fig. 75. Distribution of *Limenitis* in the western Great Basin. Numbers correspond to locations in Table 2. Histograms (scale indicated in legend) illustrate phenotypic scores for selected representative populations (1 = *L. weidemeyerii*, 2-4 = hybrids, 5 = *L. lorquini*; see text; numbered locations and histograms for Mono hybrid zone populations are in Fig. 76).

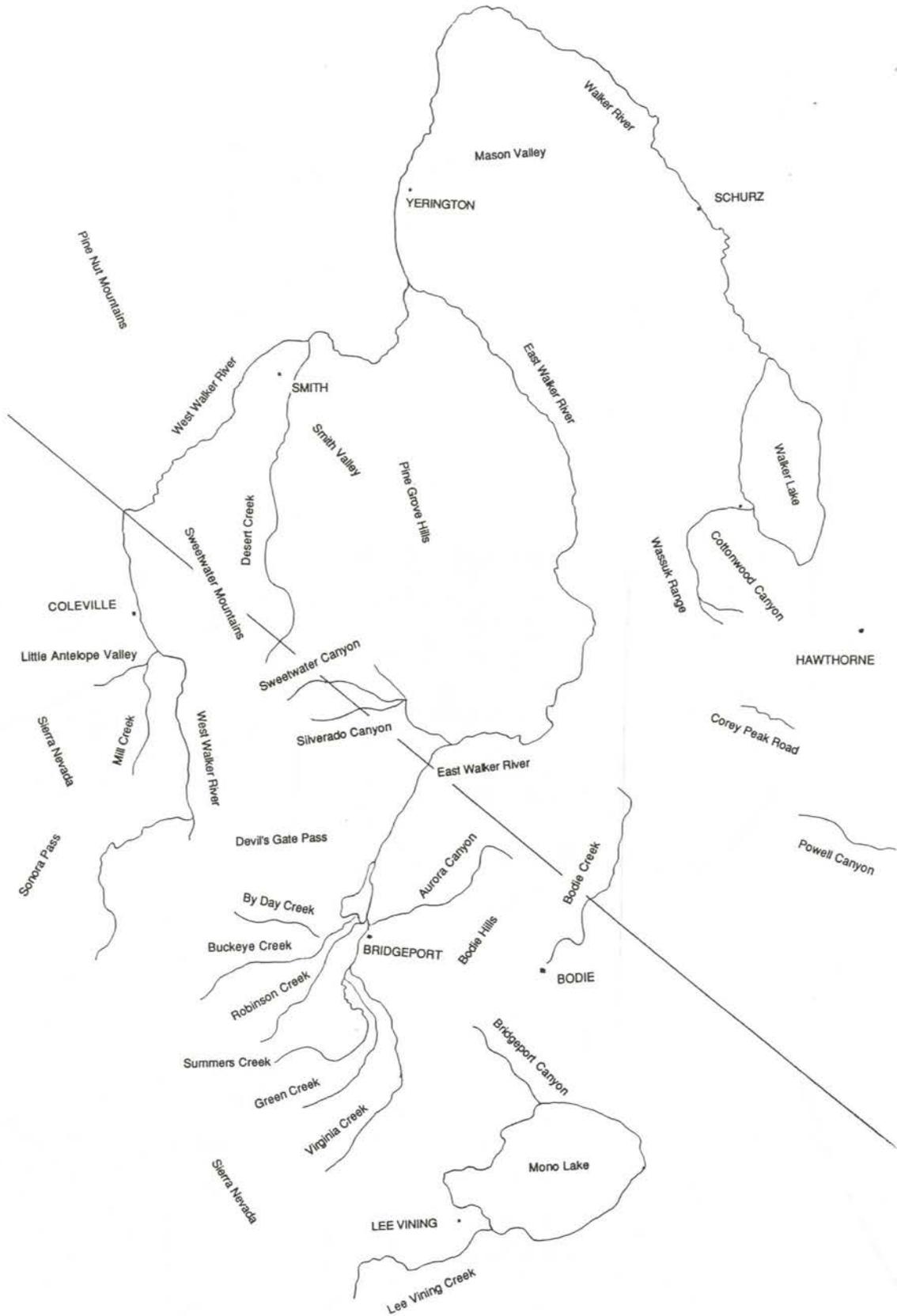


Fig. 76A. Major localities in the Mono hybrid zone as mentioned in the text.

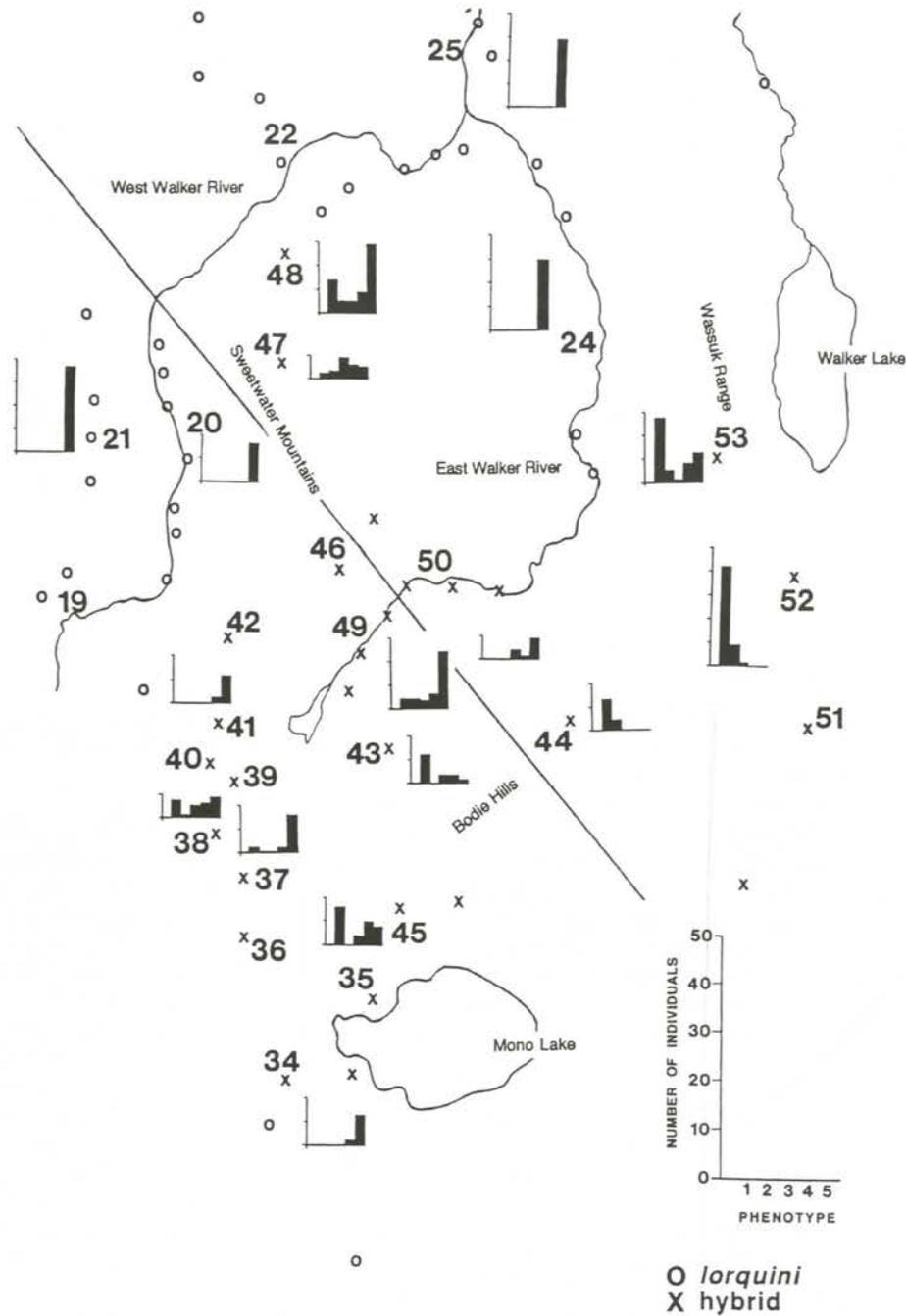


Fig. 76B. Distribution of *Limnitis* in the Mono hybrid zone and adjacent areas (explanation as in Fig. 75).

marginal macules, the development of the marginal line and the color of the mid-costa on the ventral forewing, and the development of the postmedian red-brown band and the red-brown proximad to the pale band on the ventral hindwing. This is reflected in significantly different mean scores for both *L. lorquini* and *L. weidemeyerii* in the Mono hybrid zone than outside this zone although the variances do not differ (Appendix 1c). Mono hybrid zone *L. lorquini* show significantly more variance in their scores than Mono hybrid zone *L. weidemeyerii*. "Fridayi" have significantly more variance compared to all combinations of parentals. Individuals scored as hybrids exhibit

a high proportion of intermediacy although no single character distinguishes a hybrid phenotype from one or the other of the parental species.

Form "eavesi" include 14% of the males of "Fridayi", intermediate between (but not significantly different from) the parentals. This form is found for 67% of the females, the same as for hybrid zone females of *L. weidemeyerii*, but significantly different from female *L. lorquini* (Table 4). Males of *L. lorquini* and *L. weidemeyerii* from the Mono hybrid zone have a slightly (but not significantly) greater proportion of form "eavesi" than from outside the hybrid zone while females of

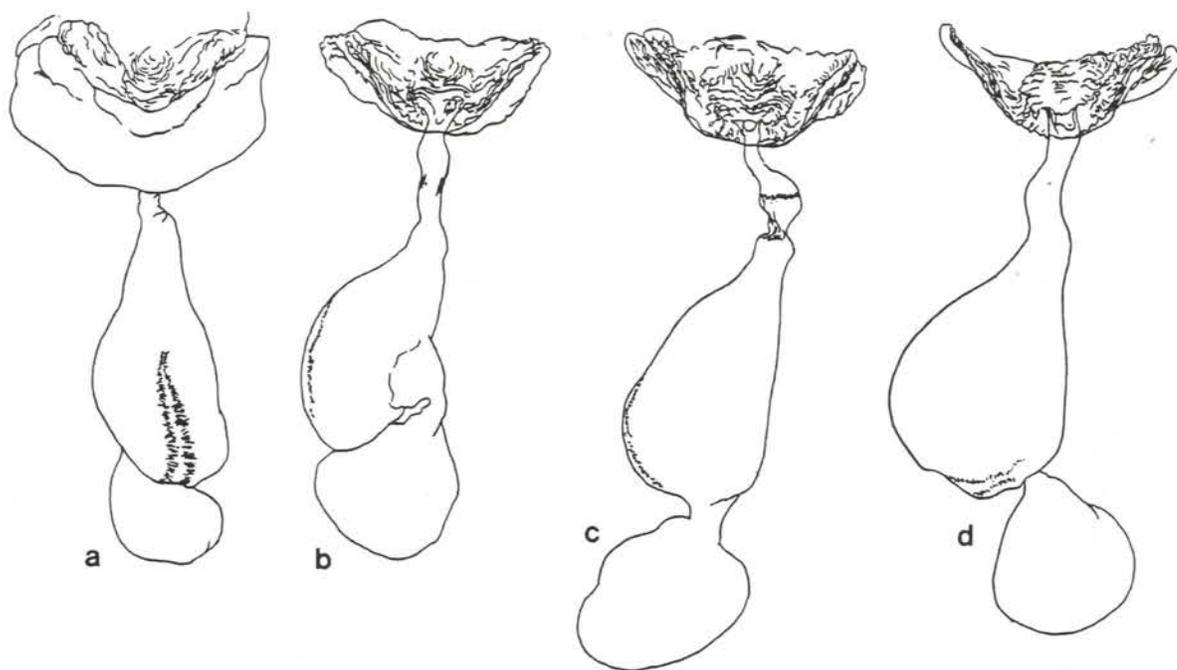


Fig. 77. Dorsal view of female genitalia of Great Basin *Limenitis* (all from Nevada): a-b. *L. lorquini* – a. Carson City (GTA #7799), b. Douglas Co. (GTA #7798); c-d. *L. weidemeyerii* – c. White Pine Co. (GTA #7801), d. Elko Co. (GTA #7800).

both species have a slightly (but again not significantly) lesser proportion. Mono hybrid zone *L. weidemeyerii* have a higher proportion of individuals with "eavesi" macules than Mono hybrid zone *L. lorquini*; the difference is significant only for females. The differences between the sexes of all phenotypes are significant.

Genital characters.—In the Mono hybrid zone, male genitalia vary continuously (scores of 0 to 8, mean = 4.5, variance = 7.0) from the phenotype of *L. weidemeyerii* to that of *L. lorquini* (Fig. 82) The mean and variance of the overall genital scores are significantly different than those of non-hybrid zone populations. Among these, there is a weak relationship between individual scores of wings and genitalia. *L. weidemeyerii* by wing score have genitalia scores ranging between 0 and 6 averaging 2.5, "fridayi" have scores between 0 and 8 averaging 4.6, and *L. lorquini* by wing score have genitalia scores from 2 to 8 averaging 6.5. These means are significantly different; the variances are not. At the population level, there is a significant positive correlation ($r = 0.945$) between scores for wings and genitalia (Fig. 83).

The valvae of non-hybrid zone *Limenitis* exhibit minor asymmetry in the number of terminal spines. Similar minor asymmetry is seen among most hybrid zone individuals. More than one-fourth (28%) hybrid zone males, however, show obvious differences in the right and left valvae, not only in the placement and number of terminal spines, but also in length and breadth characters (Fig. 84). This asymmetry occurs on males across nearly the entire ranges of both wing and genital scores. Females from the Mono hybrid zone have genitalia ranging from those typical of *L. lorquini* to those typical of *L. weidemeyerii*, these not necessarily consilient with wing phenotype.

Sex ratio. Females comprise a smaller proportion of the Mono hybrid zone parentals in comparison with non-hybrid zone populations, this significantly different. "Fridayi", likewise, are predominantly (95%) males, a significant difference from parental phenotypes from both within and outside the Mono hybrid zone (Table 5).

Phenology. The known phenology for "fridayi" in the Mono hybrid zone is similar to that of *L. weidemeyerii*, with a peak in mid-July

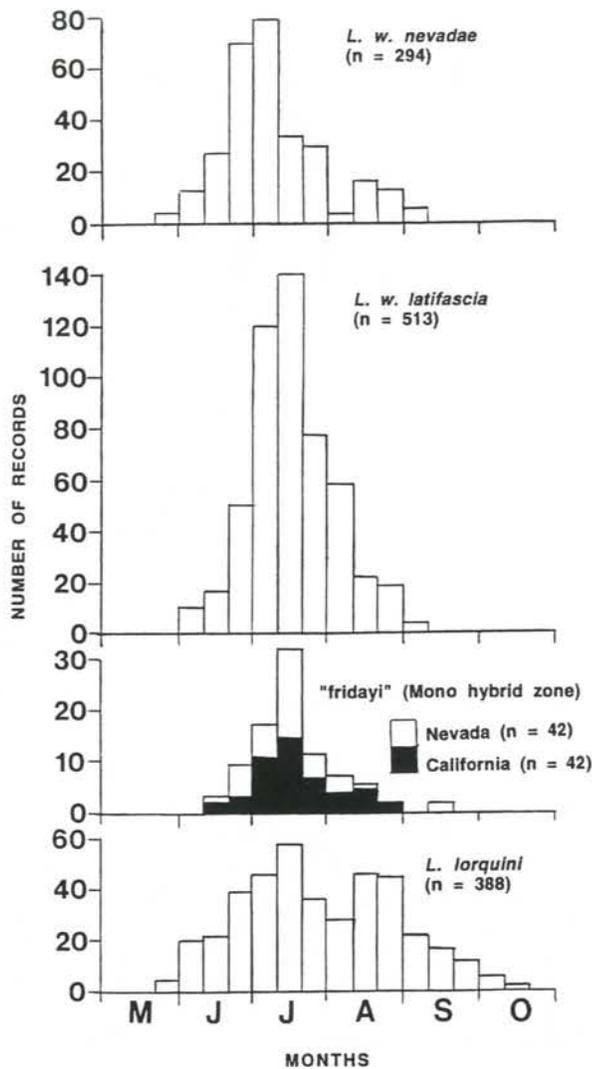
corresponding to the peak flight for that species and the peak of the first brood of *L. lorquini* (Fig. 78).

Humboldt Hybrid Zone

Distribution and ecology. Hybrid *Limenitis* populations in the Santa Rosa and Pine Forest ranges of northern Nevada were first noted by Austin and Murphy (1987), and the latter population was studied by Porter (1990). There are also reports of *L. lorquini* and "fridayi" from the vicinity of McDermitt to the north on the Oregon state line, but this material has not been examined. Peripheral populations of *L. lorquini* are known to the north and west along Virgin Creek, in southern Oregon, and in the Granite and Selenite ranges (Fig. 75). *L. weidemeyerii* occurs mostly to the south and east in the Sonoma and East ranges, at Midas and Battle Mountain, and in the Tuscarora Mountains (Fig. 75). Both species have been recorded in the Quinn River Valley, *L. weidemeyerii* near Orovada and *L. lorquini* from just north of Quinn River Crossing. There is a specimen of *L. weidemeyerii* in the California Insect Survey collection from 26 miles northwest of Gerlach (Washoe County); this location is far west of any other record for the species in northern Nevada and requires confirmation.

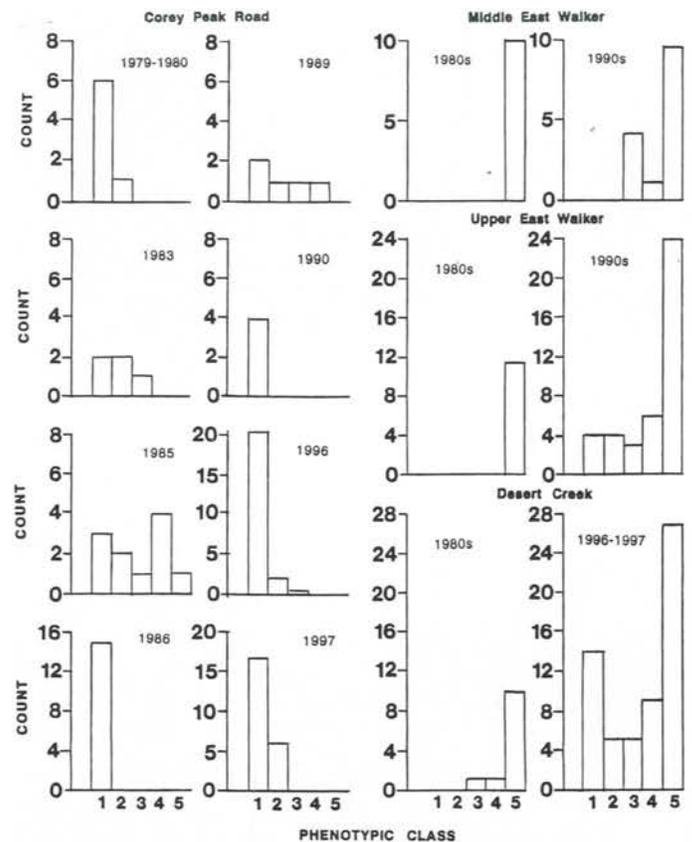
The hybrid *Limenitis* populations in northern Nevada occur along willow-lined streams and often in association with aspen, in similar habitat to that used in the Mono Lake area.

Phenotypes. Size.—Males of *L. weidemeyerii* in the Humboldt hybrid zone are the same size as those from elsewhere (Table 3). Males of "fridayi" are significantly larger than those from the Mono hybrid zone. They are the same size as their sympatric *L. weidemeyerii* and significantly smaller than non-hybrid zone *L. weidemeyerii*. Females of "fridayi" from the Humboldt hybrid zone are larger (but not significantly) than in the Mono hybrid zone (Table 3), but significantly smaller than non-hybrid zone *L. weidemeyerii* females. Both male and female Humboldt hybrid zone "fridayi" are significantly larger than non-hybrid zone *L. lorquini* (Table 3). Male "fridayi" from the Humboldt hybrid zone have significantly more variance in wing length than non-hybrid zone *L. lorquini*, but similar variance to

Fig. 78. Phenology of Great Basin *Limnitis*.

Humboldt hybrid zone and non-hybrid zone *L. weidemeyerii* and Mono hybrid zone "fridayi". Similarly, male Humboldt hybrid zone *L. weidemeyerii* have similar variance to non-hybrid zone *L. weidemeyerii*. Female Humboldt hybrid zone "fridayi" have similar variance with non-hybrid zone *L. lorquini* and *L. weidemeyerii* and Mono hybrid zone "fridayi". Other comparisons cannot be made because of the near absence of *L. lorquini* in the Humboldt hybrid zone samples.

Wing characters.— Seventy-nine *Limnitis* were scored from the Humboldt hybrid zone. In this zone, *L. weidemeyerii* and most "fridayi" have distinctly broader white bands than in the Mono hybrid zone (Fig. 50-73). This reflects its more northern position within the northeast to southwest cline of decreasing band width in *L. weidemeyerii*. Phenotypes of "fridayi" dominate in this zone, comprising over 82% of the individuals examined. Only 13 individuals (16.5%) are "pure" *L. weidemeyerii* and one (1.3%) is a "pure" *L. lorquini*. Humboldt hybrid zone *L. weidemeyerii* have a significantly greater mean score than non-hybrid zone *L. weidemeyerii* and are similar to Mono hybrid zone *L. weidemeyerii*; the variances of these scores are not significantly different. Humboldt hybrid zone "fridayi" have a significantly lower mean score than Mono hybrid zone "fridayi". The variance of scores for Humboldt hybrid zone "fridayi" is significantly greater than their sympatric *L. weidemeyerii* and significantly lower

Fig. 79. Changes in phenotypic frequencies within several Mono hybrid zone populations of *Limnitis* (1 = *L. weidemeyerii* phenotype, 2-4 = hybrid phenotypes, 5 = *L. lorquini* phenotype).

than for Mono hybrid zone "fridayi".

Form "eavesi" include 18% of the males of "fridayi" and 64% of the females (Table 4), a significant difference. The frequencies in relation to non-hybrid zone parental phenotypes are not significantly different. Too few parental phenotypes from within the hybrid zone were seen to generalize on them.

Genital characters.— In the Humboldt hybrid zone, male genitalia vary in score from 0 to 6 (mean = 2.4, variance = 1.93). Both the mean score and the variance are significantly different from those of *L. weidemeyerii*, *L. lorquini*, and Mono hybrid zone individuals. Asymmetry of the valvae occurs in about 40% of these, somewhat greater than in the Mono hybrid zone. As in the Mono hybrid zone, the female genitalia span the variation of the two species and often do not correspond with the phenotype of the wings.

Sex ratio. The sex ratios of hand-netted "fridayi" and non-hybrid phenotypes in the Humboldt hybrid zone are not significantly different from those of *Limnitis* away from hybrid zones (Table 5). There is a significant difference in the sex ratio of "fridayi" from the Humboldt and Mono hybrid zones.

Phenology. Phenology data are sparse for the Humboldt hybrid zone (and adjacent areas). *L. lorquini* apparently have a relatively long flight season, probably including two broods (records from mid July to early October), and *L. weidemeyerii* and "fridayi" have a shorter season (both recorded from late June to mid August).

DISCUSSION

Distribution and Ecology

Overall distributions of *Limnitis weidemeyerii* and *L. lorquini* and,

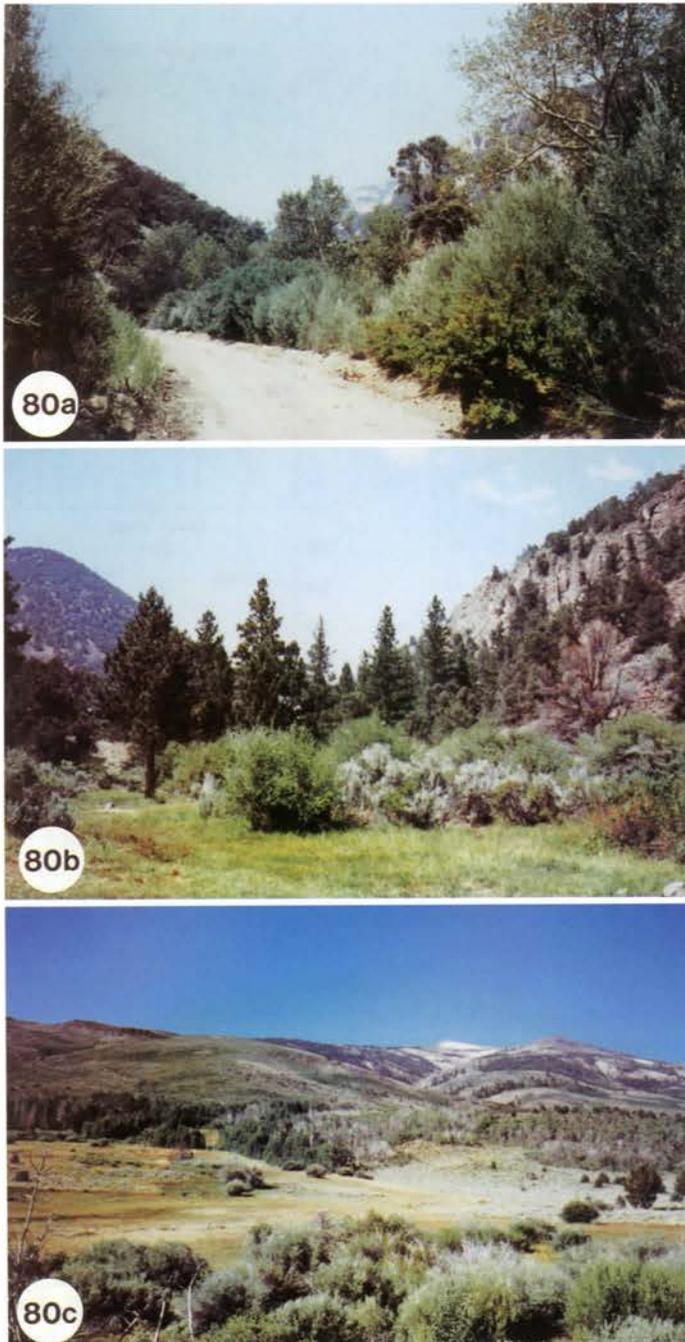


Fig. 80. Representative habitat for *Limnitis* in the Mono hybrid zone: a. NV: Mineral Co., Wassuk Range, Corey Peak Road; b. NV: Lyon Co., Sweetwater Mountains, Desert Creek; c. CA: Mono Co., Sierra Nevada, Summers Creek.

especially, their zones of hybridization are largely ignored in most general works on western North American butterflies, probably because the details are complex. In the western Great Basin, the actual distributions and overlap of these *Limnitis* are considerably less extensive than connoted by range maps. *L. lorquini* occurs only in narrow bands of riparian vegetation. *L. weidemeyerii* also occurs largely in riparian habitat, but also is found in drier montane situations. The hybridization of *Limnitis* in the southwestern Great Basin has been known for 65 years (Gunder, 1932; Brown, 1934), but aside from a few references to the "fridayi" phenotype from elsewhere, little was known of the distribution or interactions of these *Limnitis* away from the immediate vicinity of Mono Lake. Garth and Tilden (1986) stated that *L. weidemeyerii* occurs "east of the

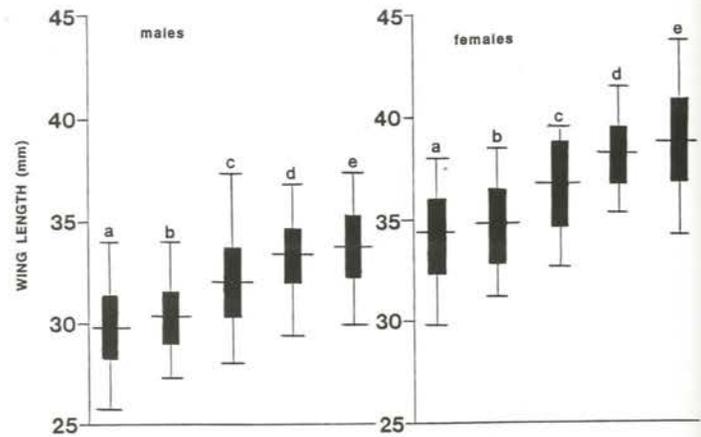


Fig. 81. Forewing length of *Limnitis* phenotypes in the western Great Basin (mean, range, standard error; sample sizes given in Table 3): a. non-hybrid zone *L. lorquini*; b. Mono hybrid zone *L. lorquini*; c. Mono hybrid zone "fridayi"; d. Mono hybrid zone *L. weidemeyerii*; e. non-hybrid zone *L. weidemeyerii*.

Sierra Nevada" despite the existence of museum records of this phenotype for localities on the east slope of these mountains; our data show that individuals of this phenotype occur in at least four Sierra Nevada canyons in the Bridgeport area. Similarly, except for Remington (1968), Scott (1986), Austin and Murphy (1987), and Porter (1990), there is little information on the hybridization of *L. weidemeyerii* with *L. lorquini* away from the immediate vicinity of Mono Lake. This study has verified the present approximate limits of this zone as recently outlined (Austin and Murphy, 1987; Porter, 1990) and added a number of localities where *Limnitis* had not been known or extensively studied. In total, the zone of overlap and hybridization in the Mono Lake area encompasses less than 1° of both latitude and longitude, considerably smaller than the approximately 2-5° latitudinal width and about 30° longitudinal length of the area of interaction between *L. astyanax* phenotypes in eastern North America (Platt and Brower, 1968).

Throughout its Great Basin range, *L. lorquini* is confined to and evidently largely disperses along riparian corridors. *L. weidemeyerii*, although it occurs principally in similar habitats, appears to be adapted to more xeric situations than is *L. lorquini* and is not as closely associated with riparian areas, even for breeding. One of its larval hostplants, *Amelanchier*, occurs widely on arid slopes and in dry canyons, far from streams and other wet areas. *L. weidemeyerii* therefore may disperse longer distances in habitat apparently unsuitable for *L. lorquini*.

Biogeography

One can only speculate as to the origins of the New World *Limnitis*. Their ancestors may have been similar to *Limnitis populi* (Linnaeus, 1758) from Eurasia (Chermock, 1950; Platt and Brower, 1968; Platt, 1983) or possibly North American *L. arthemis*, which separated into eastern and western forms, with the western form giving rise to the *weidemeyerii-lorquini* group (Platt *et al.*, 1970; Platt, 1983). The relationship between the taxa of this *weidemeyerii-lorquini* group (we treat them as species here for reasons detailed below), they undoubtedly represent independent evolutionary lines that probably differentiated in Pleistocene (or earlier) refugia from a *L. arthemis*-like or a *L. weidemeyerii*-like phenotype.

As pointed out by Endler (1977; but see Hammond, 1991), the difficulty in distinguishing primary from secondary intergradation is manifest. Yet, it seems probable that *L. weidemeyerii* and *L. lorquini*

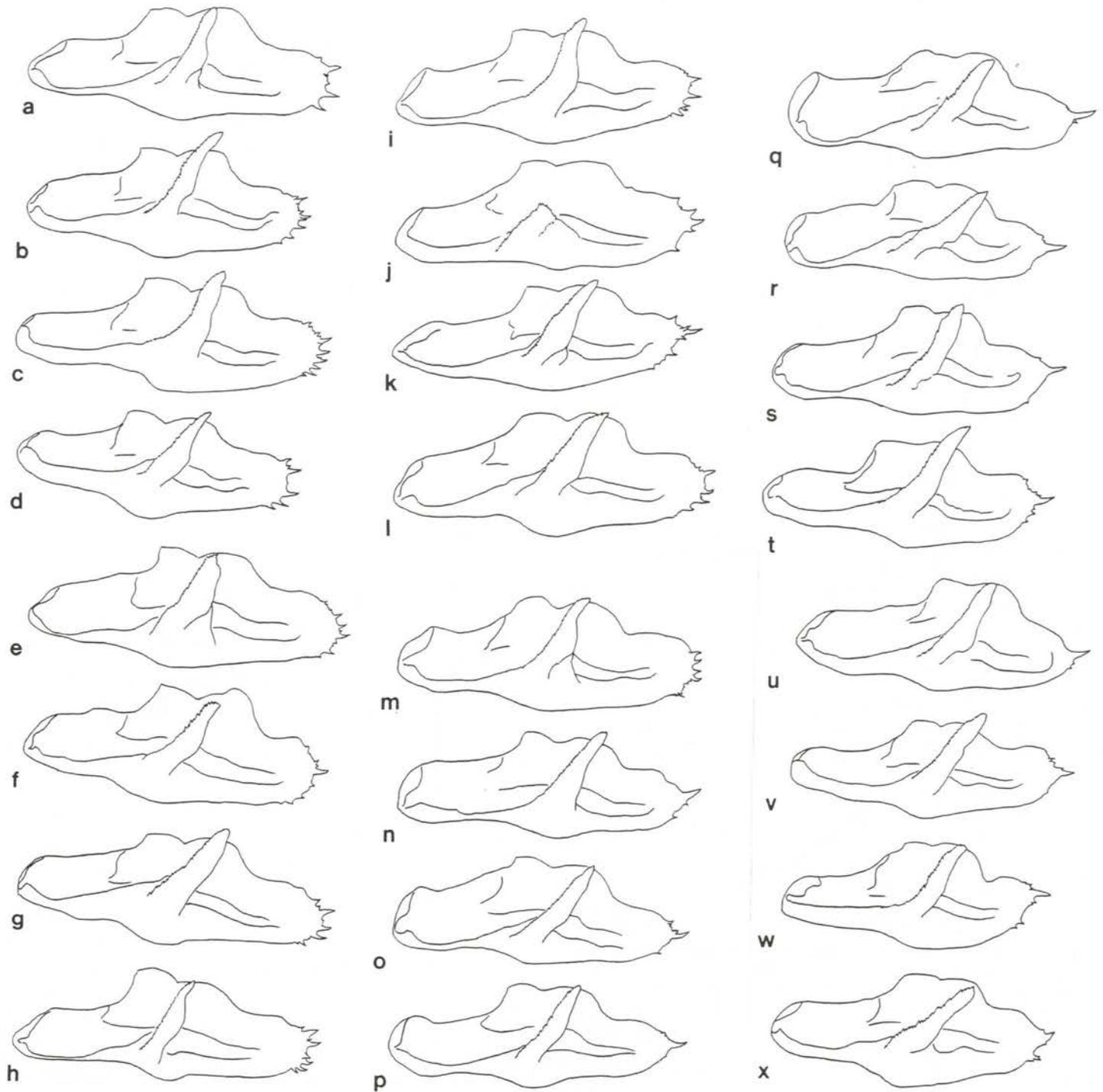


Fig. 82. Representative valvae of *Limenitis* from Desert Creek in the Mono hybrid zone (wing scores in parentheses): a-h. *L. weidemeyerii* phenotype, a. GTA #7719 (1), b. GTA #7720 (5), c. GTA #7721 (6), d. GTA #7722 (3), e. GTA #7723 (7, marginal "fridayi"), f. GTA #7727 (5), g. GTA #7728 (7, marginal "fridayi"), h. GTA #7729 (4); i-p. "fridayi" phenotype, i. GTA #7712 (20), j. GTA #7713 (25, aberrant valva), k. GTA #7714 (25), l. GTA #7715 (18), m. GTA #7716 (13), n. GTA #7717 (21), o. GTA #7718 (25), p. GTA #7730 (19); q-x. *L. lorquini* phenotype, q. GTA #7706 (33), r. GTA #7707 (32), s. GTA #7708 (34), t. GTA #7709 (33), u. GTA #7710 (33), v. GTA #7711 (32), w. GTA #7724 (31), x. GTA #7726 (31).

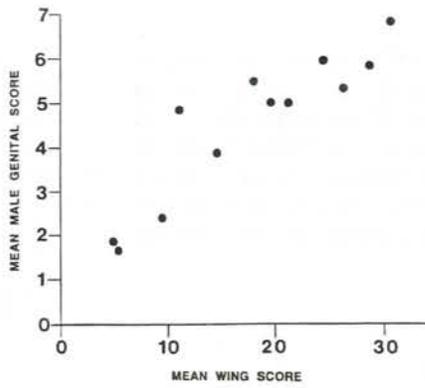


Fig. 83. Relation of mean wing and genital scores for Mono hybrid zone *Limenitis* populations ($r = 0.945$).

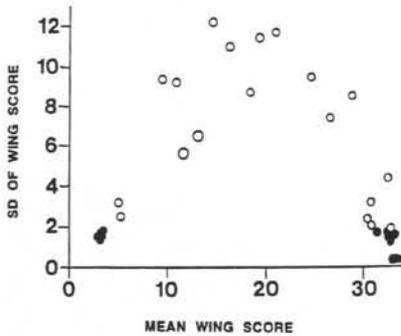


Fig. 85. Relation between mean population wing score and its standard deviation in Great Basin *Limenitis* (open circles = hybrid zone populations, closed circles = non-hybrid zone populations).

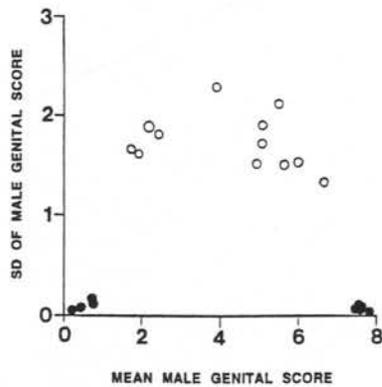


Fig. 86. Relation between mean population score of male genitalia and its standard deviation in Great Basin *Limenitis* (open circles = hybrid zone populations, closed circles = non-hybrid zone populations).

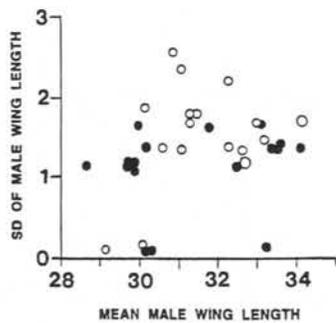


Fig. 87. Relation between mean population male forewing length and its standard deviation in Great Basin *Limenitis* (open circles = hybrid zone populations, closed circles = non-hybrid zone populations).

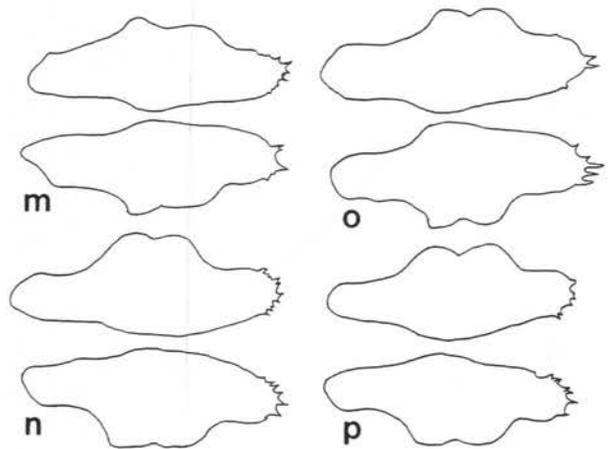
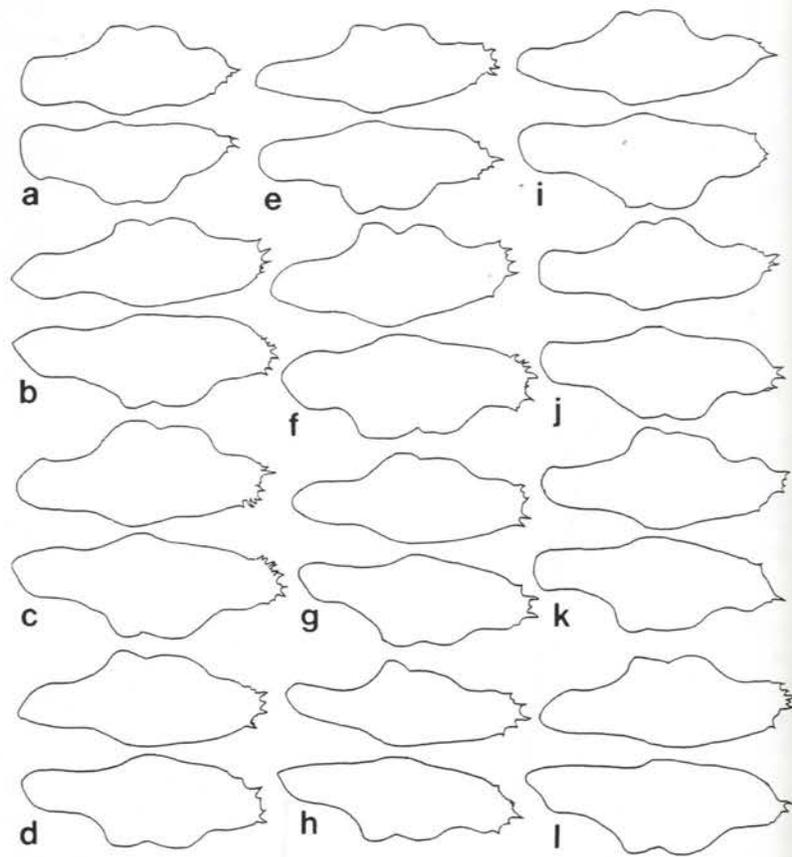


Fig. 84. Examples of asymmetry of the valvae of Great Basin hybrid zone *Limenitis* (external view): a-l. Mono hybrid zone (a, e, i-l - East Walker River, GTA #7787, 8040, 8146, 8150, 8157, 8083, respectively; b-d, f-h - Corey Peak Road, GTA #7749, 8196, 8192, 8118, 7756, 7734, respectively); m-p. Humboldt hybrid zone (all Santa Rosa Range, GTA #8977, 8993, 8990, 8996, respectively).

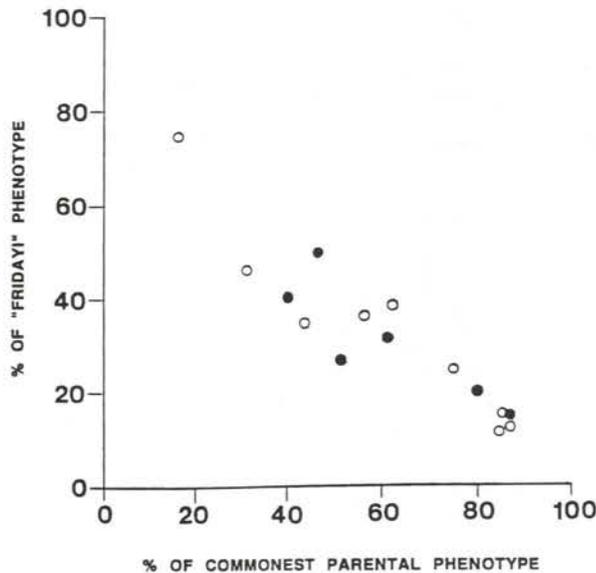


Fig. 88. Relation of proportions of "fridayi" and the commonest parental phenotype ($r = 0.949$; open circles = *L. lorquini* dominated populations, closed circles = *L. weidemeyerii* dominated populations).

differentiated in separate, probably later Pleistocene, refugia (east and west of the Sierra Nevada, respectively) and that the contact between *L. weidemeyerii* and *L. lorquini* is secondary based upon their current distributions and present knowledge of the paleoclimate and paleovegetation of western North America. Other similar situations of species pair interactions and clinal variation are known for this same general area at the western Great Basin-Sierra Nevada interface for butterflies (Grey and Moeck, 1962; Hammond, 1986; Murphy and Ehrlich, 1983; see also Austin and Murphy, 1987), moths (Collins, 1984; Collins *et al.*, 1993), birds (Johnson, 1978; see also Johnson and Zink, 1983; Johnson and Marten, 1988; Zink, 1994; Cicero and Johnson, 1995), and other organisms (Remington, 1968).

Late Wisconsin vegetation of the southwest was characterized by woodland and forest species distributed broadly in lowland habitats and the Great Basin was possibly largely dominated by sagebrush (*Artemisia*) with subalpine conifers occurring to near basal levels in the mountains (Wells, 1983; Van Devender *et al.*, 1987; Grayson, 1993). Large lakes and/or paludal habitat existed in many or most of the valleys of the Great Basin (Mifflin and Wheat, 1979), these apparently attributable to lower temperatures, especially in the summer, and perhaps a modest increase in precipitation in comparison to present climate (Van Devender *et al.*, 1987). Whatever the scenario, evidence exists for a number of Pleistocene refugia in North America which seem to explain some of the differentiation seen today. Refugial models have largely been developed for birds (Rand, 1948; Mengel, 1964, 1970; Hubbard, 1974; Zink and Hackett, 1988), but plants also show the effects of refugia (e.g., Reveal, 1979) and arthropods undoubtedly tracked the distributional changes of plants (Elias, 1991, 1994; Elias *et al.*, 1992; Elias and Van Devender, 1992; Hall *et al.*, 1989). The present distributions and diversities of some mesic taxa of insects were thought to have arisen during the Holocene (Noonan, 1990) and this has been verified by the fossil record (Elias, 1992, 1994). Mammalian taxa now characteristic of the Rocky Mountains and Great Basin were Pleistocene inhabitants of the extreme southwestern United States from western Texas to Arizona, apparently reaching their present distributions through much of the Holocene (Harris, 1990; but see Riddle, 1995).

It appears that eastern and western populations of *Limnitis* were effectively separated by the Sierra Nevada during full glacials. The present distribution and differentiation of *L. weidemeyerii* suggests several possibilities for its distribution during the Wisconsin. Two morphological and geographical groups among the six subspecies indicate the possible existence of at least two discrete refugial populations. The "angustifascia" group, including *Limnitis weidemeyerii angustifascia* (Barnes & Benjamin, 1912), *Limnitis weidemeyerii nevadae* (Barnes & Benjamin, 1924), and *Limnitis weidemeyerii siennafascia* Austin & Mullins, 1983, is united by narrow wing bands and a southwestern distribution and the "weidemeyerii" group, including *L. w. weidemeyerii*, *L. w. latifascia*, and *Limnitis weidemeyerii oberfoelli* F. M. Brown, 1960, has broad bands and a more northern distribution. It may be speculated that these resided in Pleistocene refugia in the Sonoran Desert and southern Rocky Mountains, respectively, with the former group expanding northwestward into the Spring Mountains (or where it may have been all along) and the latter group expanding north on both sides of the Rocky Mountains and westward (for potential migration routes into the Great Basin, see Reveal, 1979). The westward expansion may have been facilitated by its use of more xeric adapted shrubs as hostplants (*Amelanchier*, *Holodiscus*) in addition to the more riparian *Salix* and *Populus* and the potentially still widespread paludal and riparian habitats in the Great Basin during the early Holocene (Benson and Thompson, 1987a, b; Davis, 1982). Such westward dispersal producing the western limits of *L. weidemeyerii* was also suggested by Porter and Shapiro (1991).

Another possibility is that *L. weidemeyerii* was widespread in much of its present southern range (including the Great Basin) and its Holocene northward expansion was limited to the more eastern portion of its range. The various phenotypes seen today would then be of a more recent differentiation, resulting from an interruption in gene flow as they tracked mesic habitat as it desiccated in the valleys and retreated upward in elevation. This latter scenario could perhaps account for the cline of increasing band width of *L. w. latifascia* from southwest to northeast across the Great Basin, but does not explain the absence of the species from most of the extreme western Great Basin. Certainly there was abundant potential habitat for *L. weidemeyerii* throughout much of the Great Basin in the late Pleistocene and early Holocene as many valleys contained pluvial lakes or marshes (Hubbs and Miller, 1948; Mifflin and Wheat, 1979; Benson and Thompson, 1987a). Continuous water existed from northeastern Nevada to eastern California, much of this persisting at least into the mid-Holocene. Fluctuating lake levels (Benson and Thompson, 1987b) may have prevented long term development of continuous riparian habitat, but such undoubtedly was present along tributaries (Weide, 1976). These would, however, have provided numerous stepping stones not only within the Lake Lahontan system, but also between drainage basins across the entire Great Basin. Still another alternative refugium for Great Basin *L. weidemeyerii* may have been the Colorado Plateau which seems to have been an important refugium for Great Basin plants (Reveal, 1979) and also possibly insects (Elias *et al.*, 1992). Absence, however, of *L. weidemeyerii* on the east slope of the Sierra Nevada (except between Devils Gate Summit and Lee Vining Creek within the Mono hybrid zone), in other mountains on the California-Nevada border (e.g., White, Inyo, Excelsior, Silver Peak, Pine Nut mountains), and in the Carson, Truckee, and Walker river drainages (except the upper and middle portions which may be recent, see above) suggests that it was not in the western Great Basin during the Wisconsin and that its presence there now is a result of more recent dispersal from the east.

With Holocene warming, *L. lorquini* concomitantly was able to breach the lower passes of the Sierra Nevada and enter the riparian

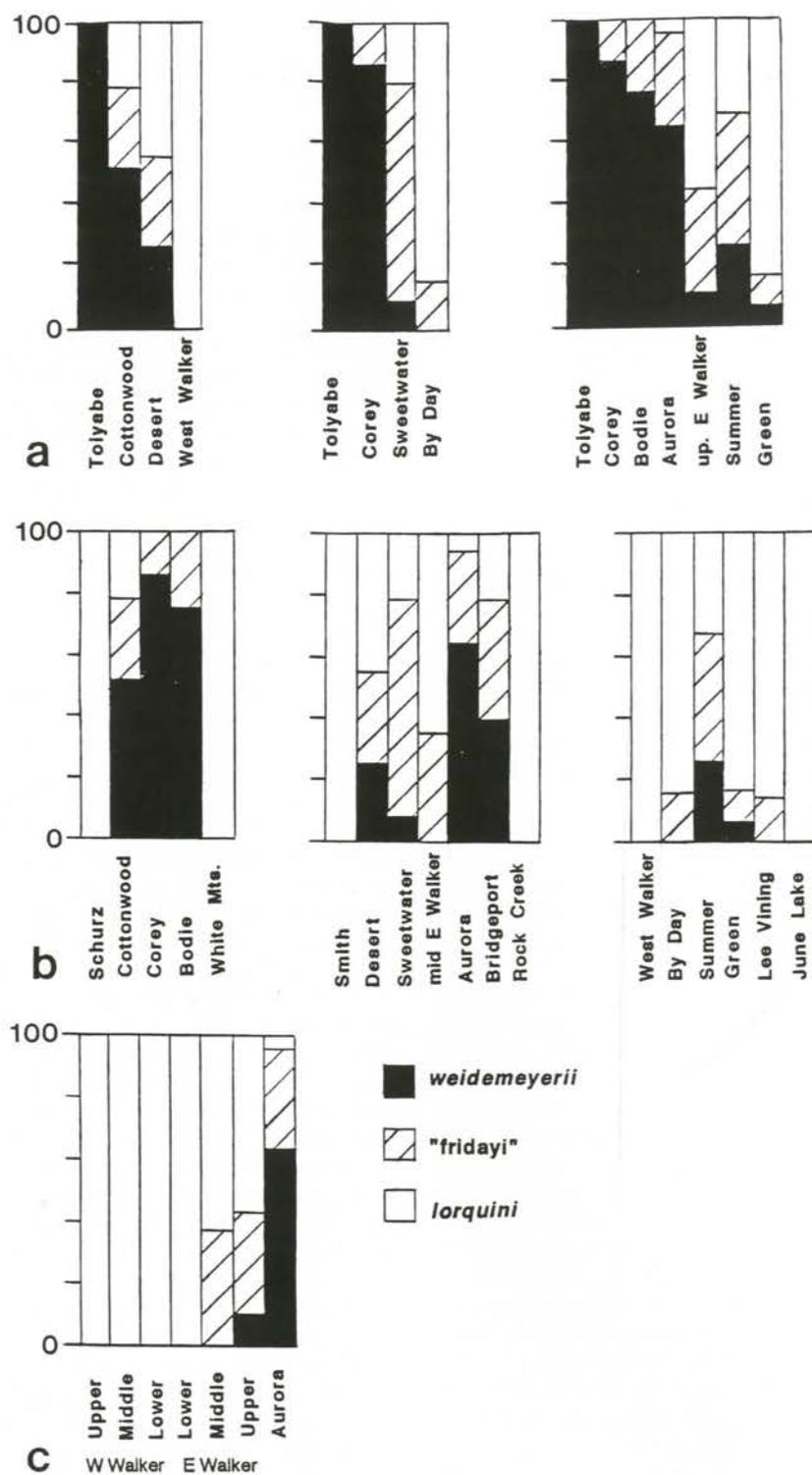


Fig. 89. Frequency (%) of various phenotypes of *Limenitis* in transects through the Mono hybrid zone: a. east to west transects; b. north to south transects; c. Walker River transect (see text).

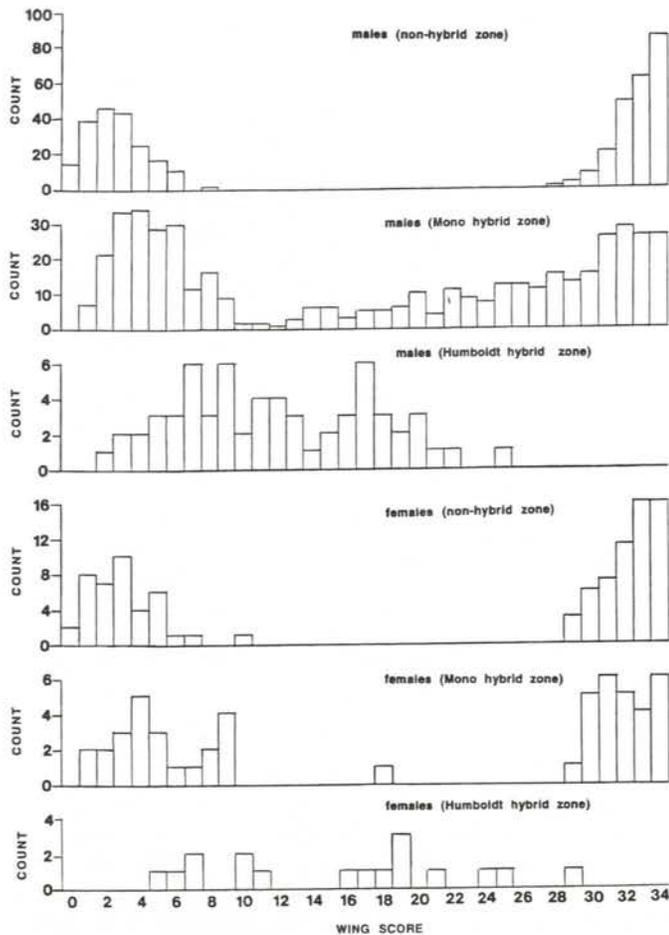


Fig. 90. Wing character frequencies of *Limenitis* from non-hybrid and hybrid populations.

areas of the western Great Basin. Since *L. lorquini* now occurs (in the south) only along river systems with direct connections to the Sierra Nevada (Walker, Carson, and Truckee rivers) and is not in the drainage of the Humboldt River proper, it appears to have arrived after considerable dessication of the Great Basin and fragmentation of continuous or stepping-stone riparian habitat. The Carson and Humboldt rivers emptied into a common sink which may have provided this corridor until at least 6900 BP (Davis, 1982).

The history appears to have been different in northern Nevada. Here, the drainage patterns are currently less continuous, more isolated, and less extensive than southward and make tracing possible dispersal routes of *Limenitis* more difficult than in the Mono hybrid zone. The only present continuous drainages are the Little Humboldt River, which drains the east slope of the Santa Rosa Range and enters the Humboldt River near Winnemucca, and the Little Owyhee River, which also drains the east slope of the Santa Rosa Mountains and flows north into Oregon. The Quinn River and its tributary, the Kings River, drain the region between the Santa Rosa and Pine Forest ranges and eventually end in the Black Rock Desert. This currently isolated drainage was originally part of the Pleistocene Lake Lahontan system. To the northwest into southern Oregon and northwestern California are a number of unconnected hydrological basins (e.g., see summary of Great Basin hydrological history in Austin, 1992). Certainly, the Little Humboldt River provides a potential corridor for *L. weidemeyerii* into the eastern portion of the Humboldt hybrid zone. The basins to the north and west provide

potential stepping stones for dispersal by *L. lorquini*.

The present eastern distributional limit of *L. lorquini* in the Great Basin may be Holocene in origin (as probably is the western limit of *L. weidemeyerii*) and its interaction with *L. weidemeyerii* is similarly recent following its range expansion during a warming climate (Remington, 1968). This is certainly one possibly scenario as Elias (1991, 1994) pointed out that, in the Rocky Mountains, present community structure has existed only since after the last glaciation, distributions changed relatively rapidly with late glacial extirpations of now northern species, and with Holocene extirpations reflecting the compression or alteration of previous distributions mostly to the east or west of the Rocky Mountains. Nowhere in the Great Basin of Nevada are three species of *Limenitis* known to occur together. *L. weidemeyerii* and *L. lorquini* co-occur in the hybrid zones, *L. weidemeyerii* occurs with *L. archippus* at various locations along the Humboldt River, and *L. lorquini* and *L. archippus* are found in the lower Carson and Truckee river drainages. *L. archippus* does not occur in the Walker River drainage (Austin, 1998); the record indicated in Stanford and Opler (1993) is based on a mislabeled specimen at the Nevada State Museum.

Phenotypes

Non-hybrid zone populations of *Limenitis* have little variation with mean scores of wing characters for *L. weidemeyerii* and *L. lorquini* below 4 and above 31, respectively, and standard deviations below 2.0 in all instances (Fig. 85). Hybrid populations have average scores ranging from 4.7 (Corey, 1990s) and 5.4 (Bodie Creek) to 32.1 and 32.5 (middle and upper, respectively, East Walker River, 1970s-1980s). The extreme means have the lower standard deviations which ranged overall from 1.8 to 12.0 (Fig. 85), a pattern also found for the scores and variation of male genitalia (Fig. 86). Rohwer and Wood (1998) found a similar phenotypic pattern among hybridizing wood warblers (Aves: Parulidae) in Washington. Although size shows a decreasing trend from "pure" *L. weidemeyerii* to "pure" *L. lorquini* (Fig. 81), a comparison between wing length and its standard deviation is less clear cut (Fig. 87). Size (in this case, wing length), however, has environmental in addition to genetic components (Gardiner, 1963; White, 1974) and the wing lengths of the two species overlap considerably. Nonetheless, hybrid populations generally are intermediate in size and exhibit greater variability than non-hybrid populations (Fig. 87).

Some authors have commented upon the phenotypes of "fridayi" populations. Brown (1934) found the Mono Lake population to be largely of the *L. weidemeyerii* phenotype with "fridayi" approaching *L. weidemeyerii* in size and pattern. Garth and Tilden (1963) spoke of an even blend without the predominance of characters of either species. Scott (1986) suggested that *L. lorquini* was rare to absent at most locales where the "fridayi" phenotype was found. Porter (1990), in contrast, found populations that not only were truly intermediate, but also others clearly most closely resembling *L. weidemeyerii*. The data presented herein for the Mono hybrid zone further support and expand these generalizations as there is a continuum from "pure" populations of *L. weidemeyerii* (e.g., central Nevada), to mixed populations of *L. weidemeyerii* and "fridayi" (Corey Peak Road, Bodie Canyon), populations with all three phenotypes (Cottonwood Canyon, Desert Creek, Sweetwater Canyon, upper East Walker River, Aurora Canyon, Bridgeport Canyon, Green Creek, Summers Creek), populations with *L. lorquini* and "fridayi" (middle East Walker River, By Day Creek, Lee Vining Creek), and "pure" populations of *L. lorquini* (e.g., West Walker River, lower East Walker River, lower Rock Creek). Parental phenotypes outnumber "fridayi" in all populations sampled except in Sweetwater Canyon (Fig. 76). Even there, parentals are 28% of the individuals captured. Some popula-

tions (e.g., Cottonwood, Desert) actually exhibit a bimodal frequency of phenotypes (Fig. 76). In the Mono hybrid zone, the pattern is generally of one parental type or one parental type and "fridayi" being numerically dominant. The rarest parental phenotype does not exceed 23% of the sample and averages 11% overall while the commonest parental phenotype varies from 17% to 87% of individual samples averaging 55%. "Fridayi" also has a broad range from 11% to 75% (averaging 34%). The proportion of "fridayi" is significantly negatively correlated ($r = 0.949$) with the proportion of the commonest parental phenotype (Fig. 88), but has no correlation with the proportion of the rarest parental. The "fridayi" phenotypes exhibit all degrees of intermediacy (see especially Fig. 5-16, 23-34, 41, 47, 53-55, 59-61, 63-67, 69-73), some truly striking. The greater variation seen among "pure" *L. weidemeyerii* and *L. lorquini* within the hybrid zone and the variation of "fridayi" itself are likely reflections of backcrossing. The phenotypic expressions of backcrossing and their underlying genetics remain to be resolved (but see Platt, 1975, 1983).

The pattern of hybridization in the Mono Lake area appears to be more complex than suggested by Porter (1990). The cline from *L. weidemeyerii* to *L. lorquini* is certainly steep and character transitions are more or less concordant (Porter, 1990). Apparently pure *L. weidemeyerii* populations occur as far west as the Clan Alpine and Desatoya mountains and possibly as far as the Pilot Mountains. Within the latitude of this hybrid zone, non-hybrid *L. lorquini* populations occur east to at least the Sierra Nevada crest and further define the hybrid zone to both the north and southwest with non-hybrid *L. weidemeyerii* only bordering on the east. This contributes to the east to west cline as shown by Porter (1990). Examined across three artificial east to west transects (see below), a transition is seen from largely *L. weidemeyerii* in the east giving way to mostly *L. lorquini* westward with hybrids prevalent at sites in the middle of the zone (Fig. 89a). Both parental phenotypes are present across most of this area. The north to south pattern may be examined along three transects, one along the east side of the zone, one more or less in the middle and one including the canyons on the Sierra Nevada east slope (Fig. 89b). These show *L. lorquini* in both the north and south, and *L. weidemeyerii* and "fridayi" at intermediate sites, with an east to west pattern of decreasing proportions of *L. weidemeyerii* and a greater proportion of "fridayi" at intermediate locations. One other and less artificial transect is of interest. This transect extends from the upper West Walker River, to the upper East Walker River, and into the Bodie Hills (Fig. 89c). A gradient exists from pure *L. lorquini* in the West Walker and lower East Walker drainages, to "fridayi" in the middle East Walker, and "fridayi" and a few *L. weidemeyerii* in the upper East Walker drainage. This strongly suggests that *L. weidemeyerii* may have dispersed into the East Walker drainage from the Bodie Hills (possibly via Aurora Canyon). The Bodie Hills also may well have been the source of *L. weidemeyerii* in the Sweetwater Mountains, at Mono Lake via Cottonwood (Bodie Hills) and Bridgeport canyons, and on the east slope of the Sierra Nevada via the East Walker River.

The general trend shown by these transects within the Mono hybrid zone, recognizing that phenotypes are not necessarily correlated with genotypes (Collins, 1991), is a decreasing proportion of *L. weidemeyerii* westward with a concomitant increase of *L. lorquini*. The "fridayi" phenotype tends to be more frequent at geographically intermediate locations. These generalizations are apparently influenced by geographically adjacent "parental" populations. Thus, Cottonwood Canyon (Wassuk Range), relatively close (30km) to the *L. lorquini* population of the lower Walker River near Schurz, has a higher proportion of *L. lorquini* and "fridayi" than the Corey Peak Road population 15km further south (one *L. weidemeyerii*,

ii, one *L. lorquini*, and two "fridayi" were taken in Powell Canyon still further south in the Wassuk Range). Likewise, the populations on the east slope (Bodie Creek) of the Bodie Hills are largely *L. weidemeyerii*, but Bridgeport Canyon on the south slope and Aurora Canyon on the west slope of these mountains have a substantial proportion of the "fridayi" phenotype and some *L. lorquini*. Three canyons on the Sierra Nevada east slope. (By Day Creek, Green Creek, Lee Vining Creek) are largely inhabited by *L. lorquini*.

Apparent anomalies do exist. In the Sweetwater Mountains, the population along Desert Creek is largely *L. lorquini*, but includes *L. weidemeyerii* and a range of "fridayi" phenotypes as well. Just 20 km to the south, along Sweetwater Creek, the population is very variable with "fridayi" phenotypes more common than parentals. Three specimens from Silverado Canyon, still further south, include one of each phenotype. These differences may, however, be accounted for by the drainage relationships (and thus likely main dispersal routes) of these canyons. Desert Creek drains into the West Walker River whereas Sweetwater and Silverado canyons drain into the East Walker River. The cline along the East Walker River was discussed above. The population in Summers Creek, 4km north of Green Creek, is different from other known Sierra Nevada populations because "fridayi" outnumbers each of the parental phenotypes and *L. weidemeyerii* comprises over 20% of the population (but note that of the two known specimens each from Robinson Creek and the Virginia Lakes Road, one is a *L. weidemeyerii* and one is a "fridayi"). The Mono Lake samples of Brown (1934) and Porter (1990) were described as closer to *L. weidemeyerii* than to *L. lorquini*.

Unfortunately, the Mono hybrid zone does not lend itself to detailed analysis of symmetry in character transitions and their concordance or even the actual width and slope of the hybrid zone. The patchiness and lineal character of *Limenitis* habitat with several apparent axes of hybridization preclude simple examination of the hybridization dynamics in the region as have been performed for hybrid zones within large blocks of continuous habitat (e.g., Rohwer and Wood, 1998). East-west or north-south transects are only instructive in examining gross changes from *L. weidemeyerii* occurring essentially east of the hybrid zone and *L. lorquini* occurring largely in the west, north, and south. The only potential natural major axis (albeit convoluted) within the Mono hybrid zone may be that from the upper West Walker River to the upper East Walker River and the Bodie Hills as previously discussed. It seems likely that each montane canyon is its own subaxis with potential immigration of either species. Thus, for example, *L. lorquini* may be immigrating into the Wassuks from the lower Walker River drainage and *L. weidemeyerii* into the canyons of the Sierra Nevada and Sweetwater Mountains from the Bodie Hills via the East Walker River. Differential immigration into these canyons from the Walker River may explain the apparent anomalies mentioned above.

Porter (1990) noted a "tail of introgression" of *L. lorquini* wing characters into *L. weidemeyerii* in the Mono Lake region, but little in reverse. The situation, as summarized above, does not seem this simplistic since *L. lorquini* characters appear as both phenotypic *L. lorquini* and as "fridayi" at the easternmost edge of the hybrid zone, this possibly a "tail" from the north (i.e., Walker River at Schurz) and phenotypic *L. weidemeyerii* have been encountered well into several canyons on the east slope of the Sierra Nevada. Similarly, *L. weidemeyerii* seems recently to have introgressed into *L. lorquini* populations in the middle and upper East Walker River drainages and in the Sweetwater Mountains. There thus appears to be introgression not only of *L. lorquini* into *L. weidemeyerii*, but also of *L. weidemeyerii* into *L. lorquini*.

The Humboldt hybrid zone is less well known and material from only two populations was available for study. These two population

are largely "fridayi" in phenotype (Fig. 75) and appear unlike any known population in the Mono hybrid zone with just over 17% parental-like individuals (mostly *L. weidemeyerii*). As pointed out by Porter (1990), suitable habitat for *Limenitis* in this region is much more isolated than in the Mono Lake area which undoubtedly contributes to reducing immigration of and gene flow between parental forms.

When character frequencies are plotted (Fig. 90), two very striking patterns emerge. The phenotypic frequency of males within the Mono hybrid zone is bimodal. *L. weidemeyerii* and *L. lorquini* phenotypes are most frequent with hybrids spanning the entire range in between. Phenotypes, however, tend toward *L. lorquini* even in populations (i.e., Cottonwood Canyon, Aurora Canyon, Bridgeport Canyon) where *L. weidemeyerii* is more abundant (see also frequency distributions for Corey Peak Road in the 1970s and 1980s and Summers Creek; Fig. 76, 79). In contrast, males in the Humboldt hybrid zone are largely hybrids, tending towards the *L. weidemeyerii* side, and parentals are notably scarce. Females from the Mono hybrid zone are also bimodal, but hybrids, unlike the males, are clustered on the *L. weidemeyerii* side. Distribution of the phenotypes of Humboldt hybrid zone females are similar to males and distinct from Mono hybrid zone females.

The variation of the male genitalia inside the hybrid zones presents an interesting comparison to variation of the wings. Overall and as expected, these have a range overlapping (completely in the case of the Mono hybrid zone) the scores for non-hybrid zone parentals. That parental-like phenotypes within the hybrid zones have a broad range of genital scores indicates that wing characteristics alone do not account for the variation within these populations. Nearly 40% of the individuals scored as parentals by wing characters have genital scores outside those seen in non-hybrid zone populations and over 50% of "fridayi" by wing scores have genital scores within the range of variation seen in non-hybrid zone populations of parentals. This also suggests that wing and genital characters are not closely linked. Hybrids between *L. archippus* and *L. arthemis*, however, were reported to have intermediate genitalia (Platt and Maudsley, 1994). The variation of female genitalia within the hybrid zones appears similar with a range of phenotypes including those of non-hybrid zone individuals and with genital phenotype not necessarily corresponding to wing phenotypes.

An asymmetry of the valvae, not previously reported for *Limenitis* in hybrid zones, does not appear to be correlated with wing or genital phenotypes. It is unknown if or how asymmetry and genital variation may affect mating (e.g., Porter and Shapiro, 1990).

Hybrid zone changes

Porter (1990) noted little apparent change in hybrid frequencies at Mono Lake since Brown's (1934) study, indicating stability within the hybrid zone. Our data, however, show that phenotypic frequencies shift at some sites, at least in the short term. Material from Corey Peak Road in Mineral County, Nevada, indicates a shift from one including a substantial proportion of hybrids (46%) from the late 1970s to 1985 to largely *L. weidemeyerii* (77%) in the 1990s. This trend, however, may be more complex. The Corey site is the only location where there are data for a series of years (Fig. 79). These reveal apparent short-term changes in phenotype perhaps reflecting drift or differential selection acting on this population. Most interesting is the predominance of hybrids in 1985 followed by no detection of hybrids by Porter (1990) in 1986. Other shifts in phenotype detected during our study were at Desert Creek and the middle and upper East Walker River where historical populations were entirely or mostly of the *L. lorquini* phenotype, but recent populations include significant numbers of "fridayi" and *L. weide-*

meyerii (Fig. 79). Further, Porter (1990) found (in 1986) the Bridgeport Canyon population to be largely *L. weidemeyerii* in phenotype; the sample from 1998 is 40% of the *L. weidemeyerii* phenotype, 40% "fridayi", and 20% *L. lorquini*. The few data available for the Humboldt hybrid zone indicate no radical changes between the 1970s and the 1980s although the population in the Pine Forest Range appears to have shifted somewhat toward *L. lorquini* between the early and late 1980s. Shifts of phenotypic frequencies within hybrid zones are known for various taxa (e.g., for data on birds see Corbin and Sibley, 1977; Rising, 1983). These changes may, at least in some instances, be due to variable and intermittent dispersal. Porter (1990), however, noted deme sizes of these *Limenitis* to be between 10 and 200 individuals (with likely much smaller effective population sizes) suggesting that some observed shifts in phenotype may be due to drift.

Sex ratio

Porter (1990) argued that, because "both sexes of hybrid phenotypes are frequently produced," there was no genetic incompatibility between *L. weidemeyerii* and *L. lorquini*. Although Porter (1990) did not see F₁ females, these do occur (e.g., see photograph in Platt, 1983). Additionally, Remington (1968) observed that *L. weidemeyerii* and *L. lorquini* interbreed "freely", although the F₂ generation between hybrids apparently had lower viability than offspring of either of the parental phenotypes.

While extensive experimental data are unavailable for *L. weidemeyerii* and *L. lorquini*, our field data suggest that Haldane's rule (Haldane, 1922; see also Coyne and Orr, 1989a,b; for examples in butterflies, see Clarke and Sheppard, 1955; Ae, 1979; Scriber *et al.*, 1990; Sperling, 1993; Hagan and Scriber, 1995) applies with a deficiency of the heterogametic sex (the female among butterflies) among hybrid phenotypes, at least in the Mono hybrid zone. Sex ratios among field caught samples of Lepidoptera are nearly always male biased (e.g., Brussard *et al.*, 1974; Brussard and Ehrlich, 1970; Brown and Ehrlich, 1980; Ehrlich *et al.*, 1984; Freitas, 1993, 1996; Tyler *et al.*, 1994), as indicated for three taxa of Great Basin *Limenitis* (Table 5), largely due to behavioral differences between the sexes. In these hand-netted *Limenitis* samples, males outnumber females by more than 3.7:1. Within the Mono hybrid zone, however, this ratio for all individuals is 6.9:1 and nearly 18:1 for "fridayi" phenotypes, both significantly different from that seen among other Great Basin *Limenitis* populations (Table 5). In fact, there is a significantly smaller proportion of females among Mono hybrid zone parental phenotypes (sex ratio = 5.2:1) than in other Great Basin *Limenitis* suggesting possible inviability of backcross hybrid females which score as parental types. Assuming that catchability of hybrid zone individuals is the same as elsewhere, the deficiency of "fridayi" females suggests some preadult heterogametic inviability. This is further reinforced by the near absence of female hybrids with wing scores between 9 and 29 (Fig. 90).

The sex ratio of Mono hybrid zone "fridayi" appears intermediate between those in other instances of intergrading or hybridizing *Limenitis*. Laboratory crosses between *L. a. arthemis* and *Limenitis arthemis astyanax* (Fabricius, 1775) produced 1:1 sex ratios (Platt and Brower, 1968; but see Collins, 1991). In contrast, all wild caught hybrids between *Limenitis archippus* and other North American *Limenitis* have been males (N = 77) (Shapiro and Biggs, 1968; Platt and Greenfield, 1971; Platt *et al.*, 1978; Platt and Maudsley, 1994). Likewise, in the laboratory, no adult females were produced among 204 progeny of *L. archippus* during initial crosses with various *L. arthemis* phenotypes (Platt, 1975), but abnormal females (27%) were obtained in later F₁ generations and backcrosses produced about 25% females (Platt, 1975; Platt *et al.*, 1978; see also Field, 1914;

Remington, 1958; Platt and Harrison, 1994). Female larvae of the F_1 crosses pupated early (fourth instar) and had malformed pupae or grew to abnormally large size and failed to metamorphose (Kean and Platt, 1973). Hybrid female pupae of some *Papilio* species are known to enter permanent diapause (e.g., Clarke and Willig, 1977; West and Clark, 1988; Scriber *et al.*, 1990; Hagan and Scriber, 1995). Remington (1958) obtained both sexes, but significantly fewer females (12 of 41 individuals), from a cross between *L. arthemis* and *L. weidemeyerii*. Crosses involving male *L. archippus* with females of other *Limenitis* species were easier to produce in the laboratory than the reciprocal (Platt *et al.*, 1978) and may likewise select against hybrids in the field.

In contrast to the Mono hybrid zone, the sex ratios of both "fridayi" and parentals in the Humboldt hybrid zone appear as that seen in non-hybrid populations at 3.6:1. This may reflect the more isolated nature of these populations, significant backcrossing allowing the elimination of incompatible combinations, and a more stable overall genotype.

Taxonomy

Most recent authors have considered *L. weidemeyerii* and *L. lorquini* to be separate species (e.g., Miller and Brown, 1981; Ferris, 1989). Scott (1986) stated that the two taxa "may" be subspecies and Porter (1990) argued for conspecificity. The data presented here provide additional taxonomically pertinent information on phenotype, phenology, and sex ratios. These are not biological species in the strictest sense (Barton and Hewitt, 1983) as they obviously do hybridize, but they may be recognized as such in a less strict sense (e.g., Bigelow, 1965; Mayr, 1982) and certainly are phylogenetic species (e.g., see Craycraft, 1989; Collins, 1991; Zink and McKittrick, 1995). Genetic exchange may occur broadly without hybridizing taxa becoming panmictic, and can possibly function to increase genetic diversity (Grant and Grant, 1992; Moore and Price, 1993; Parsons *et al.*, 1993; Bell, 1996) and allow intrageneric introgression of adaptive alleles (Barton, 1979).

Short (1969) presented a discussion of the taxonomic implications of hybridization in birds which may apply equally well to butterflies (see also Sperling, 1990). He defined "hybrid zones" as areas where only hybrids occurred and "zone of overlap and hybridization" as areas of secondary intergradation where both parental types (comprising more than 5% of the population) and hybrids were found. The presence of parental types within the zone of overlap and hybridization indicates the existence of partial isolating mechanisms (or immigration when hybrids are at a selective disadvantage) (Short, 1965; Bigelow, 1965); their proportion over 5% was thought to be relatively unimportant since this can be affected by other factors such as size of contact. Short (1965) considered such taxa as semispecies which he recognized taxonomically as species. These criteria apply to the Mono hybrid zone of *Limenitis* as parentals comprise over 5% of all populations studied. These two *Limenitis* species, along with *L. arthemis*, are a classic example of a superspecies (Mayr, 1963) with their distributions largely allopatric (Hovanitz, 1949; Platt, 1983).

Limenitis hybridize across a narrow band in the Great Basin. Occurrence and maintenance of such narrow zones have been accounted for by essentially four models. The first is "recent contact" (Endler, 1977; Barrowclough, 1980). Dispersal distances for these *Limenitis* species are unknown and cannot be calculated indirectly (Barton and Gale, 1993) because of the habitat patchiness of the hybrid zone. *Limenitis* in the vicinity of Mono Lake, however, have been in contact for at least 65 years (Gunder, 1932; Brown, 1934) and the extent of the zone has been known for 30 years. A second model involves "habitat modification" (Gill, 1980, 1997; Wake *et al.*,

1980). No habitat changes which may have affected the distributions of *Limenitis* are obvious; hybridization in the area for at least 65 years argues against human mediated habitat modification as a factor. The third model for hybrid zone maintenance relates to "hybrid superiority" in response to some climatic or ecological cline across the zone (Moore, 1977; Moore and Price, 1993). No obvious cline exists although there is the possibility that the two species are differentially adapted to some as yet unmeasured subtle environmental factor. Both species are relatively common in riparian situations with males of all three phenotypes perching similarly in the same canyons. Parental phenotypes seem to have superiority over hybrids since they are more abundant at nearly every site sampled. This observation indicates that the fourth model, the "tension-zone" model (Barton and Hewitt, 1985, 1989; Barton and Gale, 1993), wherein hybrid inferiority balanced with continued introgression of parental genes may apply to the Mono hybrid zone. This may be a reflection of general inferiority of the hybrid genotype or heterogametic incompatibility as exhibited by a deficiency of hybrid females. The shift in frequencies of phenotypes at some sites suggests temporal fluctuations in relative fitness preventing complete swamping of parentals or complete elimination of hybrids (Grant & Grant, 1992, 1993; Bell, 1997). Dispersal in either direction, for example, may be hindered by unidentified physiological and/or ecological limitations. Lack of swamping, however, may be a result of the continued immigration of parentals; this apparently occurs. Geographically proximate populations with very different proportions of the various phenotypes (Desert vs Sweetwater, Green vs Summers) and the absence of *L. weidemeyerii* from the West Walker and lower East Walker drainages suggest, however, a relatively slow dispersal rate. Additionally, Porter's (1990) genetic data showed an apparently decreased gene flow through the hybrid zone.

The Humboldt hybrid zone, however, presents a different picture. Although this area of hybridization has been known for only 25 years, recent contact is unlikely, especially in light of the paucity of parental phenotypes within the two populations studied. Habitat modification seems unlikely for the same reasons as in the Mono hybrid zone. Immigration may be even less of a factor in the Humboldt hybrid zone than near Mono Lake. The *Limenitis* populations in the general area are widely separated by unsuitable habitat (as pointed out by Porter, 1990). Here, although parental-like phenotypes (particularly *L. weidemeyerii*) comprise more than 5% of the two populations examined, the vast majority of individuals are "fridayi" at an apparently "normal" sex ratio. This may be the result of low rate of immigration and the greater chance of backcrossing and potentially a more stabilized genotype. The possible greater genetic compatibility within these, as indicated by their apparently balanced sex ratio, suggests that hybrids in the Santa Rosa and Pine Forest ranges may be superior to parentals (Moore and Buchanan, 1985; Moore and Price, 1993). The region is characterized by relatively few mountains which appear drier than those to the west and east, and by the absence of major riparian corridors, these features possibly contributing to a transitional habitat. Such differences between different hybrid zones of the same two species have been noted for other taxa (e.g., Brower, 1959; Rising, 1973, 1983; Sperling, 1987, 1990; Collins, 1991).

With the apparent stability in the distribution and width of the Mono hybrid zone, it is likely that *L. weidemeyerii* and *L. lorquini* are different species (Mayr, 1982). Judging stability, however, is complicated and may well take 100s-1000s of generations to document (Barton and Hewitt, 1983). The two taxa appear to be sister species, but this does not necessarily need to be the case (Sperling, 1987; Zink, 1994; Freeman and Zink, 1995; Burns, 1998); each may be evolving independently (McKittrick and Zink, 1988).

Zink and McKittrick (1995) suggested that complete fusion of such taxa may require a period longer than the estimated average time of existence for the majority of species. Bigelow (1965) suggested that gene flow, and not hybridization, is the key to reproductive isolation. While Porter's (1990) allozyme data indicated some apparent gene flow, there are inherent difficulties in interpreting these for phylogenetic studies (Buth, 1984). Investigations of mitochondrial DNA may shed additional insights on the relationships of these two taxa (Avisé *et al.*, 1987; Harrison, 1991). Furthermore, recognizing two hybridizing taxa as conspecific anticipates introgression and fusion and ignores their status as historical entities (Barton and Hewitt, 1983).

Collins (1991; see also Barton and Hewitt, 1983) observed that hybrid zones are narrow clines, their steepness reinforced by a balance between genetic incompatibility and gene flow. Their clinal nature is reflected as a continuum of recombinant genotypes and in their resultant phenotypes (Harrison, 1993). Hybrid zones and intraspecific clines may be difficult to distinguish using morphological characters (Endler, 1977), but differences in these characters (Hammond, 1991), the presence of both parental phenotypes across the entire span of the Mono hybrid zone, along with a suggestion of selection indicate that the Mono Lake area is a hybrid zone between two *Limenitis* species rather than an intraspecific cline. It appears to be a case of overlap of two species without strong prezygotic isolating mechanisms, but constrained at least by the lack of full genetic compatibility reflected in a reduction of gene flow (Porter, 1990) and a deficiency of female hybrids. This situation is intermediate between apparent complete intraspecific compatibility of *L. a. arthemis* and *L. a. astyanax* and the high degree of interspecific incompatibility of *L. archippus* with various other *Limenitis* (Platt and Brower, 1968; Platt, 1975). Incompatibility between *L. weidemeyerii* and *L. lorquini* may also be less than that between them and *L. arthemis*. Platt (1983) observed that females of the F₁ crosses with *L. arthemis* were large in size and although mating was possible, eggs were difficult to obtain. Female "fridayi" in the Mono hybrid zone are intermediate in size between their parental species.

The interactions between these *Limenitis* are different in form from those exhibited in the hybrid zone of *Hyalophora* (Lepidoptera: Saturniidae) just to the north of the Mono hybrid zone of *Limenitis*. In these *Hyalophora*, hybrid zone individuals are variable morphologically (Collins, 1984) resembling the pattern seen in the Sweetwater Canyon population of *Limenitis*. The *Hyalophora* situation also differs in the parentals having different fixed alleles, these appearing at varying frequencies within the hybrid zone (Collins *et al.*, 1993).

Phenology

The absence of "fridayi" during the second brood flight of *L. lorquini* suggests developmental differences between *L. lorquini* and *L. weidemeyerii*. This phenology perhaps indicates dominance of the *L. weidemeyerii* threshold of sensitivity to photoperiod that triggers diapause; "fridayi" (based on its phenology) appears similar to *L. weidemeyerii* in its sensitivity to photoperiod length, which is known to trigger diapause in *L. archippus* (Clark and Platt, 1969; Hong and Platt, 1975; see also Hagen and Scriber, 1989, 1995). Apparent differences in sensitivity may cause diapause disorganization in "fridayi" heterozygous for this trait.

Genetics

Porter (1990) showed genetic similarity between *L. weidemeyerii* and *L. lorquini*, but these data showed a reduction of gene flow between them. Further interpretation of his data revealed additional information which was not originally elaborated. Eleven of the 18 resolved loci were polymorphic including 41 alleles. Populations assigned to *L. weidemeyerii* were polymorphic at eight of these loci

including 30 alleles (two additional alleles were found in *L. w. angustifascia*; Porter, 1989). *L. lorquini* populations were also polymorphic at eight loci (seven of these also polymorphic in *L. weidemeyerii*) including 31 alleles, and "fridayi" was similarly polymorphic at eight loci including 32 alleles. In "fridayi", five of the polymorphic loci were also polymorphic in *L. weidemeyerii* and six were polymorphic in *L. lorquini*. Of the alleles, *L. lorquini* had two unique alleles and shared four others with "fridayi" (note that one of these is also found in *L. w. angustifascia*; Porter, 1989), but not with *L. weidemeyerii*, *L. weidemeyerii* had two unique alleles and two shared with "fridayi" but not with *L. lorquini*, and "fridayi" had 6 unique alleles (but note that one of these apparently also occurs in *L. w. angustifascia*; Porter, 1989). Unique alleles found only in hybrid zones are known for a variety of taxa (Barton and Hewitt, 1985; Woodruff, 1989; Collins *et al.*, 1993).

One final comment is warranted on the analysis of genetic data by Porter (1990). He noted no significant deviations from expected frequencies in a Hardy-Weinberg analysis, but noted the small sample sizes as limiting. Hardy-Weinberg analysis, however, assumes random mating and no gene flow and is not sensitive to reduced fecundity (Endler, 1986). No data are available for mating patterns in these *Limenitis*, at least some gene flow was shown to exist, and the sex ratio of hybrids is suggestive of a measure of female hybrid inviability which thus can influence fecundity.

Identification

The phenotype of "fridayi" has been characterized as similar to *L. weidemeyerii* (Perkins and Perkins, 1967; Ferris and Brown, 1981; Garth and Tilden, 1986; Tilden and Smith, 1986; Scott, 1986), usually having white submarginal macules (Gunder, 1932; Perkins and Perkins, 1967), but with red-brown forewing apices (Ferris and Brown, 1981; Garth and Tilden, 1986; Tilden and Smith, 1986; Scott, 1986) and red-brown in the submarginal line on the ventral hindwing (Perkins and Perkins, 1967; Garth and Tilden, 1986; Scott, 1986). More than 90% of the hybrids have submarginal macules on the forewing and 35% have these on the hindwing. Nearly all *L. weidemeyerii* have these macules on the forewing (only a few from the hybrid zone do not) and more than 80% have them on the hindwing while about one-third of *L. lorquini* have faint macules on the forewing and almost none have these present on the hindwing. *L. lorquini* always has a red-brown dorsal forewing apex while this is nearly always black on *L. weidemeyerii* (a few hybrid zone individuals otherwise scored as *L. weidemeyerii* have red-brown at the apex); 90% of "fridayi" have red-brown apices. *L. lorquini* always has a red-brown submarginal line on the ventral hindwing whereas on *L. weidemeyerii*, this line is always black; 71% of "fridayi" have some red-brown in this area (note that the ventral forewing submarginal line is similarly distinctive).

The vast majority of *Limenitis* may be readily placed into their proper phenotype using the above noted "classic" characters and without time consuming scoring. Before the scoring system was devised, 120 *Limenitis* from the hybrid zone were subjectively categorized as *L. weidemeyerii*, *L. lorquini*, or "fridayi"; 91% corresponded with their later scores. Of the errors were eight "fridayi" originally identified as *L. weidemeyerii* (all having scores of 7 or 8) and three *L. lorquini* which were originally placed as "fridayi" (with scores of 28, 28, and 31).

Future research

Investigations of hybrid zones are key to understanding several components of population biology (genetics, selection, dispersal, habitat selection, physiology, etc.) and remain more than curiosities which challenge or support one or another species concept (Mayr,

1963; Endler, 1977; Barton, 1979; Barton and Hewitt, 1985, 1989; Collins, 1991; Collins *et al.*, 1993; Barton and Gale, 1993; Moore and Price, 1993; Gill, 1997) and the study of their ecology and genetics are important in the understanding of speciation (Jiggins *et al.*, 1996). The data presented herein suggest various patterns indicative of interspecific hybridization including selective mating and/or selection against hybrids, apparent female hybrid inviability, and possible disruption of physiological mechanisms regulating diapause and voltinism (see Lorkovic, 1978, 1986; Oliver, 1979 for discussions of genetic disturbances possible with interspecific hybridization). Mating preferences may be based on ultraviolet reflectance of the pale wing bands because color, especially reds, may not be perceived (Porter, 1990) although courtship behavior of North American *Limenitis* is virtually unstudied (Ritland, 1990; Platt and Maudsley, 1994). These data also document a recent shift in the distribution in the frequencies of these *Limenitis* phenotypes within the Mono hybrid zone and, more importantly, provide a base from which future investigations may commence and be evaluated.

Future research must include additional samples from critical areas which are potentially inhabited by *Limenitis*, including the west slope of the Sweetwater Mountains, the Excelsior Mountains, southern Wassuk Mountains, the Pine Grove Hills, additional samples from the Pilot Mountains, and various ranges between Walker Lake and the Toiyabe Range. The Humboldt hybrid zone and surrounding regions require more study. In addition, more detailed examination needs to address continued sampling at known sites near and within the hybrid zone to document short- and long-term changes in phenotypic frequencies; identification of axes within the zone; finely partitioned samples for analyses of asymmetry and character concordance; breeding experiments designed to examine such factors as character inheritance, hybrid fitness, fecundity, and diapause control; behavioral studies to determine dominance, habitat preferences or partitioning, and mate choice; experiments to discover potential physiological differences between the taxa in their responses to heat, aridity, and/or other factors; and additional genetic studies including mitochondrial DNA. Similar studies need also to be conducted in regions of interaction north of the Great Basin.

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LITERATURE CITED

- Ae, S. A.
1980. The phylogeny of some *Papilio* species based on interspecific hybridization data. *Syst. Ent.* (London), 4:1-16.
- Austin, G. T.
1981. Book review: A catalogue/checklist of the butterflies of America north of Mexico. By L. D. Miller and F. M. Brown. *J. Res. Lepid.* (Beverly Hills), 19:241-243 (1980).
- 1985a. Nevada butterflies: preliminary checklist and distribution. *J. Lepid. Soc.* (Los Angeles), 39:95-118.
- 1985b. Lowland riparian butterflies of the Great Basin and associated areas. *J. Res. Lepid.* (Beverly Hills), 24:117-131.
1992. *Cercyonis pegala* (Fabricius) (Nymphalidae: Satyrinae) in the Great Basin: new subspecies and biogeography. *Bull. Allyn Mus.* (Sarasota), 135:1-59.
1998. *Limenitis archippus* (Cramer) (Lepidoptera: Nymphalidae) in western United States with special reference to its biogeography in the Great Basin. In T. C. Emmel (ed.), *Systematics of Western North American Butterflies*, 751-762. Gainesville: Mariposa Pr.
- Austin, G. T., and J. F. Emmel
1998. New subspecies of butterflies (Lepidoptera) from Nevada and California. In T. C. Emmel (ed.), *Systematics of Western North American Butterflies*, 501-522. Gainesville: Mariposa Pr.
- Austin, G. T., and D. D. Mullins
1983. A new *Limenitis weidemeyerii* from southeastern Arizona. *J. Res. Lepid.* (Beverly Hills), 22:225-228.
- Austin, G. T., and D. D. Murphy
1987. Zoogeography of Great Basin butterflies: patterns of distribution and differentiation. *Great Basin Nat.* (Provo), 47:186-201.
1988. Book review: A Field Guide to Western Butterflies, by J. W. Tilden and A. C. Smith. *J. Res. Lepid.* (Beverly Hills), 26:278-283 (1987).
- Avise, J. C., J. Arnold, R. M. Ball, E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reeb, and C. A. Saunders
1987. Intraspecific phylogeography: the mitochondrial DNA bridge between genetics and systematics. *Ann. Rev. Ecol. Syst.* (Palo Alto), 18:489-522.
- Bailowitz, R. A., and J. P. Brock
1991. *Butterflies of Southeastern Arizona*. Tucson: Sonoran Arthropod Studies. 342pp.
- Barrowclough, G. F.
1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. *Auk* (Lawrence), 97:655-668.
- Barton, N. H.
1979. The dynamics of hybrid zones. *Heredity* (Edinburgh), 43:333-339.
- Barton, N. H., and K. S. Gale
1993. Genetic analysis of hybrid zones. In R. G. Harrison (ed.), *Hybrid Zones and the Evolutionary Process*, 13-45. New York: Oxford Univ. Press. 364pp.
- Barton, N. H., and G. M. Hewitt
1983. Hybrid zones as barriers to gene flow. In G. S. Oxford and D. Rollinson (eds.), *Protein Polymorphism: Adaptive and Taxonomic Significance*, 341-359. Oxford: Blackwell. 405pp.
1985. Analysis of hybrid zones. *Ann. Rev. Syst.* (Palo Alto), 16:113-148.
1989. Adaptation, speciation and hybrid zones. *Nature* (London), 341:497-503.
- Bauer, D. L.
1954. An apparent hybrid *Limenitis* from Arizona. *Lepid. News* (Los Angeles), 8:129-130.
- Bell, D. A.
1996. Genetic differentiation, geographical variation and hybridization of gulls of the *Larus glaucescens-occidentalis* complex. *Condor* (Berkeley), 98:527-546.
1997. Hybridization and reproductive performance in gulls of the *Larus glaucescens-occidentalis* complex. *Condor* (Berkeley), 99:585-594.
- Benson, L., and R. S. Thompson
1987a. The physical record of lakes in the Great Basin. In W. F. Ruddiman and H. E. Wright, Jr. (eds.), *North America and Adjacent Oceans During the Last Deglaciation*, 241-260. Boulder, Colo.: Geological Soc. of America, vol. K-3. 501pp.
- 1987b. Lake-level variation in the Lahontan Basin for the past 50,000 years. *Quaternary Res.* (New York), 28:69-85.
- Bigelow, R. S.
1965. Hybrid zones and reproductive isolation. *Evol.* (Lancaster), 19:449-458.
- Bird, C. D., G. J. Hilchie, N. G. Kondla, E. M. Pike, and F. A. H. Sperling
1995. *Alberta Butterflies*. Edmonton: Prov. Museum of Alberta. 349pp.
- Brower, L. P.
1959. Speciation in butterflies of the *Papilio glaucus* group. II. Morphological relationships and hybridization. *Evol.* (Lancaster), 13:40-63.
- Brown, C.
1934. Notes on *Basilarchia lorquini* Bdv., form *fridayi* Gun. (Lepid. Nymphalidae). *Ent. News* (Lancaster), 45:205-206.
- Brown, I. L., and P. R. Ehrlich
1980. Population biology of the checkerspot butterfly, *Euphydryas chalcedona*. Structure of the Jasper Ridge colony. *Oecologia* (Berlin), 47:239-

- 251.
- Brown, J. W., H. G. Real, and D. K. Faulkner**
1992. *Butterflies of Baja California, Faunal Survey, Natural History, Conservation Biology*. Beverly Hills: Lepidoptera Research Foundation. 129pp.
- Brussard, P. F., and P. R. Ehrlich**
1970. The population structure of *Erebia episodea* (Lepidoptera: Satyrinae). *Ecol.* (Brooklyn), 51:119-129.
- Brussard, P. F., P. R. Ehrlich, and M. L. Singer**
1974. Adult movements and population structure of *Euphydryas editha*. *Evol.* (Lancaster), 28:408-415.
- Burns, K. J.**
1998. Molecular phylogenetics of the genus *Piranga*: implications for biogeography and the evolution of morphology and behavior. *Auk* (Lawrence), 115:621-634.
- Buth, D. G.**
1984. The application of electrophoretic data in systematic studies. *Ann. Rev. Ecol. Syst.* (Palo Alto), 15:501-522.
- Carpenter, G. D. H., and B. M. Hobby**
1944. On *Limenitis bredowii* Geyer (Lep., Nymphalidae) with description of a new subspecies and revival of another. A study in geographical distribution and speciation. *Trans. Roy. Ent. Soc. London*, 94:311-346.
- Chermock, R. L.**
1950. A generic revision of the Limenitini of the world. *Am. Midl. Nat.* (Notre Dame), 43:513-569.
- Cicero, C., and N. K. Johnson**
1995. Speciation in sapsuckers (*Sphyrapicus*): III. Mitochondrial-DNA sequence divergence at the Cytochrome-B locus. *Auk* (Lawrence), 112:547-563.
- Clark, S. H., and A. P. Platt**
1969. Influence of photoperiod on development and larval diapause in the viceroys butterfly, *Limenitis archippus*. *J. Insect Physiol.* (Oxford), 15:1951-1957.
- Clarke, C. A., and P. M. Sheppard**
1955. A preliminary report on the genetics of the *machaon* group of swallowtail butterflies. *Evol.* (Lancaster), 9:182-201.
- Clarke, C. A., and A. Willig**
1977. The role of alpha-ecdysone to break permanent diapause of female hybrids between *Papilio glaucus* L. female and *Papilio rutulus* Lucas male. *J. Res. Lepid.* (Beverly Hills), 16:245-248.
- Collins, M. M.**
1984. Genetics and ecology of a hybrid zone in *Hyalophora* (Lepidoptera: Saturniidae). *Univ. Calif. Publ. Entomol.* (Berkeley), 104:1-93.
1991. Speciation: a review of concepts and studies with special reference to the Lepidoptera. *J. Res. Lepid.* (Beverly Hills), 30:45-81.
- Collins, M. M., H. B. Britten, and V. Rivers**
1993. Allozyme analysis of a known hybrid zone between *Hyalophora euryalus* and *H. columbia gloveri* (Lepidoptera: Saturniidae) in the California Sierra Nevada. *J. Res. Lepid.* (Beverly Hills), 32:79-88.
- Comstock, J. A.**
1927. *Butterflies of California*. Los Angeles. 334pp.
- Corbin, K. W., and C. G. Sibley**
1977. Rapid evolution in orioles of the genus *Icterus*. *Condor* (Berkeley), 79:335-342.
- Coyne, J. A., and H. A. Orr**
1989a. Two rules of speciation. In D. Otte and J. A. Endler (eds.), *Speciation and its Consequences*, 180-207. Sunderland, Ma: Sinauer Assoc. 679pp.
1989b. Patterns of speciation in *Drosophila*. *Evol.* (Lancaster), 43:362-381.
- Craycraft, J.**
1989. Speciation and its ontogeny: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In D. Otte and J. A. Endler (eds.), *Speciation and its Consequences*, 28-59. Sunderland, Ma: Sinauer Assoc. 679pp.
- Cross, F. C.**
1937. Butterflies of Colorado. *Proc. Colo. Mus. Nat. Hist.* (Denver), 16:3-28.
- Davis, J. O.**
1982. Bits and pieces: the last 35,000 years in the Lahontan area. In D. B. Madsen and F. J. O'Connell (eds.), *Man and Environment in the Great Basin*, 53-75. Soc. Amer. Archaeol. Papers, no. 2. 242pp.
- Dornfeld, E. J.**
1980. *The Butterflies of Oregon*. Forest Grove, Or: Timber Pr. 276pp.
- dos Passos, C. F.**
1964. Synonymic list of Nearctic Rhopalocera. *Lepid. Soc. Mem.* (Los Angeles), 1:1-145.
- Ehrlich, P. R., A. E. Launer, and D. D. Murphy**
1984. Can sex ratio be defined or determined? The case of a population of checkerspot butterflies. *Amer. Nat.* (Salem), 124:527-539.
- Elias, S. A.**
1991. Insects and climate change. Fossil evidence from the Rocky Mountains. *BioSci.* (Washington), 41:552-559.
1992. Late Quaternary zoogeography of the Chihuahuan Desert insect fauna, based on fossil records from packrat middens. *J. Biogeogr.* (Oxford), 19:285-297.
1994. *Quaternary Insects and Their Environments*. Washington: Smithsonian Inst. Pr. 284pp.
- Elias, S. A., J. I. Mead, and L. D. Agenbroad**
1992. Late Quaternary arthropods from the Colorado Plateau, Arizona and Utah. *Great Basin Nat.* (Provo), 52:59-67.
- Elias, S. A., and T. R. Van Devender**
1992. Insect fossil evidence of late Quaternary environments in the northern Chihuahuan Desert of Texas and New Mexico: comparisons with the paleobotanical record. *Southwest. Nat.* (Lubbock), 37:101-116.
- Emmel, J. F., T. C. Emmel, and S. O. Mattoon**
1998. The types of California butterflies named by Jean Alphonse Boisduval: designation of lectotypes and a neotype, and fixation of type localities. In T. C. Emmel (ed.), *Systematics of Western North American Butterflies*, 3-78. Gainesville: Mariposa Pr.
- Emmel, J. F., O. Shields, and D. E. Breedlove**
1970. Larval foodplant records for North American Rhopalocera. *J. Res. Lepid.* (Beverly Hills), 9:233-242.
- Emmel, T. C., and J. F. Emmel**
1973. *The Butterflies of Southern California*. Los Angeles: Nat. Hist. Mus. Los Angeles Co. 139pp.
- Endler, J. A.**
1977. *Geographic Variation, Speciation and Clines*. Princeton: Princeton Univ. Pr. 246pp.
1986. *Natural Selection in the Wild*. Princeton: Princeton Univ. Pr. 336pp.
- Ferris, C. D. (ed.)**
1989. Supplement to: A catalogue/checklist of the butterflies of America north of Mexico. *Lepid. Soc. Mem.* (Los Angeles), 3:1-103.
- Ferris, C. D., and F. M. Brown (eds.)**
1981. *Butterflies of the Rocky Mountain States*. Norman: Univ. Oklahoma Pr. 442pp.
- Field, W. L.**
1914. Hybrid butterflies of the genus *Basilarchia*. *Psyche* (Cambridge, Ma), 21:115-117.
- Freeman, S., and R. M. Zink**
1995. A phylogenetic study of the blackbirds based on variation in mitochondrial DNA restriction sites. *Syst. Biol.* (Washington), 44:409-420.
- Freitas, A. V. L.**
1993. Biology and population dynamics of *Placidula euryanassa*, a relict ithomiine butterfly (Nymphalidae: Ithomiinae). *J. Lepid. Soc.* (Los Angeles), 47:87-105.
1996. Population biology of *Heterosais odessa* (Nymphalidae) and its associated Atlantic Forest Ithomiinae community. *J. Lepid. Soc.* (Los Angeles), 50:273-289.
- Gage, E. V.**
1970. A record of a naturally occurring *Limenitis* hybrid (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 24:270.
- Gardiner, B. O. C.**
1963. Genetic and environmental variation in *Pieris brassicae*. *J. Res. Lepid.* (Beverly Hills), 2:127-136.
- Garth, J. S., and J. W. Tilden**
1963. Yosemite butterflies. *J. Res. Lepid.* (Beverly Hills), 2:1-96.
1986. *California Butterflies*. Berkeley: Univ. Calif. Pr. 246pp.
- Gill, F. B.**
1980. Historical aspects of hybridization between blue-winged and golden-winged warblers. *Auk* (Lawrence), 97:1-18.
1997. Local cytonuclear extinction of the golden-winged warbler. *Evol.* (Lancaster), 51:519-525.
- Grant, B. R., and P. R. Grant**
1993. Evolution of Darwin's finches caused by a rare climatic event. *Proc. Roy. Soc. Lond.*, (B) 251:111-117.
- Grant, P. R., and B. R. Grant**
1992. Hybridization and bird species. *Science* (Washington), 256:193-197.
- Grayson, D. K.**
1993. *The Desert's Past. A Natural Prehistory of the Great Basin*. Washington: Smithsonian Inst. Pr. 356pp.
- Grey, L. P., and A. H. Moeck**
1962. Notes on overlapping subspecies. I. An example in *Speyeria zerene* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 16: 81-97.
- Gunder, J. D.**
1932. New Rhopalocera (Lepidoptera). *Can. Ent.* (Ottawa), 64:276-284.

Hagen, R. H., and J. B. Scriber

1989. Sex-linked diapause, color and allozyme loci in *Papilio glaucus*: linkage analysis and significance in a hybrid zone. *J. Heredity* (Washington), 80:179-185.
1995. Sex chromosomes and speciation in tiger swallowtails. In J. M. Scriber, Y. Tsubaki, and R. C. Lederhouse (eds.), *Swallowtail Butterflies: their Ecology and Evolutionary Biology*, 211-227. Gainesville: Scientific Publ. 459pp.

Haldane, J. B. S.

1922. Sex-ratio and unisexual sterility in hybrid animals. *J. Genetics* (Lancaster), 12:101-109.

Hall, W. E., C. A. Olson, and T. R. Van Devender

1989. Late Quaternary and modern arthropods from the Ajo Mountains of southwestern Arizona. *Pan-Pac. Ent.* (San Francisco), 65:322-347.

Hammond, P. C.

1986. A rebuttal to the Arnold classification of *Speyeria callippe* (Nymphalidae) and defense of the subspecies concept. *J. Res. Lepid.* (Beverly Hills), 24:197-208 (1985).
1991. Patterns of geographic variation and evolution in polytypic butterflies. *J. Res. Lepid.* (Beverly Hills), 29:54-76 (1990).

Harris, A. H.

1990. Fossil evidence bearing on southwestern mammalian biogeography. *J. Mamm.* (Baltimore), 71:219-229.

Harrison, R. G.

1991. Molecular changes at speciation. *Ann. Rev. Ecol. Syst.* (Palo Alto), 22:281-308.
1993. *Hybrid zones and the Evolutionary Process*. New York: Oxford Univ. Pr. 364pp.

Hong, J. W., and A. P. Platt

1975. Critical photoperiod and day-length threshold differences between northern and southern populations of the butterfly *Limenitis archippus*. *J. Insect Physiol.* (Oxford), 21:122-129.

Hovanitz, W.

1949. Increased variability in populations following natural hybridization. In G. L. Jepson, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution*, 339-355. Princeton: Princeton Univ. Pr. 474pp.

Howe, W. H. (ed.)

1975. *The Butterflies of North America*. Garden City: Doubleday. 633pp.

Hubbard, J. P.

1974. Avian evolution in the aridlands of North America. *Living Bird* (Ithaca), 12:155-196.

Hubbs, C. L., and R. R. Miller

1948. The zoological correlation between fish distribution and hydrographic history in the desert basins of western United States. *Bull. Univ. Utah Biol. Ser.* (Salt Lake City), 38:17-166.

Jiggins, C. D., W. O. McMillan, W. Neukirchen, and J. Mallet.

1996. What can hybrid zones tell us about speciation? The case of *Heliconius erato* and *H. himeris* (Lepidoptera: Nymphalidae). *Biol. J. Linn. Soc.* (London), 59:221-242.

Johnson, K.

1973. The butterflies of Nebraska. *J. Res. Lepid.* (Beverly Hills), 11:1-64 (1972).

Johnson, N. K.

1978. Patterns of avian geography and speciation in the intermountain region. *Great Basin Nat. Mem.* (Provo), 2:137-159.

Johnson, N. K., and J. A. Marten

1988. Evolutionary genetics of flycatchers. II. Differentiation in the *Empidonax difficilis* complex. *Auk* (Lawrence), 105:177-191.

Johnson, N. K., and R. M. Zink

1983. Speciation in sapsuckers (*Sphyrapicus*): I. Genetic differentiation. *Auk* (Lawrence), 100:871-884.

Jones, J. R. J.

1951. An annotated check list of the Macrolepidoptera of British Columbia. *Ent. Soc. Br. Col., Occas. Pap.* (Victoria), 1:1-143.

Kean, P. J., and A. P. Platt

1973. Methods for externally sexing mature larvae and pupae of *Limenitis* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 27:122-129.

Klots, A. B.

1956. Lepidoptera. In S. L. Tuxen (ed.), *Taxonomist's Glossary of Genitalia in Insects*, 97-111. Copenhagen: Munksgaard. 283pp.

Kohler, S.

1980. Checklist of Montana butterflies (Rhopalocera). *J. Lepid. Soc.* (Los Angeles), 34:1-19.

Layberry, R. A., P. W. Hall, and J. D. Lafontaine

1998. *The Butterflies of Canada*. Toronto: Univ. Toronto Pr. 280pp.

Lorkovic, Z.

1978. Types of hybrid sterility in diurnal Lepidoptera: speciation and

taxonomy. *Acta Ent. Jugoslav.* (Zagreb), 14:13-26.

1986. Enzyme electrophoresis and interspecific hybridization in Pieridae (Lepidoptera). *J. Res. Lepid.* (Beverly Hills), 24:334-358 (1985).

Martin, L. M., and S. F. Truxal

1955. A list of North American Lepidoptera in the Los Angeles County Museum. Part I. Butterflies (suborder Rhopalocera). *Los Angeles Co. Mus. Sci. Series* (Los Angeles), no. 18, Zool., no. B.

Mayr, E.

1963. *Animal Species and Evolution*. Cambridge, Ma: Belknap Pr. 797pp.
1982. *The Growth of Biological Thought*. Cambridge, Ma: Belknap Pr. 974pp.

McDunnough, J.

1938. Check list of the Lepidoptera of Canada and the United States of America. Part I. Macrolepidoptera. *Mem. So. Calif. Acad. Sci.* (Los Angeles), 1:1-272.

McKittrick, M. C., and R. M. Zink

1988. Species concepts in ornithology. *Condor* (Berkeley), 90:1-14.

Mengel, R. E.

1964. The probable history of species formation of some northern wood warblers (Parulidae). *Living Bird* (Ithaca), 3:9-43.
1970. The North American central plains as an isolating agent in bird speciation. In W. Dart, Jr. and J. K. Jones, Jr. (eds.), *Pleistocene and Recent Environments of the Central Great Plains*, 279-340. Lawrence: Univ. Kansas, Dept. Geol. (Spec. Publ. 3).

Mifflin, M. D., and M. M. Wheat

1979. Pluvial lakes and estimated pluvial climates of Nevada. *Bull. Nevada Bur. Mines and Geology* (Reno), 94:1-57.

Miller, L. D., and F. M. Brown

1981. A catalogue/checklist of the butterflies of America north of Mexico. *Lepid. Soc. Mem.* (Los Angeles), 2:1-280.

Moore, W. S.

1977. An evaluation of narrow hybrid zones in vertebrates. *Qtr. Rev. Biol.* (Baltimore), 52:263-277.

Moore, W. S., and D. B. Buchanan

1985. Stability of the northern flicker hybrid zone in historical times: implications for adaptive speciation theory. *Evol.* (Lancaster), 41:135-151.

Moore, W. S., and J. T. Price

1993. Nature of selection in the northern flicker hybrid zone and its implications for speciation theory. In R. G. Harrison (ed.), *Hybrid Zones and the Evolutionary Process*, 196-225. New York: Oxford Univ. Pr. 364pp.

Murphy, D. D., and P. R. Ehrlich

1983. Biosystematics of the *Euphydryas* of the Great Basin with the description of a new subspecies. *J. Res. Lepid.* (Beverly Hills), 22:254-261.

Nakahara, W.

1924. A revision of the genus *Basilarchia* (Rhopalocera: Nymphalidae). *Bull. Brooklyn Ent. Soc.* (Lancaster), 19:166-180.

Noonan, G. R.

1990. Biogeographical patterns of North American *Harpalus* Latreille (Insecta: Coleoptera: Carabidae). *J. Biogeogr.* (Oxford), 17:583-614.

Oliver, C. G.

1979. Genetic differentiation and hybrid viability within and between some Lepidoptera species. *Amer. Nat.* (Salem), 114:681-694.

Orsak, L. J.

1977. The butterflies of Orange County, California. *Univ. Calif., Irvine. Mus. Syst. Biol., Res. Ser.* (Irvine), 4:1-349.

Parsons, T. J., S. L. Olson, and M. J. Braun

1993. Unidirectional spread of secondary sexual plumage traits across an avian hybrid zone. *Science* (Washington), 260:1643-1646.

Perkins, E. M., and E. V. Gage

1970. On the occurrence of *Limenitis archippus* x *L. lorquini* hybrids (Nymphalidae). *J. Res. Lepid.* (Beverly Hills), 9:223-226.

Perkins, E. M., Jr., and J. S. Garth

1973. *Limenitis weidemeyerii angustifascia* X *L. astyanax arizonensis* = ? *ab. doudoroffi* (Gunder), 1934 in the Allan Hancock Foundation collection (Nymphalidae). *J. Res. Lepid.* (Beverly Hills), 11:229-234. (1972)

Perkins, E. M., Jr., and S. F. Perkins

1966. A review of the *Limenitis lorquini* complex (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 20:172-176.

Perkins, S. F., and E. M. Perkins, Jr.

1967. Revision of the *Limenitis weidemeyerii* complex, with description of a new subspecies (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 21:213-234.

Pinel, H. W., and N. G. Kondla

1985. Skippers and butterflies of the Police Coulee area, Alberta. *Blue Ja*

- (Edmonton), 43:213-223.
- Platt, A. P.**
1975. Monomorphic mimicry in Nearctic *Limenitis* butterflies: experimental hybridization of the *L. arthemis-astyanax* complex with *L. archippus*. *Evol.* (Lancaster), 29:120-141.
1983. Evolution of North American admiral butterflies. *Bull. Ent. Soc. Am.* (Lanham), 29:10-22.
- Platt, A. P., and L. P. Brower**
1968. Mimetic versus disruptive coloration in intergrading populations of *Limenitis arthemis* and *astyanax* butterflies. *Evol.* (Lancaster), 22:699-718.
- Platt, A. P., S. D. Frearson, and P. N. Graves**
1970. Statistical comparisons of valval structure within and between populations of North American *Limenitis* (Nymphalidae). *Can. Ent.* (Ottawa), 102:513-533.
- Platt, A. P., and J. C. Greenfield, Jr.**
1971. Inter-specific hybridization between *Limenitis arthemis astyanax* and *L. archippus* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 24:278-284.
- Platt, A. P., and S. J. Harrison**
1994. First record of an heterotic adult female hybrid *Limenitis* (*Basilarchia*) "rubicus" (Strecker) (Lepidoptera: Nymphalidae). *Ent. News* (Philadelphia), 105:33-38.
- Platt, A. P., and J. R. Maudsley**
1994. Continued interspecific hybridization between *Limenitis* (*Basilarchia*) *arthemis astyanax* and *L. (B.) archippus* in the southeastern U.S. (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 48:190-198.
- Platt, A. P., G. W. Rawson, and G. Balogh**
1978. Inter-specific hybridization involving *Limenitis archippus* and its congeneric species (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 32:289-303.
- Porter, A. H.**
1988. Courtship of a model (*Adelpha*; Nymphalidae) by its probable Batesian mimic (*Limenitis*; Nymphalidae). *J. Res. Lepid.* (Beverly Hills), 26:255-256.
1989. Genetic evidence for reproductive isolation between hybridizing *Limenitis* butterflies (Lepidoptera: Nymphalidae) in southwestern New Mexico. *Amer. Midl. Nat.* (Notre Dame), 122:275-280.
1990. Testing nominal species boundaries using gene flow statistics: the taxonomy of two hybridizing admiral butterflies (*Limenitis*; Nymphalidae). *Syst. Zool.* (Lawrence), 39:131-147.
- Porter, A. H., and A. M. Shapiro**
1990. The lock-and-key hypothesis: lack of mechanical isolation in a butterfly hybrid zone. *Ann. Ent. Soc. Am.* (College Park), 83:107-114.
1991. Genetics and biogeography of the *Oeneis chryxus* complex (Satyrinae) in California. *J. Res. Lepid.* (Beverly Hills), 28:263-276 (1989).
- Poulton, E. B.**
1909. Mimicry in butterflies of North America. *Ann. Ent. Soc. Amer.* (Lanham), 2:203-242.
- Pyle, R. M.**
1981. *The Audubon Society Field Guide to North American Butterflies*. New York: A. A. Knopf. 916pp.
- Rand, A. L.**
1948. Glaciation, an isolating factor in speciation. *Evol.* (Lancaster), 2:314-321.
- Remington, C. L.**
1958. Genetics of populations of Lepidoptera. *Proc. 10th Int. Cong. Ent.*, 2:787-805.
1968. Suture-zones of hybrid interaction between recently joined biotas. *Evol. Biol.* (New York), 2:321-428.
- Reveal, J. L.**
1979. Biogeography of the intermountain region, a speculative appraisal. *Mentzelia* (Reno), 4:1-92.
- Riddle, B. R.**
1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): the late Cenozoic development of a North American aridlands rodent guild. *J. Mamm.* (Baltimore), 76:283-301.
- Rising, J. D.**
1973. Morphological variation and status of the orioles, *Icterus galbula*, *I. bullockii*, and *I. abeillei*, in the northern Great Plains and in Durango, Mexico. *Can. J. Zool.* (Ottawa), 51:1267-1273.
1983. The progress of oriole hybridization in Kansas. *Auk* (Lawrence), 100:885-897.
- Ritland, D. B.**
1990. Localized interspecific hybridization between mimetic *Limenitis* butterflies (Nymphalidae) in Florida. *J. Lepid. Soc.* (Los Angeles), 44:163-173.
- Rohwer, S., and C. Wood**
1998. Three hybrid zones between hermit and Townsend's warblers in Washington and Oregon. *Auk* (Lawrence), 115:284-310.
- Royer, R. A.**
1988. *Butterflies of North Dakota, an Atlas and Guide*. Minot, ND: Minot St. Univ. 192pp.
- Scott, J. A.**
1974. Survey of ultraviolet reflectance of Nearctic butterflies. *J. Res. Lepid.* (Beverly Hills), 12:151-160 (1973).
1986. *The Butterflies of North America: a Natural History and Field Guide*. Stanford: Stanford Univ. Pr. 583pp.
- Scriber, J. M., R. V. Dowell, R. C. Lederhouse, and R. H. Hagen**
1990. Female color and sex ratio in hybrids between *Papilio glaucus* and *P. eurymedon*, *P. rutulus*, and *P. multicaudatus* (Papilionidae). *J. Lepid. Soc.* (Los Angeles), 44:229-244.
- Shapiro, A. M., and J. D. Biggs**
1968. A hybrid *Limenitis* from New York. *J. Res. Lepid.* (Beverly Hills), 7:149-152.
- Shields, O.**
1963. A trip into California and Oregon for *Speyeria*. *J. Lepid. Soc.* (Los Angeles), 17:111-116.
- Short, L. L.**
1965. Hybridization in the flickers (*Colaptes*) of North America. *Bull. Amer. Mus. Nat. Hist.* (New York), 129:307-428.
1969. Taxonomic aspects of avian hybridization. *Auk* (Lawrence), 86:84-105.
- Simpson, R. G., and D. Pettus**
1976. Records of *Limenitis* hybrids from Colorado. *J. Res. Lepid.* (Beverly Hills), 15:163-168.
- Sperling, F. A. H.**
1987. Evolution of the *Papilio machaon* species group in western Canada. *Quaest. Ent.*, 23:198-315.
1990. Natural hybrids of *Papilio* (Insecta: Lepidoptera): poor taxonomy or interesting evolutionary problem? *Can. J. Zool.* (Ottawa), 68:1790-1799.
1993. Mitochondrial DNA phylogeny of the *Papilio machaon* species group (Lepidoptera: Papilionidae). *Mem. Ent. Soc. Can.* (Ottawa), 165:233-242.
- Stanford, R. E., and P. A. Opler**
1993. *Atlas of Western USA Butterflies, Including Adjacent Parts of Canada and Mexico*. Denver and Fort Collins. 275pp.
- Thormin, T. W., N. G. Kondla, and C. D. Bird**
1980. Further records of skippers and butterflies from the Milk River-Lost River area of southeastern Alberta. *Blue Jay* (Edmonton), 38:5-10.
- Tilden, J. W., and A. C. Smith**
1986. *A Field Guide to Western Butterflies*. Boston: Houghton Mifflin. 368 pp.
- Toliver, M. E., and R. Holland**
1991. *Distribution of Butterflies in New Mexico (Lepidoptera: Hesperioidea and Papilionoidea)*. Albuquerque. 239pp. (1977)
- Tyler, H. A., K. S. Brown, Jr., and K. H. Wilson**
1994. *Swallowtail Butterflies of the Americas: a Study in Biological Dynamics, Ecological Diversity, Biosystematics, and Conservation*. Gainesville: Scientific Publ. 376pp.
- Van Devender, T. R., R. S. Thompson, and J. L. Betencourt**
1987. Vegetation history of the deserts of southwestern North America; the nature and timing of the late Wisconsin-Holocene transition. In W. F. Ruddiman and H. E. Wright, Jr. (eds.), *North America and Adjacent Oceans During the Last Deglaciation*, 323-352. Boulder: Geological Soc. Amer. (vol. K-3). 501pp.
- Wake, D. B., S. Y. Yang, and T. J. Papenfuss**
1980. Natural hybridization and its evolutionary implications in Guatemalan plethodontid salamanders, genus *Bolitoglossa*. *Herpetol.* (Lawrence), 36:335-345.
- Weide, D. L.**
1976. The altithermal as an archaeological "non-problem" in the Great Basin. *Nevada Archaeol. Survey, Research Paper* (Carson City), 8:175-184.
- Wells, P. V.**
1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecol. Monog.* (Durham), 53:341-382.
- West, D. A., and C. A. Clarke**
1988. Suppression of the black phenotype in females of *P. glaucus* group (Papilionidae). *J. Res. Lepid.* (Beverly Hills), 26:187-200.
- White, R. R.**
1974. Food plant defoliation and larval starvation of *Euphydryas editha*. *Oecologia* (Berlin), 14:307-315.
- Woodruff, D. S.**
1989. Genetic anomalies associated with *Cerion* hybrid zones: the origin and

maintenance of new electromorphic variants called hybrizynes. *Biol. J. Linn. Soc.* (London), 36:281-294.

Zar, J. H.

1974. *Biostatistical Analysis*. Englewood Cliffs: Prentice-Hall. 620pp.

Zink, R. M.

1994. The geography of mitochondrial DNA variation, population structure, hybridization, and species limits in the fox sparrow (*Passerella iliaca*). *Evol.* (Lancaster), 48:96-111.

Zink, R. M., and S. J. Hackett

1988. Historical biogeographic patterns in the avifauna of North America. In H. Ouellet (ed.), *Acta XIX Congressus Internationalis Ornithologici*, 2574-2580. Ottawa: Natl. Mus. Nat. Sci.

Zink, R. M., and M. C. McKittrick

1995. The debate over species concepts and its implications for ornithology. *Auk* (Lawrence), 112:701-719.

APPENDIX Ia. Wing length significance for male *Limenitis* (numbers in bold are significant, data above diagonal are values of *t* for mean wing length, below are values for *F* for wing length variance; na = not applicable, NHZ = non-hybrid zone, MHZ = Mono hybrid zone, HHZ = Humboldt hybrid zone).

	N	NHZ <i>L. lorq.</i>	NHZ <i>L. weid.</i>	MHZ <i>L. lorq.</i>	MHZ <i>L. weid.</i>	MHZ "fridayi"	HHZ <i>L. weid.</i>	HHZ "fridayi"
NHZ <i>L. lorquini</i>	165	-	25.66	2.53	na	11.54	na	142.24
NHZ <i>L. weidemeyerii</i>	183	1.13	-	na	2.99	9.39	1.12	25.86
MHZ <i>L. lorquini</i>	131	1.01	na	-	17.34	8.72	na	na
MHZ <i>L. weidemeyerii</i>	115	na	1.13	1.02	-	6.44	0	na
MHZ "fridayi"	120	1.69	1.50	1.71	1.69	-	na	4.14
HHZ <i>L. weidemeyerii</i>	11	na	1.48	na	1.67	na	-	0.02
HHZ "fridayi"	47	1.25	1.11	na	na	1.34	1.33	-

APPENDIX Ib. Wing length significance for female *Limenitis* (numbers in bold are significant, data above diagonal are values of *t* for mean wing length, below are values for *F* for wing length variance; na = not applicable, nd = no data, NHZ = non-hybrid zone, MHZ = Mono hybrid zone, HHZ = Humboldt hybrid zone).

	N	NHZ <i>L. lorq.</i>	NHZ <i>L. weid.</i>	MHZ <i>L. lorq.</i>	MHZ <i>L. weid.</i>	MHZ "fridayi"	HHZ <i>L. weid.</i>	HHZ "fridayi"
NHZ <i>L. lorquini</i>	54	-	11.77	1.38	na	3.75	na	19.18
NHZ <i>L. weidemeyerii</i>	40	1.26	-	na	1.21	2.56	nd	2.11
MHZ <i>L. lorquini</i>	25	1.05	na	-	5.84	2.59	na	na
MHZ <i>L. weidemeyerii</i>	14	na	1.96	1.64	-	1.72	nd	na
MHZ "fridayi"	8	1.45	1.16	1.39	2.27	-	na	0.78
HHZ <i>L. weidemeyerii</i>	-	na	nd	na	nd	na	-	nd
HHZ "fridayi"	14	1.21	1.04	na	na	1.20	nd	-

APPENDIX Ic. Wing score significance for male + female *Limenitis* (numbers in bold are significant, data above diagonal are values of *t* for mean score, below are values for *F* for score variance; na = not applicable, NHZ = non-hybrid zone, MHZ = Mono hybrid zone, HHZ = Humboldt hybrid zone).

	N	NHZ <i>L. lorq.</i>	NHZ <i>L. weid.</i>	MHZ <i>L. lorq.</i>	MHZ <i>L. weid.</i>	MHZ "fridayi"	HHZ <i>L. weid.</i>	HHZ "fridayi"
NHZ <i>L. lorquini</i>	288	-	225.37	7.39	na	35.83	na	55.91
NHZ <i>L. weidemeyerii</i>	231	1.63	-	na	4.55	30.98	12.42	28.97
MHZ <i>L. lorquini</i>	168	1.95	na	-	149.20	25.32	na	na
MHZ <i>L. weidemeyerii</i>	142	na	1.40	1.43	-	25.27	0.54	na
MHZ "fridayi"	131	27.49	16.92	13.82	19.83	-	na	3.73
HHZ <i>L. weidemeyerii</i>	14	na	1.77	na	1.33	na	-	6.68
HHZ "fridayi"	65	14.07	8.66	na	na	1.92	15.29	-

APPENDIX Id. Chi-square values for frequencies of form "eavesii" in populations of *Limenitis* (numbers in bold are significant, data above diagonal are values for males, below are values for females; na = not applicable, NHZ = non-hybrid zone, MHZ = Mono hybrid zone, HHZ = Humboldt hybrid zone). No calculations were made for *L. lorquini* or *L. weidemeyerii* from the Humboldt hybrid zone since there were no meaningful data.

	N	NHZ	NHZ	MHZ	MHZ	MHZ	HHZ
	(males)	<i>L. lorq.</i>	<i>L. weid.</i>	<i>L. lorq.</i>	<i>L. weid.</i>	"fridayi"	"fridayi"
NHZ <i>L. lorquini</i>	168	-	2.13	0.83	na	2.62	3.61
NHZ <i>L. weidemeyerii</i>	190	18.14	-	na	1.90	0.07	0.67
MHZ <i>L. lorquini</i>	140	0.06	na	-	2.90	0.47	na
MHZ <i>L. weidemeyerii</i>	133	na	0.38	6.19	-	1.03	-
MHZ "fridayi"	134	4.92	0.26	4.52	0	-	1.27
HHZ "fridayi"	51	5.74	0.59	na	na	0.01	-
N (females)	-	54	40	26	15	9	14

APPENDIX Ie. Chi-square values for frequencies of sex ratios in populations of *Limenitis* (numbers in bold are significant; na = not applicable, NHZ = non-hybrid zone, MHZ = Mono hybrid zone, HHZ = Humboldt hybrid zone).

	N	NHZ	NHZ	MHZ	all MHZ	MHZ	HHZ	all HHZ	HHZ
		<i>L. lorq.</i>	<i>L. weid.</i>	<i>L. lorq.</i> + <i>L. weid.</i>	indiv.	"fridayi"	<i>L. lorq.</i> + <i>L. weid.</i>	indiv.	"fridayi"
<i>L. archippus</i>	329	0.18	<0.01	na	na	na	na	na	na
NHZ <i>L. lorquini</i>	409	-	0.37	4.44	15.02	23.50	0.01	0.02	0.02
NHZ <i>L. weidemeyerii</i>	190		-	2.95	12.95	21.38	0.01	0.03	0.03
NHZ <i>L. lorq.</i> + <i>L. weid.</i>	1043			4.27	17.14	23.53	<0.01	<0.01	<0.01
MHZ <i>L. lorq.</i> + <i>L. weid.</i>	341			-	na	11.74	0.28	na	na
all MHZ individuals	508				-	na	na	4.52	na
MHZ "fridayi"	167					-	na	na	13.66
HHZ <i>L. lorq.</i> + <i>L. weid.</i>	14						-	na	<0.01
all HHZ individuals	79							-	na
HHZ "fridayi"	65								-

APPENDIX If. Genital score significance for male *Limenitis* (numbers in bold are significant, data above diagonal are values of *t* for mean score, below are values for *F* for score variance; na = not applicable, NHZ = non-hybrid zone, MHZ = Mono hybrid zone).

	N	NHZ	NHZ	MHZ	MHZ	MHZ
		<i>L. lorq.</i>	<i>L. weid.</i>	<i>L. lorq.</i>	<i>L. weid.</i>	"fridayi"
NHZ <i>L. lorquini</i>	10	-	32.27	2.18	na	4.80
NHZ <i>L. weidemeyerii</i>	17	1.18	-	na	5.88	9.85
MHZ <i>L. lorquini</i>	106	5.78	na	-	18.25	7.93
MHZ <i>L. weidemeyerii</i>	116	na	11.28	1.29	-	8.95
MHZ "fridayi"	114	9.14	13.78	1.60	na	-