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LOCALIZED INTERSPECIFIC HYBRIDIZATION BETWEEN MIMETIC *LIMENITIS* BUTTERFLIES (NYMPHALIDAE) IN FLORIDA

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ABSTRACT. Viceroy and red-spotted purple butterflies (*Limenitis archippus* and *Limenitis arthemis astyanax*) are broadly sympatric in the eastern United States, but very rarely interbreed in most areas. However, the butterflies hybridize relatively frequently in northern Florida and southern Georgia; I recorded seven hybrid individuals in a 13-month period in 1986–87, as well as two mating pairs of viceroy and red-spotted purple. I propose that this elevated hybridization is due to a unique combination of ecological and biogeographic (genetic) factors, which interact to locally weaken the premating reproductive barrier between viceroys and red-spotted purples. First, habitat overlap (and therefore encounter rate) between the two species of butterflies is unusually high because they share a larval foodplant. Second, red-spotted purples may be less discriminating in mate choice because of their comparative rarity (viceroy : red-spotted purple ratio is 9:1), which must affect the economics of mate choice. Finally, viceroys in northern Florida also may be prone to mismating because they represent intraspecific hybrids between two geographic races (*L. a. archippus* and *L. a. floridensis*), the latter of which is largely allopatric from red-spotted purples and may not have evolved effective pre-mating isolating mechanisms. This combination of ecological and genetic factors apparently creates a unique conduit of gene flow (introgression) between red-spotted purples and viceroys.

Additional key words: *Limenitis archippus, Limenitis arthemis astyanax, Salix caroliniana,* introgression, mate choice.

Interspecific hybrids are often striking individuals, blending the morphological, behavioral, and ecological traits of two parental types into novel patterns. Studying natural hybridization can elucidate ecological and genetic barriers between taxa and plays an important and continuing role in the development of evolutionary thought and speciation theory (e.g., Wallace 1889, Fisher 1930, Mayr 1963, Barton & Hewitt 1985). "Hybridization" encompasses a spectrum of phenomena, ranging from clinal intergradation involving geographic subspecies to *bona fide* hybridization between nominally distinct species. Most investigations of interspecific hybridization have focussed on "hybrid zones" (geographically-limited regions of contact and interbreeding between parapatric species: e.g., Remington 1968). However, isolated interspecific hybrids also occur between species that are broadly sympatric; two species may be well-isolated reproductively in some locales but interbreed in others (e.g., the sparrows *Passer domesticus* and *P. hispaniolensis* in Europe: Mayr 1963).

In contrast to the extensive literature on hybrid zones between parapatric taxa, few studies have addressed the causes and implications of such localized hybridization events involving distinct, broadly-sympat-

ric species. In this paper, I consider a case involving southeastern United States populations of two congeneric nymphalid butterflies: the viceroy, *Limenitis archippus* (Cramer), and the red-spotted purple, *L. arthemis astyanax* (Fabricius) (Nymphalidae).

Parapatric taxa of the genus *Limenitis* provide the best examples of interspecific hybridization among North American butterflies. *Limenitis* taxonomy is currently being reassessed (Porter 1989), but four nominal species are generally recognized in North America: *L. arthemis* (Drury), *L. archippus*, *L. weidemeyerii* (Edwards), and *L. lorquini* (Boisduval). Each of these hybridizes (sometimes frequently) with its parapatric congeners in areas where they meet in narrow contact zones (e.g., Remington 1968, Platt 1983, Porter 1989). In contrast, the two taxa that are most broadly sympatric—the viceroy (*L. archippus*) and the red-spotted purple (*L. arthemis astyanax*)—interbreed surprisingly infrequently. From 1872 to present, only 33 natural hybrids between these butterflies have been reported, all as single, isolated individuals (Platt 1983, 1987a). These hybrids are designated as form "rubidus" (Strecker 1878). Platt (1975) has crossed viceroys and red-spotted purples in the laboratory, confirming that wild-collected "rubidus" phenotypes are indeed interspecific hybrids (Platt & Greenfield 1971).

The rarity of "rubidus" hybrids in nature presumably is due to a combination of genetic incompatibility (evidenced by a deficit of females in laboratory crosses: Platt 1987a) and effective premating reproductive isolation of the two butterflies resulting from morphological, behavioral, and habitat differences (Platt et al. 1978). In addition, it has been suggested that "rubidus" may be selected against by attracting increased adult predation (Platt & Greenfield 1971). Viceroys and red-spotted purples both mimic distasteful butterflies (viceroys resemble monarchs, *Danaus plexippus* (L.), and queens, *Danaus gilippus* (Cramer) (Danainae); red-spotted purples mimic the pipevine swallowtail, *Battus philenor* (L.) (Papilionidae)). The efficacy of each mimetic pattern has been experimentally demonstrated (Brower 1958, Platt et al. 1971, Ritland unpubl.). The intermediate coloration of "rubidus" hybrids, however, does not closely approximate either the monarch or the pipevine swallowtail, so the hybrids may lose their mimetic protection (although this hypothesis is untested).

HYBRIDIZATION RECORDS

Collection records of individual "rubidus" hybrids extend from New Mexico to New York, but only two individuals have been reported previously from the southeastern U.S. (Platt et al. 1978, Platt 1987a). I now report seven new "rubidus" hybrids discovered in Florida and

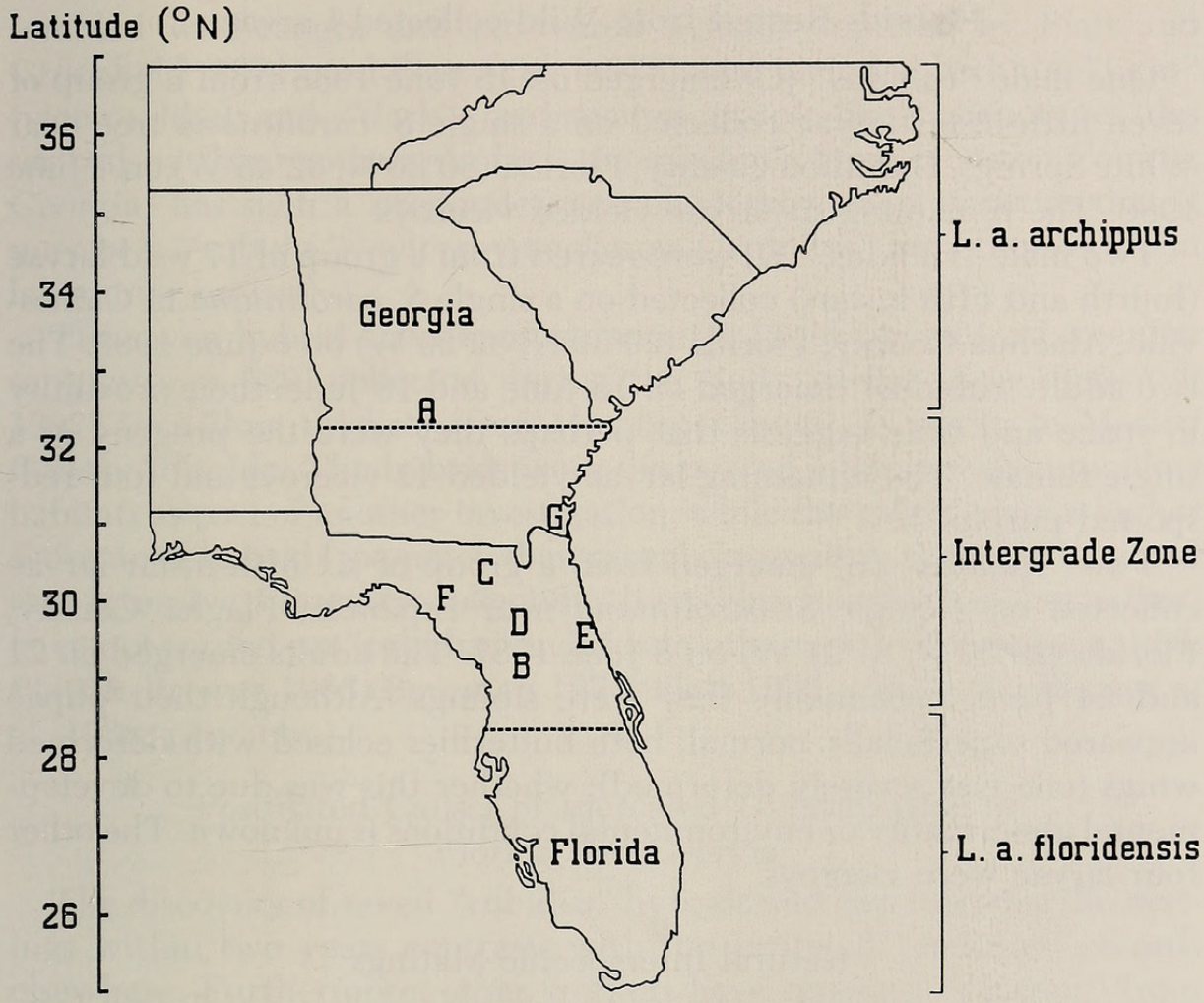

FIG. 1. Collections and observations of "rubidus" hybrids (A–E) and interspecific matings (F–G) between viceroys (*Limenitis archippus*) and red-spotted purples (*L. arthemis astyanax*) in 1986–88. Letters refer to individual records described in text. Also indicated (by two dotted lines) is the approximate location of a phenotypic intergrade zone between northern viceroys (*Limenitis a. archippus*) and Florida viceroys (*L. a. floridensis*) (Ritland 1990).

Georgia between June 1986 and July 1987, as well as two observations of interspecific mating between viceroy and red-spotted purple. Each independent hybridization event is designated by a letter, and the corresponding collection locales are depicted in Fig. 1.

Hybrids Collected as Adults

An adult male "rubidus" (A) was captured near Perry, Houston County, Georgia (32°22′N, 83°45′W) on 8 June 1986 in a thicket of black willow (*Salix nigra* Marsh) (Salicaceae).

A very small male "rubidus" (B) was sighted, but not captured, in a clump of coastal-plain willow (*Salix caroliniana* Michx.) (Salicaceae) near Dunnellon, Marion County, Florida (29°02′N, 82°31′W) on 7 July 1987.

Hybrids Reared from Wild-collected Larvae

One male "rubidus" (C) emerged on 15 June 1986 from a group of seven fifth-instar larvae collected on a single *S. caroliniana* tree near White Springs, Hamilton County, Florida (30°20'N, 82°45'W) on 7 June 1986. The remaining six larvae yielded viceroys.

Two male "rubidus" (D) were reared from a group of 17 wild larvae (fourth and fifth instars) collected on a single *S. caroliniana* in Gainesville, Alachua County, Florida (29°39'N, 82°20'W) on 6 June 1986. The two adult "rubidus" emerged on 16 June and 18 June; their proximity in space and time suggests that perhaps they were the progeny of a single female. The remaining larvae yielded 11 viceroys and four red-spotted purples.

Two "rubidus" (E) emerged from a group of six fifth-instar larvae collected on a single *S. caroliniana* near Espanola, Flagler County, Florida (29°30'N, 81°21'W) on 8 June 1987. The adults emerged on 21 and 24 June; presumably they were siblings. Although their pupae appeared superficially normal, both butterflies eclosed with deformed wings (one was severely deformed); whether this was due to developmental abnormality or environmental conditions is unknown. The other four larvae were viceroys.

Natural Interspecific Matings

Two mating pairs of male viceroy and female red-spotted purple were collected in 1988; one pair (F) was taken near Mayo, Lafayette County, Florida (30°03'N, 83°11'W) on 29 April, and the other (G) was collected near Woodbine, Camden County, Georgia (30°56'N, 81°45'W) on 14 June. Both viceroys involved were *L. a. archippus–L. a. floridensis* intergrades. These mismatings may not have resulted necessarily in successful hybridization, but they do provide evidence of mate-choice breakdown (see below). Attempts to obtain eggs from the females failed in both cases, possibly due to interruption of spermatophore transfer during their capture *in copula* (although captive female *Limenitis* often fail to oviposit: A. P. Platt, pers. comm.).

Further sampling is required to determine the magnitude and persistence of interbreeding between viceroys and red-spotted purples in Florida and Georgia; such influences as winter survivorship and population dynamics of the two species presumably affect the degree of interaction and hybridization that occurs between them.

DISCUSSION

All of the "rubidus" discovered were males (a female "rubidus" has never been taken in the wild: Platt 1987a) and all were intermediate in wing pattern between viceroys and red-spotted purples. They re-

sembled wild-caught and lab-reared hybrids depicted by Platt and Greenfield (1971) and Platt et al. (1978), and included both the "light" (viceroy-like) and "dark" (red-spotted purple-like) phenotypes described by these authors. In fact, the specimen from Houston County, Georgia, has such a preponderance of viceroy characteristics that it may be a "rubidus"—viceroy backcross ("rubidus" are often fertile in laboratory crosses).

The seven hybrid specimens represent 1.1% of the entire *Limenitis* sample (n = 629) collected during the study period (Apr 1986–Aug 1987) in willow thickets from Houston County, Georgia, to Marion County, Florida. The hybrids were discovered while surveying willow habitats as part of another investigation; while this might yield a higher estimate of hybrid frequency than casual observation, it should be noted that intensive *Limenitis* collections (involving hundreds of butterflies) have not turned up "rubidus" hybrids in other areas (Remington 1968; Platt & Brower 1968; Bergman 1971; Platt 1975, 1987b; Waldbauer et al. 1988; pers. obs.).

Postulated Causes of Increased Hybridization in Florida and Georgia

The discovery of seven "rubidus" hybrids and two interspecific matings within two years contrasts with the rarity of "rubidus" records elsewhere. Furthermore, other workers have reported "rubidus" from northern Florida: one collected in Volusia County by G. W. Rawson (Platt et al. 1978) and three collected in Columbia County by James Maudsley (Platt & Maudsley, unpublished). Why should Florida/Georgia populations of viceroy and red-spotted purple hybridize more frequently than populations elsewhere? At least two possibilities exist: (1) matings between viceroys and red-spotted purples occur more frequently in this area than elsewhere (i.e., there is reduced pre-mating reproductive isolation), or (2) interspecific matings are no more frequent, but the few hybrids that are produced are more viable than those elsewhere (i.e., there is reduced post-mating reproductive isolation).

There is no *a priori* reason to expect that post-mating isolating mechanisms (genetic incompatibility or hybrid breakdown) are any weaker in Florida and Georgia than elsewhere, but the appropriate breeding studies have not been conducted. On the other hand, I propose three reasons to suspect a partial breakdown of pre-mating isolating mechanisms, which could result in more frequent intermating.

1) Habitat overlap

Although the two butterflies share a broad geographic range, red-spotted purples commonly rely on a different larval foodplant (black

cherry, *Prunus serotina* Ehrh.; Rosaceae) than do viceroys (willows and poplars; Salicaceae) (e.g., Remington 1968, Opler & Krizek 1984). Willow and black cherry often occur in different microhabitats (Elias 1987), and viceroys and red-spotted purples feeding on them are reportedly somewhat habitat-segregated (Shapiro & Biggs 1968). In fact, in Maryland and Wisconsin willow patches, larvae of viceroys outnumber those of red-spotted purples by from 30:1 to 100:1 (A. Platt & D. Flaim, pers. comm.; pers. obs.). This habitat segregation has been proposed as one component of pre-mating isolation between the two species (Platt et al. 1978).

However, in northern Florida and southern Georgia, red-spotted purples occasionally switch from black cherry to the viceroy's larval foodplants, coastal plain willow (*Salix caroliniana*) and black willow (*S. nigra*). In fact, red-spotted purples comprise up to 35% of mixed *Limenitis* larvae collected from Florida willow thickets (pers. obs.), and the adult butterflies are forced into microsympatry (Table 1). Thus, the butterflies probably encounter one another more frequently in this region than elsewhere. Such habitat overlap is commonly cited as a cause of hybridization between normally habitat-segregated species (e.g., Chapin 1948, Anderson 1949, Mayr 1963, Williams 1983), including *Limenitis* (Greenfield & Platt 1974). In sampled willow thickets, adult red-spotted purples were most abundant early in the year (26% of combined *Limenitis* sample), becoming virtually absent later (Fig. 2). Perhaps autumnal senescence of black cherry in northern Florida forces late-season red-spotted purples to oviposit primarily on willow; the overwintering larvae then give rise to early-spring adults that find themselves in willow thickets surrounded by viceroys. This elevated encounter rate in the spring may explain why the Florida hybrids occurred fairly early in the year (median date = 8 June), rather than in late summer, as Platt (1987a) reported for "rubidus" elsewhere. Likewise, the two mismated pairs of viceroy and red-spotted purple were discovered early in the season.

2) "Economics" of red-spotted purple mate choice

The low density of red-spotted purples relative to viceroys in willow habitats may compel red-spotted purples to "settle for" viceroys as mates. In willow thickets where both butterflies were observed (Apr 1986–Aug 1987), viceroys outnumbered red-spotted purples by approximately 9:1 (Table 1). Increased hybridization when one species is comparatively rare is well documented in various taxa (e.g., Hubbs 1955, Mayr 1963, Wittenberger 1983), including butterflies (*Limenitis*: Greenfield & Platt 1974, Simpson & Pettus 1976, Platt et al. 1978; *Pieris*: Chew 1980). Theoretical considerations of mate choice "eco-

TABLE 1. Documented microsympatry of adult viceroys (*Limenitis archippus*) and red spotted purples (RSPs; *L. arthemis astyanax*) in willow thickets in Florida and Georgia (April 1986–August 1987). Data include only thickets in which both butterflies were found, and sites at which "rubidus" or interspecific matings were observed have the city name underlined. Note: localities are in N to S order; north of Houston County, Georgia (32°30'N), RSPs occur but were not observed in willow thickets; south of Marion County, Florida (29°N), RSPs do not occur.

Location		Total number	
County	City	of *Limenitis*	Percent RSPs
Georgia			
Houston	Perry	10	10
Dooly	Unadilla	14	7
Liberty	Flemington	13	8
McIntosh	Eutonia	16	12
Tift	Chula	26	8
Cook	Adel	15	13
Camden	Woodbine	13	8
Lowndes	Valdosta	49	10
Brooks	Quitman	17	6
Georgia subtotals:		173	9
Florida			
Hamilton	Wht. Sprgs	39	8
Duval	Baldwin	7	14
Columbia	Lake City	9	11
Lafayette	Mayo	15	7
Union	Lake Butler	28	14
Alachua	Waldo	28	7
	Gainesville	163	10
	Hawthorne	35	14
	Micanopy	24	17
Gilchrist	Bell	12	25
Flagler	Espanola	9	11
Marion	Dunnellon	30	3
Florida subtotals:		404	10
Overall:		577	10

nomics" (Wilson & Hedrick 1982) predict that female red-spotted purples will be less discriminating in choosing mates if conspecific males are absent (which they often are; most red-spotted purples that I encountered in willow thickets were single females). Likewise, male red-spotted purples that are unable to locate conspecific females may be unusually persistent in courting female viceroys. Probably it is the combination of microsympatry and red-spotted purple mate-choice economics that sets the stage for hybridization.

3) Biogeography and genetics

An intriguing biogeographic correlation suggests that in northern Florida, red-spotted purples encounter viceroys that differ in mate

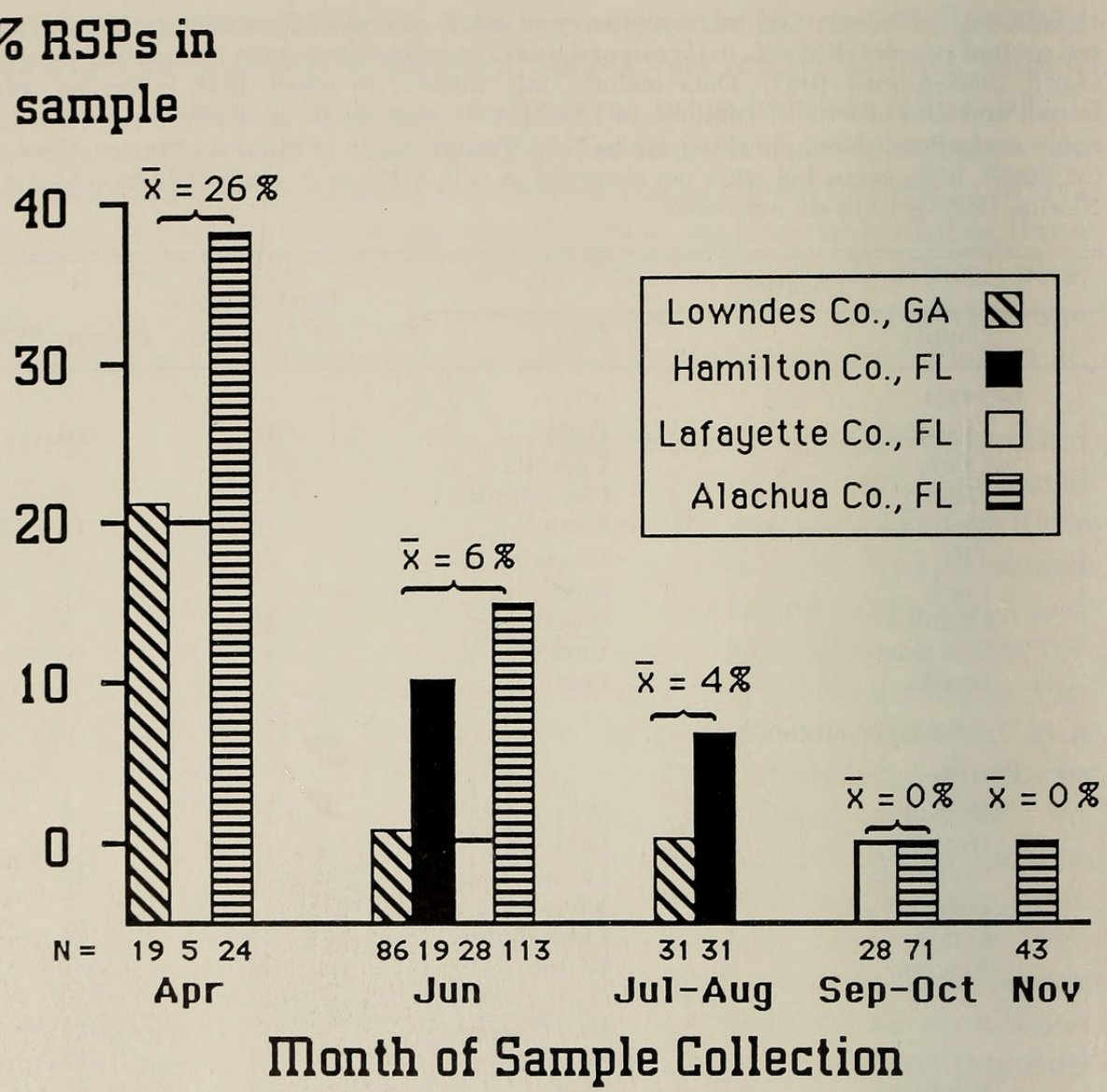

FIG. 2. Seasonal decline in the relative frequency of red-spotted purples (RSPs; *Limenitis arthemis astyanax*) in willow thickets from four areas in northern Florida and southern Georgia (1986–88). Bars (coded by site as indicated) depict percentage of RSPs in the total adult *Limenitis* sample collected during different months. Mean RSP percentage across all sites is indicated by month as well. A seasonal decline in RSPs is evident in both individual and pooled site data. Total sample size (no. viceroys + no. RSPs) is indicated beneath each bar. Some sites were not sampled every month.

choice behavior from viceroys they encounter elsewhere. The "rubidus" collection sites coincide geographically with an intraspecific hybrid zone between two subspecies of the viceroy (Fig. 1). This hybrid zone, which is characterized by a latitudinal cline in wing color, connects the light orange northern viceroy, *L. a. archippus* (Cramer), and the dark mahogany-brown Florida viceroy, *L. a. floridensis* (Strecker). *L. a. archippus* ranges widely over eastern North America and is broadly sympatric with the red-spotted purple, but *L. a. floridensis,* in peninsular Florida, occupies a largely disjunct geographic range to the south of other *Limenitis* species. Thus, *L. a. floridensis* may have "escaped"

selection for sensitive mate-discrimination abilities (Bigelow 1965, Dobzhansky et al. 1968, Barton & Hewitt 1985), and *L. a. floridensis* genotypes immigrating into the intergrade zone could therefore be prone to mismating with the unfamiliar red-spotted purples that they encounter there. Furthermore, the dark wing color of Florida viceroys perhaps masks critical pattern elements that normally allow a red-spotted purple to recognize a viceroy as a heterospecific.

Moreover, "hybrid" viceroys may exhibit atypical mate choice because they represent mixtures of the *L. a. archippus* and *L. a. floridensis* genomes. These genomes apparently differ in alleles besides those for wing color (e.g., larval characters: Edwards 1884; and diapause control: Williams and Platt 1987), so hybrid viceroy mating behavior conceivably could be affected by novel allele combinations or intragenic recombination (e.g., Spieth 1968, Barton et al. 1983, Golding & Strobeck 1983; but *cf.* Barton 1983 *re* polygenic traits). This hypothesis is supported by the two observations of intergrade viceroys *in copula* with red-spotted purples. Finally, to the extent that mate choice and courtship in *Limenitis* are mediated by wing pattern or coloration, the variable ground color of viceroys within the intergrade zone (ranging from light orange to dark mahogany-brown: Ritland, 1990) may contribute to more frequent mismating by viceroys here than occurs in monotypic populations. These arguments remain speculative, because mate choice in viceroys and red-spotted purples is poorly understood; however, the proposed mechanisms identify several avenues of research that should be pursued in attempting to explain the elevated hybridization in this area.

Potential Consequences of Viceroy–Red-spotted Purple Hybridization

Locally-elevated hybridization between red-spotted purple and viceroy populations may allow limited genetic introgression (Anderson 1949) between the two species. Introgression is possible because "rubidus" males are fertile in laboratory backcrosses to both parental species (Platt 1983). The unpredictable effects of novel allele combinations created through introgression (Alston 1967, Ford 1971, Naveira & Fontdevila 1985) and the diffusion of adaptive alleles from one taxon to another (Barton 1979) represent potential evolutionary catalysts in Lepidoptera (e.g., Clarke & Sheppard 1960, Hovanitz 1963). Introgressive hybridization between red-spotted purples and viceroys conceivably could affect traits ranging from mimetic coloration and chemical defense to diapause dynamics and foodplant utilization ability. Thus, if local hybridization in Florida and Georgia does represent a significant and

persistent breach in the normal species barrier, this area may be a "hot spot" in the continuing evolution of the two butterflies.

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