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CONTINUED INTERSPECIFIC HYBRIDIZATION BETWEEN *LIMENITIS (BASILARCHIA) ARTHEMIS ASTYANAX* AND *L. (B.) ARCHIPPUS* IN THE SOUTHEASTERN U.S. (NYMPHALIDAE)

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ABSTRACT. Interspecific hybridization between North American admiral butterflies is briefly reviewed and updated. Records of 77 wild male F_1 hybrids between the viceroy, *Limenitis archippus* subspecies, and other nearctic *Limenitis* are noted. Among these are six new records of the hybrid form "rubidus" Strecker (*L. archippus* × *L. arthemis astyanax*), including three each from two localities, one in Athens, Georgia and the other in northern Florida. Four of these new hybrids were reared from eggs and larvae wild-collected from willows (*Salix* spp.). Topics reviewed include 1) the present status of viceroy mimicry, and 2) the intense hybridization between phenotypically variable populations of *L. archippus* and *L. arthemis astyanax* observed recently in the Georgia/Florida region. Ecological, phenotypic, and behavioral reasons underlying this phenomenon are considered.

Additional key words: admirals, *L. archippus floridensis*, hybrid "rubidus," mimicry, selection.

Interspecific hybridization among North American *Limenitis* is well-known and has received much attention in the literature (see reviews by Platt et al. 1978, Platt 1983, Ritland 1990). Of particular interest to both lepidopterists and biologists are those crosses involving the viceroy, *L. archippus* (Cramer), a known mimic of various danaine models, and the other congeneric admirals with which *L. archippus* is broadly sympatric. These include butterflies of the eastern *L. arthemis-astyanax* complex (Platt & Brower 1968, Platt 1975, 1987a, 1994) and species of the two western complexes, *L. lorquini* Boisduval (Perkins & Perkins 1966, Gage 1970, Perkins & Gage 1970) and *L. weidemeyerii* Edwards (Cross 1936, 1937, Perkins & Perkins 1967, Simpson & Pettus 1976). Such crosses involving *L. archippus* and its congeners yield phenotypically intermediate F_1 males, which are somewhat variable in terms of their relative light (orange) or dark (brownish-black) ground coloration, and also their partial postmedial white banding.

These naturally occurring hybrid forms have been variously named (see below), depending upon the species (or subspecies) involved. These interspecific hybrids are quite rare, usually occurring as from one to several specimens in widely distributed, but geographically isolated,

localities. Some of these locales are referred to by collectors as hybrid "hot spots." In such areas, low levels of interspecific cross-breeding take place over a number of years (and insect generations) in the same locality. Such wild hybrids presumably result from "stray" matings between individuals belonging to the two different taxa involved [e.g., 1) *L. arthemis arthemis* × *L. archippus*, 2) *L. arthemis astyanax* × *L. archippus*, 3) *L. weidemeyerii* × *L. archippus*, and 4) *L. lorquini* × *L. archippus*]. Including the specimens to be reported in this paper, a total of 77 published and unpublished records of such interspecific hybrids presently are known to the senior author. The most recent of these records are from south-central Louisiana in September 1991 (Kemp 1991) and southwestern Kentucky in September 1993 (Covell 1994, pers. comm.). These breakdown as follows:

1) hybr. "arthechippus" Scudder = 11 (including the type specimen of hybr. "rubrofasechippus" Gunder)
2) hybr. "rubidus" Strecker = 45
3) hybr. "weidechippus" Cross = 12
4) hybrid unnamed (*L. lorquini* × *L. archippus*) = 9

All of these wild-caught specimens are males. However, a single heterotic female specimen of hybr. "rubidus" has been lab-reared from Maryland strains (Platt & Harrison 1994). Similar female morphs occur in laboratory backcrosses involving the F_1 hybrid males as well (Platt 1975, Platt et al. 1978).

Hybrid "rubidus" Strecker

Particularly well known are the F_1 hybrids between the two mimetic butterflies, *L. arthemis astyanax* and *L. archippus* subspecies. Such hybrids are broadly distributed from Arizona and New Mexico across the mid-western U. S. into New England and south to Florida. The two parent insects belong to two separate well-known mimicry complexes, and themselves are very different in appearance (Figs. 1 & 4). Thus, the morphologically intermediate F_1 hybrids represent a complete breakdown of both mimetic patterns (Fig. 3), and they quite likely are at a selective disadvantage from predation (by birds), when compared to either of the parental types. Because the known wild F_1 hybrids all are males, they most certainly are at a mating disadvantage as well. The hybrid morphs are not known to persist in nature, and backcross specimens at present are known only from laboratory crosses (Platt 1975, 1983, Platt et al. 1978).

Presently, little is known regarding courtship behavior in nearctic admirals. Possibly visual, tactile, and pheromonal cues are important to the insects, as has been shown for closely related palearctic species

(Lederer 1960). Both parental species possess distinctive apical morphology of the male valvae (Platt et al. 1970), but apparently this precopulatory reproductive isolating mechanism is not perfect. The hybrids possess intermediate genitalic morphology.

Results of laboratory hybridization studies (Platt 1975, 1983) reveal that some degree of inter-fertility is possible in reciprocal crosses, although a greater number of the few interspecific pairings encountered in nature involve female *L. arthemis astyanax* and male *L. archippus archippus* (Klots 1959, Ritland 1990). Apparently, the specialized elongate, sickle-shaped valval tips of *L. archippus* subspecies are efficient mating structures which may play an important functional role in interspecific hybridization among the nearctic *Limenitis.* However, recent observations by Covell (1994) in southwestern Kentucky and by S. Mertens (pers. comm.) in north central Wisconsin, demonstrate that the reciprocal crosses involving female *L. archippus archippus* × male *L. arthemis astyanax* and *L. arthemis arthemis* sometimes do take place in nature in the following article (Covell 1994:199).

Present Status of Viceroy Mimicry

Recently, the queen/Florida viceroy relationship (and hence, by inference, the monarch/viceroy relationship as well) has been shown to be a Müllerian one, rather than a Batesian one, as classically believed (Brower 1992, Ritland 1991, Ritland & Brower 1991a, 1991b, Vane-Wright 1991, Walker 1991). These findings confirm those of J. V. Z. Brower (1958a, 1958b) and Platt et al. (1971) that certain avian predators (scrub jays, *Aphelocoma coerulescens coerulescens* Bosc. and blue jays, *Cyanocitta cristata bromia* Oberholser; Corvidae) find viceroy butterflies unpalatable in caged experimental situations.

RESULTS

This paper reports the collecting of six additional wild "rubidus" hybrids, three each from Clarke Co., Georgia and Columbia Co., Florida. All were taken between 1973 and 1986 by J. R. M. The Athens records probably involve the nominate subspecies, *L. archippus archippus,* whereas those from Florida most likely involve the southern chocolate-brown subspecies, *L. archippus floridensis* Strecker, or *L. archippus/floridensis* intergrade forms, which are prevalent in northern Florida and southeastern Georgia. Four of these records represent specimens reared from wild-collected eggs and larvae found on willows (*Salix* spp.; Salicaceae). These records (presented chronologically) are as follows:

1) A worn adult male was collected at Belmont Road and Shoal

Creek in Athens (Clarke Co.), Georgia on 19 September 1973. The willow thicket was part of an ecotone habitat between the wooded bottomlands along Shoal Creek and an open cow pasture.

2) A fresh adult male was captured at the "Beaver Pond" site in Athens, on 17 May 1984. This area consists of a two- to three-acre beaver pond surrounded on three sides by open "old field" habitat, and by a mature pine plantation. The specimen was taken in a willow thicket between the beaver pond and the pine plantation.

3) A third hybrid male eclosed on 1 August 1984 from a single larva collected several weeks earlier on *Salix nigra* Marsh at the Athens "Beaver Pond" site.

4) Finally, three other male hybrids, all dark morphs of "rubidus," were among 12 admirals reared from a group of 11 young larvae and two eggs collected along a 30 m stand of willow shrubs (believed to be *Salix caroliniana* Michx.) between a service road and a cypress swamp, located just north of the entrance to O'leno State Park (Columbia Co.), Florida on 11 July 1986. At the time, the willow leaves showed few signs of larval feeding, and only one freshly eclosed light orange female *L. archippus archippus* was seen flying in the area.

This collection of eggs and larvae was made between summer broods of the adult admirals. Only 12 butterflies were reared, since one of the eggs failed to hatch. These insects were lab-reared at room temperature on *Salix nigra*, and eclosed between 19 July and 5 August 1986. Eclosion dates for the three hybrids were 19, 23, & 29 July. Also, reared in this sample were seven *L. arthemis astyanax* (4 males & 3 females) and two male *L. archippus floridensis*. All except one male *L. arthemis astyanax* represent the iridescent greenish form "viridis" Strecker.

Intense Hybridization in the Florida/Georgia Subspecific "Suture-zone"

Assuming that all like butterflies were siblings, the 12 individuals must represent eggs laid by at least three different wild females. The last three hybrids well may involve the dark brown Florida subspecies of *L. archippus* (Fig. 2), although specimens seen and taken at this locality represent intraspecific intergrades, and vary greatly in ground color (ranging from bright orange to orange-brown to brown). This region, of course, represents an area of intergradation between the typical orange colored eastern viceroy and the darker peninsular subspecies *L. archippus floridensis* (Remington 1958, 1968).

Ritland (1990) reports seven additional hybr. "rubidus" records from Georgia and northern Florida obtained in 1986 and 1987. Five of his records, likewise, were obtained from wild-collected larvae taken on *Salix caroliniana*. There are, in addition, two earlier records of hybr.

"rubidus" from this region (Platt et al. 1978). All 13 of the wild "rubidus" hybrids recently collected by J. R. M. & D. B. R. from this area represent progeny of either spring or early summer interspecific matings of the parental butterflies. Further north, and in western regions of the country, the majority of such crosses seem to occur in the late summer or fall (Platt 1987b). According to Ritland (1990), *L. arthemis astyanax* is absent from local habitats where *L. archippus archippus* and *L. archippus floridensis* fly during the late summer and fall seasons.

Ritland (1990) discussed possible reasons for this cross-breeding. They include the following:

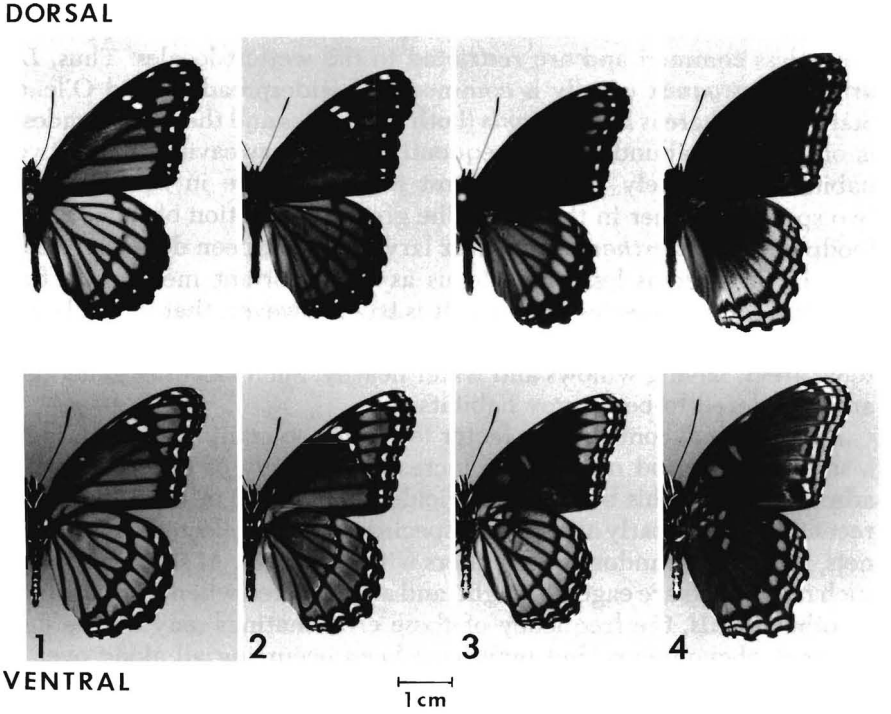
1) The existence of the subspecific intergrade zone between *L. archippus archippus* and *L. archippus floridensis* in southern Georgia and northern Florida, which creates greater genetic and phenotypic variability within populations of this often phenotypically uniform species. This greater genetic diversity within these viceroy populations may contribute to more labile female mate-choice.

2) The general scarcity of *L. arthemis astyanax* in many regions of Florida, at least relative to *L. archippus archippus*, and the utilization of similar microhabitats by both species in the southeastern U.S., especially during the early part of the year (April–June). [However, in northern Florida, *L. arthemis astyanax* populations can be reasonably common, locally.]

3) In this area *L. arthemis astyanax* switches to greater dependence on salicaceous foodplants, since its main rosaceous foodplants, such as *Prunus serotina* Ehrh., become restricted to dry woodland habitats, and generally do not occur in the moist open meadow habitats, usually frequented only by viceroys.

DISCUSSION

Our present studies reveal the existence of phenotypic intergradation between *L. archippus archippus* and *L. archippus floridensis* in Georgia and northern Florida, as reported previously by Remington (1958, 1968). In fact, viceroy populations as far north as Athens, Georgia show tendencies toward this phenotypic blending with the darker southern subspecies. Such individuals usually are a darker orange-brown color than that of nominate *L. archippus*. Many of these specimens have forewings that are a shade darker than their hindwings, and some even possess ventral hindwing basal orange spots, like those characteristic of *L. arthemis astyanax* (Fig. 1). This last trait appears in *L. archippus archippus* because of differences in hues of the ventral hindwing ground color and of the basal spots themselves. Laboratory crosses between the two viceroy subspecies clearly show that the appearance of these ventral



FIGS. 1–4. Specimens of the different forms of *Limenitis* from the southeastern U. S. **1)** *L. archippus archippus*, no. 84-1, Athens (Clarke Co.) Georgia, Aug. 1984, J. R. M.; **2)** *L. archippus floridensis*, no. 86-7, eclosed 3 Aug. 1986; **3)** hybr. "rubidus", no. 86-11, eclosed 23 July 1986; & **4)** *L. arthemis astyanax*, no. 86-3, eclosed 27 July 1986. All four specimens are males, reared on *Salix* sp. Specimens 2–4 reared from eggs and larvae collected on *Salix* sp. near O'leno State Park (Columbia Co.), Florida, 11 July 1986, by J. R. M. All specimens deposited in the insect collection at U.M.B.C.

basal spots can occur without any cross-breeding involving viceroys and red-spotted purples. Thus, in itself, this trait among viceroys is not an indicator of such interspecific genetic introgression.

Although throughout much of Florida *L. arthemis astyanax* seems to be relatively scarce compared to *L. archippus,* this does not appear to be the case in the O'leno State Park region of northern Florida. This area includes mesic habitat laced with ribbons of wet bottomlands and sink holes. These wetter low areas usually are wooded. The higher, more dry uplands form a patchwork of open fields, farmlands, and islands of either pines (*Pinus* spp.; Pinaceae) or oaks (*Quercus* spp.; Fagaceae). Within the more open pine areas and throughout the old fields, wild cherries and wild plums (*Prunus* spp.; Rosaceae) are among

the most common successional tree species. Willows (*Salix* spp.) are much less common and are restricted to the wettest locales. Thus, *L. arthemis astyanax* usually is common and widespread around O'leno State Park, whereas *L. archippus* (both subspecies and their intergrades) is only locally abundant. Consequently, the interweaving of the two habitats quite likely plays the most important role in bringing the two species together in this area. The greater utilization of salicaceous foodplants by *L. arthemis astyanax* larvae has not been demonstrated, and, in fact, seems less likely to us as an important mechanism for bringing the two species together. It is true, however, that virtually all hybr. "rubidus" have been collected in rather open moist field or ecotonal areas, having willows and water nearby. Such localities generally are considered to be viceroy habitats.

An additional contributing factor to finding so many hybrids in such a short time period may be the increased intensity of collecting wild admiral larvae. This by itself has yielded nine (69%) of the 13 hybrids recently taken. Nearly all previous specimens were collected with handnets, following "random" encounters with collectors. At the same time, such rare insects are eagerly sought, and are collected whenever possible. In other words, the frequency of these cross-matings may not be just a recent phenomenon, but may have been occurring all along over a prolonged period of time. Such crosses simply may be an indication of the extremely close affinities between *L. arthemis astyanax* and *L. archippus* subspecies, as belied by their very similar developmental stages. It is likely that the red-spotted purple (*L. arthemis astyanax*) has evolved as a mimetic form from *L. arthemis arthemis* in comparatively recent times. Thus, it may have spread southward into the vicinity of northern Florida very recently (geologically speaking) as well.

Four of the hybr. "rubidus" specimens collected by J. R. M. are in his personal collection. The other two hybr. "rubidus" and the remaining Florida specimens are in the U.M.B.C. insect collection.

CONCLUSIONS

Evidently, both the Beaver Pond site in Athens, Georgia, and the O'leno State Park locality in northern Florida represent the interspecific "hot spot" locales referred to earlier in this paper. In such habitats, ecological conditions including temperature, light, moisture, and food plant types and distributions, together with the relative abundances of the two parental species (with one being prevalent, but the other much scarcer) produce conditions leading to "microsympatry" at certain times of the year (Ritland pers. comm.). As long as such conditions persist,

elevated levels of hybridization can continue to occur at these specific locales.

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