# MIMICRY-RELATED VARIATION IN WING COLOR OF VICEROY BUTTERFLIES (*LIMENITIS ARCHIPPUS*):
## A Test of the Model-Switching Hypothesis
### (LEPIDOPTERA: NYMPHALIDAE)

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**ABSTRACT.**– The viceroy butterfly (*Limenitis archippus*) is well known as a superb mimic of its chemically defended model, the monarch (*Danaus plexippus*). However, viceroy populations in both the southeastern and southwestern United States appear to have switched phenotypically from mimicking the tawny-orange monarch to mimicking two subspecies of a darker mahogany-brown model, the queen (*Danaus gilippus*). This paper, combining field censuses and computer-assisted wing-color analyses, supports the hypothesis of "model-switching" by the viceroy. Specifically, we demonstrate that in the southeastern United States, a latitudinal cline in viceroy wing color (darkening from orange to mahogany southward from Georgia through Florida) is geographically correlated with a latitudinal shift in relative abundance of monarchs and queens, with the latter becoming more prevalent southward. We therefore view the cline in viceroy coloration as an adaptive adjustment to a latitudinal selective gradient associated with danaine relative abundance. This work supports the hypothesis that the viceroy's mimetic wing-color pattern is regionally "fine-tuned," phenotypically tracking different models in different areas.

**KEY WORDS**: *Basilarchia*, clinal change, *Danaus*, geographic variation, hybrid zone, introgression, monarch, Nearctic.

Few phenomena illustrate the power and creativity of natural selection as clearly as the various forms of mimicry. In particular, defensive mimicry — in which one prey species escapes some predation by resembling a second, protected prey species — has been instrumental in elucidating both the process and the product of adaptive evolution (Riley, 1871; Turner, 1977; Platt, 1975; Brower, 1988, 1992, 1996; Charlesworth, 1994). The Lepidoptera, with their bold and intricate color patterns, have for decades played a key role in the formulation and testing of mimicry theory.

A premier example of lepidopteran mimicry involves the viceroy butterfly, *Limenitis archippus* (Cramer) (Nymphalidae: Nymphalinae), a remarkably accurate mimic of its variably distasteful model, the monarch, *Danaus plexippus* (Linnaeus) (Nymphalidae: Danainae). The striking resemblance between viceroy and monarch (Fig. 1) has made this relationship a widely cited textbook example of defensive mimicry, and the relationship continues to shed light on the complexities and dynamics of mimicry and predator–prey relationships (Ritland and Brower, 1991; Ritland, 1994, 1998).

However, as Fig. 1 illustrates, not all viceroys closely resemble monarchs; indeed, viceroys from different regions, generally considered geographic subspecies (Miller and Brown, 1981; Platt, 1983), vary considerably in wing color and pattern, and appear to mimic different danaine models. Thus, the widespread *L. archippus archippus* — the orange, monarch-mimicking phenotype of textbook fame — is replaced in the southeastern United States by *L. archippus floridensis*, a dark, mahogany-brown butterfly that resembles in hue the locally predominant danaine: the Florida queen, *Danaus gilippus berenice* (Cramer). In riparian habitats of the southwestern United States deserts, a pale viceroy race, *L. archippus obsoleta*, coexists with a similarly colored and distributed form of the queen, *D. gilippus strigosus* (Bates). Early observers (Walsh and Riley, 1869; Scudder, 1870; Strecker, 1878; Edwards, 1884; Poulton, 1908, 1909, 1914) noted the phenotypic and distributional correlations among these viceroy-danaine pairs and proposed a logical explanation: viceroy populations in different areas have diverged from their ancestral coloration, evolutionarily switching from one danaine mimicry model to another. This explanation, which we term the "model-switching hypothesis," holds that

geographic variation in viceroy wing color is due to mimicry-related natural selection; predators selectively attack viceroys, avoiding those phenotypes most similar to the local danaine, thereby exerting selective pressures leading to the improvement of viceroy mimicry. The result is the evolution of regional viceroy races that are adapted to mimic the locally predominant danaine. Similar model-switching has been postulated in a number of other Batesian and Müllerian mimics (e.g., Clarke and Sheppard, 1960; Ford, 1975; Turner *et al.*, 1979; Heal, 1982; Gordon, 1987). This paper describes an assessment of the viceroy model-switching hypothesis, concentrating on the two model-mimic pairs in the eastern United States: *L. a. archippus* & *D. plexippus*, and *L. a. floridensis* & *D. gilippus berenice*.

Figure 1 illustrates the approximate latitudinal distributions of the *L. a. archippus* and *L. a. floridensis* subspecies in the eastern United States, based on literature records (Howe, 1975; Opler and Krizek, 1984; Scott, 1986). Between *L. a. archippus* and *L. a. floridensis* lies a transition zone, in which individual viceroys are intermediate between the two extreme phenotypes (Remington, 1958, 1968).

It is intriguing that the spatial distribution of *L. a. archippus* overlaps the summer breeding range of the monarch, and the range of *L. a. floridensis* roughly coincides with that of the Florida queen, and it is this large-scale biogeographical correlation that spawned and undergirds the model-switching hypothesis. However, Florida viceroys could be darker in color for reasons not directly related to contemporary mimicry-related selection; for instance, their coloration might be related to abiotic (e.g., climatic) factors (Ritland, 1991; A. P. Platt, pers. comm.) or perhaps reflect genetic divergence (perhaps via inbreeding; A. P. Platt, pers. comm.) of a population isolated in Florida during the Pleistocene. To evaluate the model-switching hypothesis in relation to such alternative hypotheses, two points need to be addressed. First, the ecological mechanism purported to favor model-switching--selective predation by danaine--conditioned birds--must be demonstrated. Ritland (1998) presents such a demonstration, revealing that monarch-conditioned predators preferentially attack dark rather than light viceroys, while queen-conditioned birds attack light rather than dark phenotypes.

L. a. archippus          D. plexippus
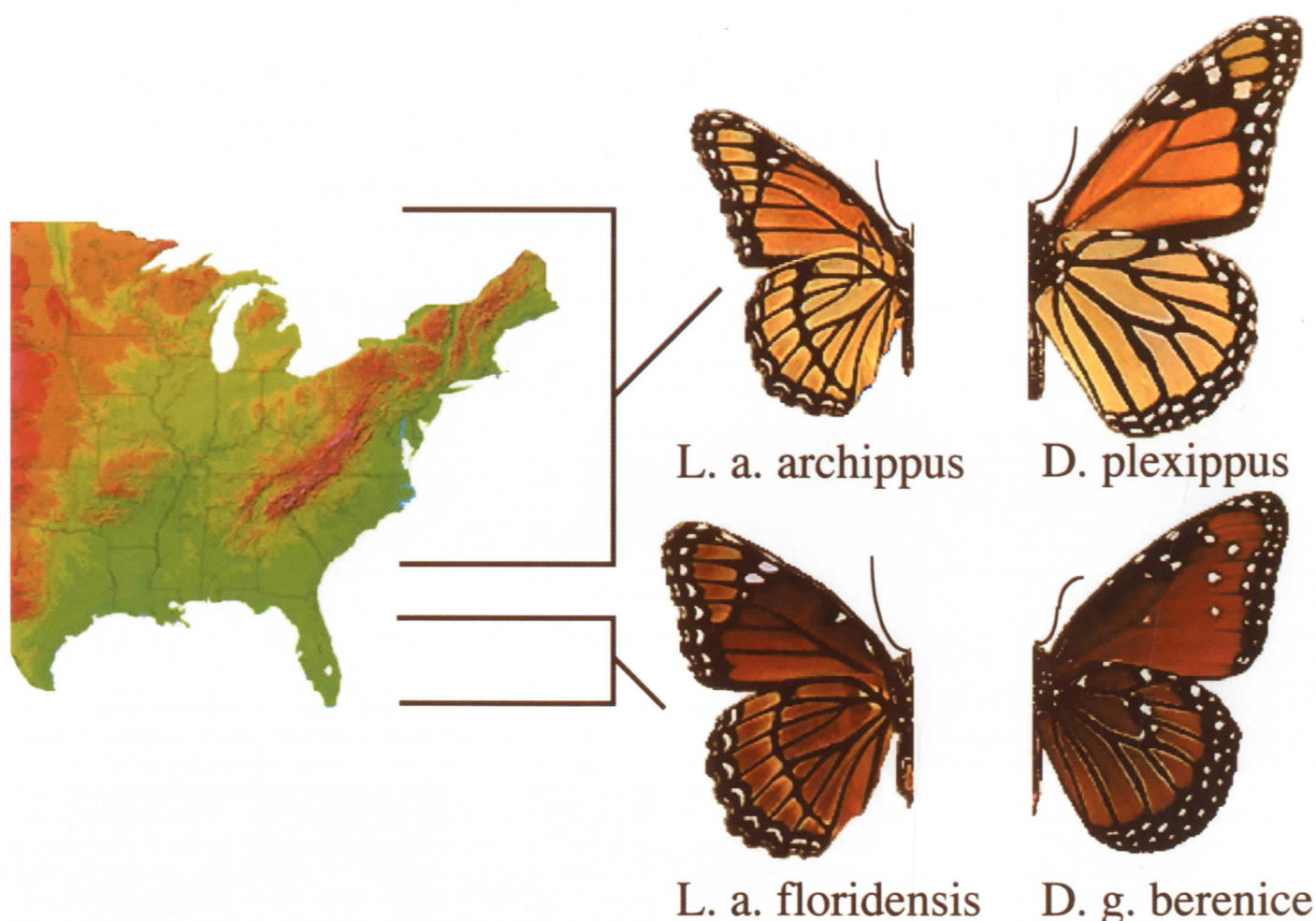
L. a. floridensis        D. g. berenice

Fig. 1. Representative specimens of the typical or northern viceroy (*Limenitis archippus archippus*), the Florida viceroy (*L. archippus floridensis*), and their two danaine "models": the monarch (*Danaus plexippus*) and the Florida queen (*D. gilippus berenice*). Distribution brackets indicate approximate geographic ranges of the *L. a. archippus* and *L. a. floridensis* phenotypes in the eastern United States; a phenotypic transition zone occurs between the two subspecies in southern Georgia and northern Florida.

Second, the presumed correlation between viceroy coloration and the geographic pattern of monarch/queen distribution in the eastern United States must be quantitatively documented. In this paper, we describe quantitatively the latitudinal pattern of viceroy wing coloration in the southeastern United States and seek evidence of a geographic correlation between viceroy wing color and monarch/queen biogeography.

**Methods**

Our study area ranged over 650 linear miles (1080 km) from southern peninsular Florida (latitude = 25°N) to the northern segment of the coastal plain province in central Georgia (latitude = 33°N). This latitudinal region encompasses and extends beyond the reported transition zone between the *L. a. archippus* and *L. a. floridensis* phenotypes (Remington, 1968). In the transition zone, viceroy wing color is variable, and both monarchs and queens occur at least seasonally. The model-switching hypothesis makes the specific prediction that within this region, local viceroy wing color should be correlated with monarch/queen relative abundance. If the latitudinal cline in viceroy wing color is instead due to other factors, no such latitudinal correlation between viceroy coloration and monarch/queen abundance would necessarily exist.

We sampled viceroys from over 200 sites within our study area, which was divided into 16 half-degree latitudinal belts for analysis

(belt 1 = extreme southern Florida; belt 16 = central Georgia; see Fig. 3). Collections were made from March 1986 to September 1991. We employed computer-interfaced video microscopy coupled with image-analysis software to quantify the brightness (luminance) of each viceroy's orange or mahogany ground color (details in Ritland, 1991). Briefly, color video images of butterflies were captured, digitized, and converted to gray-scale images. The image-analysis program was then used to calculate "brightness values" for the orange to mahogany ground color (with black veins/wing margins and white spots excluded) of standardized wing areas. These gray-scale brightness values were measured on a scale from 0 = black to 255 = white. Actual ground-color brightness values obtained in this study ranged from 28 for the darkest butterfly to 174 for the lightest.

Separate brightness readings were taken for dorsal and ventral surfaces of forewings and hindwings; these readings can be averaged to yield an "overall" brightness value for each butterfly (since both dorsal and ventral surfaces are probably important in anti-predator signaling). In this paper, we focus on the mean overall brightness values calculated for 15 latitudinal belts (no specimens were obtained from belt 1). The higher the brightness value, the closer a butterfly is to the light, *L. a. archippus*-like phenotype. Generally, parametric statistics and tests are reported, since <25% of latitudinal belt samples exhibited any significant skewness or
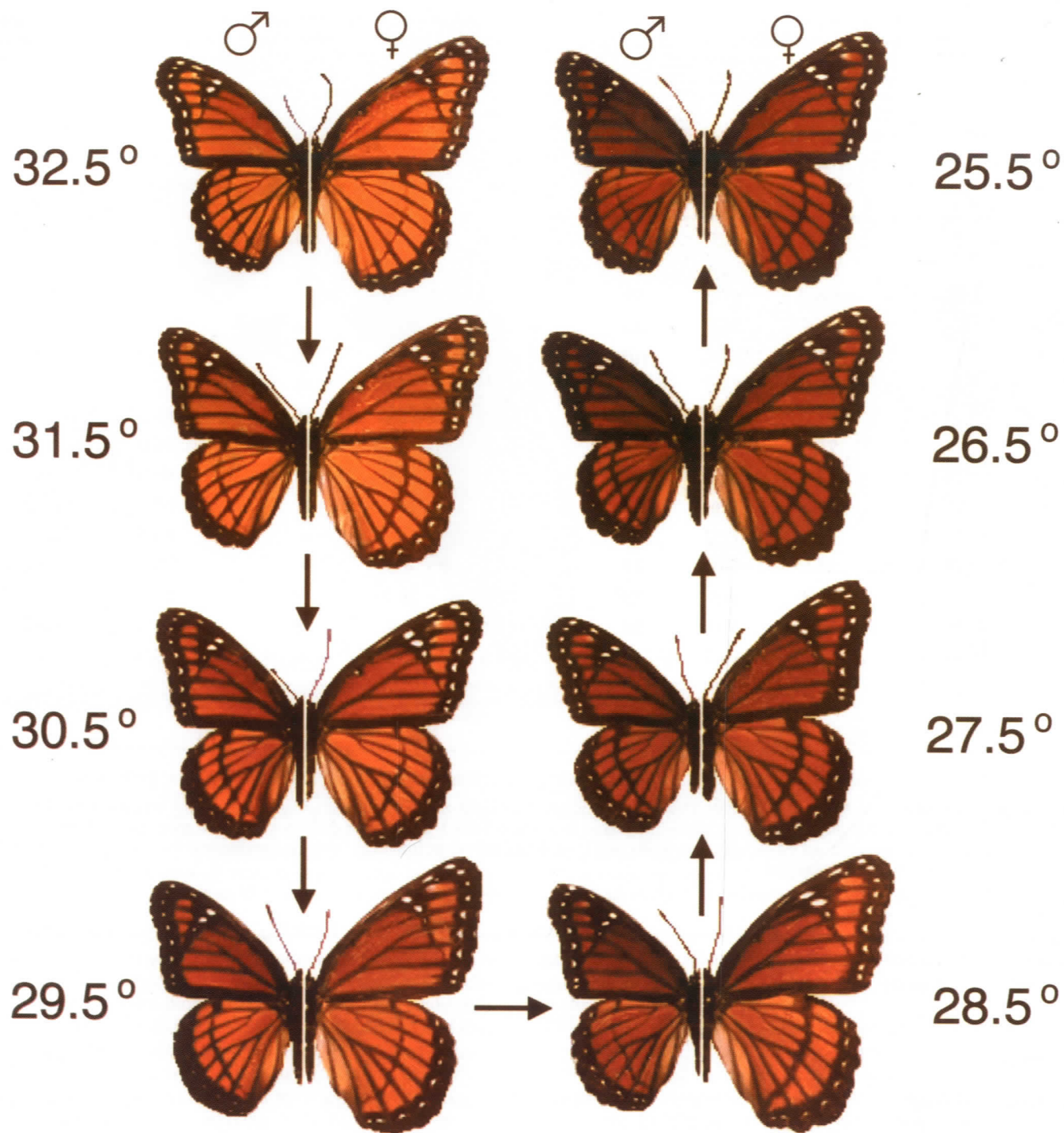
Fig. 2. Viceroy specimens representing average brightness values for paired half-degree latitudinal belts in Georgia and Florida. Each "composite" specimen consists of a male (left) and a female half, representing the male and female average overall brightness values for a given pair of latitudinal belts (see Table 2). Thus, the composite specimen labeled 15/16 represents the unweighted average of belt 15 and belt 16 values for males (left) and females (right). Composite specimens are presented in sequential latitudinal order from central Georgia (upper left, belts 15/16, 32.5° median latitude) to southern Florida (upper right, belts 1/2, 25.5° median latitude).

TABLE 1. Average wing brightness (= meam of dorsal and ventral brightness readings) by half-degree latitudinal belt for 1265 male and female viceroy butterflies sampled from Florida and Georgia, 1986-1991.

Average brightness is measured on a gray scale from 0 = black to 255 = white. Pooled values for brightness and standard deviation (S.D.) are the unweighted (due to unequal sample sizes) means of male and female values for each latitudinal belt. Brightness values for paired belts (e.g., 15/16) are unweighted averages of values from the two belts, and represent estimates of the mean brightness for a 1° latitudinal region. No females were available from belt 6, and "pooled" data for that belt are based on male specimens only. No butterflies were collected from belt 1.

| Latitudinal Belt | Median Latitude | Male Average Brightness | Male S.D. | Male N | Female Average Brightness | Female S.D. | Female N | Pooled Average Brightness | Pooled S.D. | Pooled N |
|---|---|---|---|---|---|---|---|---|---|---|
| 16 | 32.75° | 108.4 | 6.9 | 6 | 118.6 | 16.3 | 8 | 113.5 | 11.6 | 14 |
| 15 | 32.25° | 106.0 | 16.4 | 64 | 115.8 | 18.3 | 6 | 110.9 | 17.4 | 70 |
| 14 | 31.75° | 102.3 | 51.0 | 58 | 112.5 | 11.9 | 29 | 107.4 | 31.4 | 87 |
| 13 | 31.25° | 98.6 | 16.1 | 40 | 103.7 | 20.1 | 16 | 101.1 | 18.1 | 56 |
| 12 | 30.75° | 86.3 | 15.0 | 103 | 97.3 | 15.6 | 36 | 91.8 | 15.3 | 139 |
| 11 | 30.25° | 82.1 | 15.1 | 204 | 92.6 | 15.2 | 48 | 87.4 | 15.2 | 252 |
| 10 | 29.75° | 77.2 | 15.9 | 185 | 85.3 | 15.1 | 85 | 81.2 | 15.5 | 270 |
| 9 | 29.25° | 71.6 | 14.1 | 77 | 80.3 | 14.1 | 20 | 76.0 | 14.1 | 97 |
| 8 | 28.75° | 54.8 | 9.8 | 25 | 71.1 | 12.0 | 10 | 63.0 | 10.9 | 35 |
| 7 | 28.25° | 55.6 | 9.6 | 31 | 71.0 | 14.7 | 11 | 63.3 | 12.2 | 42 |
| 6 | 27.75° | 64.5 | 12.0 | 8 | -- | -- | -- | 64.5 | 12.0 | 8 |
| 5 | 27.25° | 54.0 | 10.0 | 13 | 65.6 | 4.5 | 4 | 59.8 | 7.2 | 17 |
| 4 | 26.75° | 49.8 | 6.5 | 58 | 62.0 | 10.2 | 18 | 55.9 | 8.4 | 76 |
| 3 | 26.25° | 54.7 | 8.0 | 58 | 61.6 | 7.9 | 18 | 58.2 | 8.0 | 76 |
| 2 | 25.75° | 55.4 | 10.2 | 18 | 61.5 | 3.5 | 8 | 58.4 | 6.8 | 26 |
| 1 | 25.25° | -- | -- | 0 | -- | -- | 0 | -- | -- | 0 |

TABLE 2. Average wing brightness for 1265 male and female viceroy butterflies sampled from Florida and Georgia, 1986-1991.

Reported brightness values, which represent the unweighted means of values from a pair of adjacent latitudinal belts (e.g., 15/16), represent estimates of the mean brightness for a 1° latitudinal region. Paired-belt averages are calculated from sata in Table 1. Male/female difference represents results of t-tests performed to detect significant differences between male and female coloration within each 1° latitudinal increment. Results of t-tests are recorded only for paired-belt samples represented by at least 20 male and 20 female butterflies.

| Latitudinal Belt | Median Latitude | Male Average Brightness | Male N | Female Average Brightness | Female N | Pooled Average Brightness | Pooled N | M/F Difference t | M/F Difference df | M/F Difference p |
|---|---|---|---|---|---|---|---|---|---|---|
| 15/16 | 32.5° | 107.2 | 70 | 117.2 | 14 | 112.2 | 84 | | | |
| 13/14 | 31.5° | 100.4 | 98 | 108.1 | 45 | 104.3 | 143 | 3.1 | 141 | < 0.01 |
| 11/12 | 30.5° | 84.2 | 307 | 95.0 | 84 | 89.6 | 391 | 5.9 | 389 | < 0.01 |
| 9/10 | 29.5° | 74.4 | 262 | 82.8 | 105 | 78.6 | 367 | 4.9 | 365 | < 0.01 |
| 7/8 | 28.5° | 55.2 | 56 | 71.1 | 21 | 63.1 | 77 | 5.8 | 75 | < 0.01 |
| 5/6 | 27.5° | 59.2 | 21 | 65.6[1] | 4 | 62.4 | 25 | | | |
| 3/4 | 26.5° | 52.2 | 116 | 61.8 | 36 | 57.0 | 152 | 6.3 | 150 | < 0.01 |
| 1/2 | 25.5° | 55.4[2] | 18[2] | 61.5[2] | 8[2] | 58.4[2] | 26[2] | | | |

[1] Datum based only on belt 5, as no females were available from belt 6.
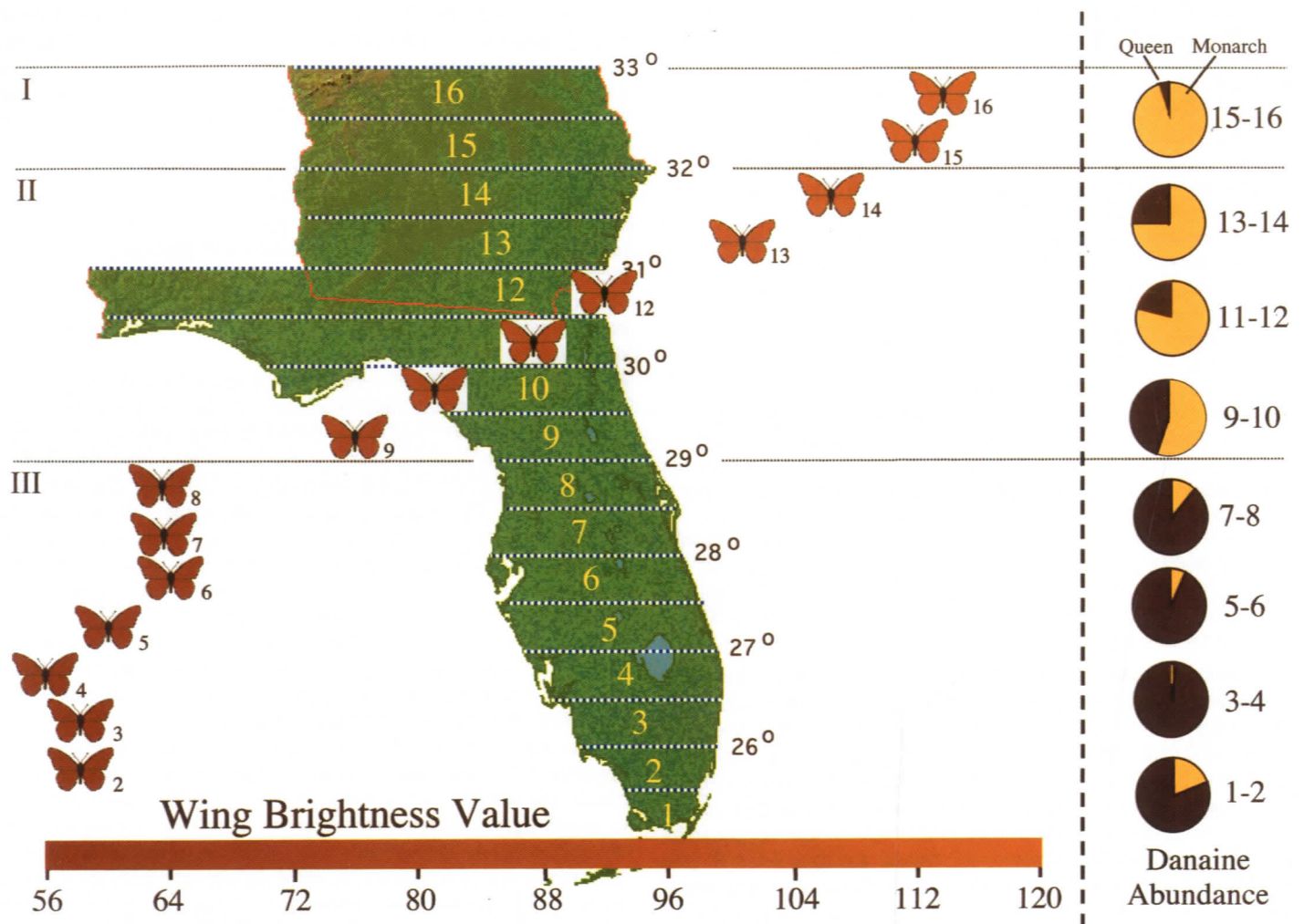[2] Data based only on belt 2, as no butterflies were available from belt 1.

Fig. 3. The large left panel presents the latitudinal pattern of variation in viceroy wing brightness. Each butterfly icon represents the mean overall brightness value (pooled sexes) for its associated half-degree latitudinal belt. Icons are arranged vertically by latitude and horizontally along a wing brightness value axis. Right panel presents, for each pair of half-degree latitudinal belts, pie charts showing the annually averaged relative abundance of monarchs (light portion) and queens (dark portion) (data from Table 3). Overall, a spatial correlation exists between viceroy wing brightness and danaine relative abundance. In Zone I (latitudinal belts 15-16), monarchs predominate and viceroys are relatively light in color. In Zone II (belts 9–14), a southward increase in queen abundance is tracked by a concomitant darkening of viceroy wing color. In Zone III (belts 2–8), where queens predominate, viceroys are relatively invariable and very dark in color.

kurtosis, and then never for both sexes.

To obtain data on spatiotemporal patterns of danaine relative abundance for comparison to patterns of viceroy wing color variation, we conducted a biogeographic survey of the study area. Our goal was not to quantify the absolute abundance of danaines throughout the study area; rather, we focused on their relative abundance in willow (*Salix*) – blackberry (*Rubus*) – buttonbush (*Cephalanthus*) associations frequented by viceroys. We employed a transect census procedure, walking a timed transect through favorable viceroy/danaine habitats (within ~0.5 km of a known viceroy breeding area) and counting every adult danaine seen within ~2m on either side of the transect. A mark-release procedure reduced inaccuracies due to recounts (details in Ritland, 1991). Over 100 census sites were sampled from 1986–1991, and many were visited repeatedly over the course of the year, both to quantify seasonal variation in abundance and to reduce errors associated with one-time sampling of dynamic populations. In this paper, data from spring, summer, and autumn samples are combined to yield a single "annually averaged" estimate of danaine relative abundance for each of the 16 half-degree latitiudinal belts. We use these relative abundance data (condensed into eight one-degree latitiudinal indices)

to relate the geographic pattern of danaine occurrence and abundance to the geographic pattern of viceroy wing color variation.

**Results and Discussion**

As predicted based on the previous work of Remington (1958, 1968), Platt (1983), and Thomas Manley (pers. comm.), our computerized image-analysis procedure identified a general southward darkening in viceroy wing color within the study area (Tables 1 and 2; Fig. 2). The lighter viceroy populations of central Georgia grade, through a series of intermediate populations, into dark southern Florida phenotypes. Males and females exhibit similar latitudinal patterns, or clines, with females slightly but significantly lighter than males (Table 2, Fig. 2).

Notably, however, the rate of latitudinal change in wing brightness (i.e., the slope of the cline) is not uniform throughout the region. Figure 3 illustrates this, graphically depicting the geographic pattern of viceroy variation by plotting mean overall brightness value against latitude. Three phenotypic zones are evident.

• In the two latitudinal belts composing Zone I (central Georgia), the average brightness is a relatively light, *L. a. archippus*-like orange. Pooled-sex brightness values for belts 15

and 16 differ by only 2.5 units, and no statistically significant difference exists between these latitudinal belts in either male or female average brightness (t-tests; male: t = 0.3, df = 68, p = 0.7; female: t = 0.3, df = 12, p = 0.8).

• By contrast, in Zone II, viceroys undergo a dramatic southward darkening, with pooled-sex average brightness values decreasing 31 units (29%) in a 3° latitudinal span. These populations, which apparently form a clinal transition zone between *L. a. archippus* and *L. a. floridensis*, are phenotypically variable; a single deme often contains both fairly light and fairly dark individuals, as well as a range of intermediates. The darkening in wing color from belt 14 southward to belt 9 is highly significant (correlation between latitude and pooled-sex mean wing color in half-degree increments: r = 0.995, r² = 0.99, n = 6, p < 0.01).

• Finally, in Zone III (central and southern Florida), wing brightness becomes more stabilized, hovering around the dark, *L. a. floridensis* phenotype. This is not to say that Zone III wing brightness is invariable; statistically significant differences exist between the darkest and lightest latitudinal belts (4 vs. 8) for both males (t = 2.7, df = 81, p < 0.01) and females (t = 2.1, df = 26, p = 0.04). However, the latitudinal pattern of southward darkening so clearly evident in Zone II is not apparent here, and the difference between overall means for the lightest and darkest latitudinal belts is only 7 units (compared to 31 units for Zone II).

The key question is this: Does the viceroy wing-color cline correspond geographically to the shifting pattern of monarch/queen abundance in the region? Table 3 contains the annually averaged relative abundance data for monarchs and queens in the study area, and Figure 3 graphically presents these data in conjunction with the viceroy wing-color data. Perusal of the relative-abundance pie charts in Fig. 3 reveals that in Zone I (the "light viceroy" zone), monarchs far outnumber queens. Moving southward through Zone II (the viceroy transition zone), a notable shift in danaine relative abundance occurs; queens become substantially more prevalent south-

TABLE 3. Annually averaged relative abundance of monarchs and queens sampled in viceroy-frequented coastal plain habitats from southern Florida to central Georgia.

Significant seasonal fluctuations in relative abundance occur (e.g., Ritland, 1991; Knight, 1998; Moranz and Brower, 1998); for the purposes of this study, the values reported represent the average relative abundances calculated from data collected in spring, summer, and fall. Each datum, the unweighted (due to unequal sample size) mean of values from a pair of adjacent latitudinal belts (e.g., 15/16), provides an estimate of the actual relative abundance for a 1° latitudinal region. N = total number of monarchs + queens sampeld in a given pair of latitudinal belts. Estimates based on small sample sizes (i.e., belts 13/14 and 15/16) must be considered tentative, but are in accord with literature records on monarch and queen distribution (e.g., Burns, 1966; Harris, 1972; Howe, 1975).

| Latitudinal Belt | Median Latitude | % Monarchs | % Queens | N |
|---|---|---|---|---|
| 15/16 | 32.5° | 92 | 8 | 11 |
| 13/14 | 31.5° | 80 | 20 | 5 |
| 11/12 | 30.5° | 79 | 21 | 41 |
| 9/10 | 29.5° | 55 | 45 | 273 |
| 7/8 | 28.5° | 11 | 89 | 62 |
| 5/6 | 27.5° | 7 | 93 | 35 |
| 3/4 | 26.5° | 1 | 99 | 899 |
| 1/2 | 25.5° | 19 | 81 | 327 |

ward, increasing from 20% of the danaine total in belt 14 to 54% in belt 9. Finally, in Zone III (the "dark viceroy" zone), queens generally predominate, though monarchs do represent some 20% of the combined total in latitudinal belts 1–2, where year-round resident monarch populations exist (Knight, 1998; Knight and Brower, in press).

Figure 3 thus reveals an intriguing correlation between viceroy coloration and danaine biogeography. In the northern subset of latitudinal belts, where monarchs predominate, the viceroys are relatively light in color. Moving southward through Zone II, the increase in queen abundance is apparently "tracked" by a darkening of viceroy wing color. In the southern Zone III, where queens predominate, the viceroys are dark and much less variable in coloration.

This demonstration of a geographical correlation between viceroy wing-color brightness and danaine relative abundance offers substantial support for the model-switching hypothesis, which proposes that in general, viceroy coloration is evolutionarily "tuned" to the presence and relative abundance of different danaines in a given region. Specifically, viceroy wing-color variation in the southeastern United States appears to be related to a latitudinally changing selective environment created by the latitudinal shift in monarch/queen relative abundance. Viceroys essentially switch models along a latitudinal selective gradient.

But do viceroys actually gain any additional protection from this geographic model-switching? A recently reported laboratory study (Ritland, 1998) suggests that they do. In that study, red-winged blackbird (*Agelaius phoeniceus*) predators exposed to a series of queens and then offered the opportunity to attack light and dark viceroys exhibited a significantly greater aversion to the dark, queen-like viceroys. Conversely, monarch-conditioned birds tended to avoid light, monarch-like viceroys, attacking instead the dark viceroys offered. These results suggest that in nature, dark viceroys do have a selective advantage over lighter conspecifics in areas where queens predominate, while light viceroys are favored in areas where monarchs are the predominant model. This work demonstrates the type of selective mechanism on which the model-switching hypothesis is predicated.

Alternative explanations for the observed geographic pattern of viceroy wing-color variation have not yet been investigated. Such potential explanations include the influence of climatic or other abiotic variables, or geologically recent genetic introgression between light mainland and dark Florida viceroy populations postulated to have been segregated by a water barrier during the Pleistocene Epoch (Remington, 1968). However, of the various alternative hypotheses, only the model-switching hypothesis predicts not just the existence of a viceroy wing-color transition zone, but also its specific geographic location AND the latitudinal pattern of wing-color variation within the transition zone. This hypothesis specifically predicts that the origin and maintenance of the *L. a. archippus* and *L. a. floridensis* phenotypes, and the existence of a broad *L. a. archippus/L. a. floridensis* transition zone, can be understood in terms of selective predation on viceroys by danaine-conditioned predators. Thus, the cline in viceroy coloration is viewed as an adaptive adjustment to a latitudinal selective gradient associated with danaine relative abundance, and the viceroy transition zone represents an "adaptive boundary" (Yablokov et al., 1979) between light- and dark-phenotype viceroy populations.

The model-switching hypothesis is now supported both by a documented geographic correlation between viceroy coloration and danaine abundance, and by a laboratory demonstration of selective predation on viceroys by danaine-conditioned birds (Ritland, 1998). While it remains to elucidate the multi-locus genetic nature of the transition zone and to further investigate questions of its origin,

maintenance, and stability, the model-switching hypothesis currently offers the most compelling explanation for the observed geographic pattern of viceroy wing-color variation. It is anticipated that further studies — particularly a northward extension of the study area, a comparison among coastal and inland viceroy/danaine assemblages in both wing brightness and palatability (see also Moranz and Brower, 1998), and elucidation of allele-frequency clines for a series of metabolic enzymes — will shed light not only on the intricacies of viceroy butterfly mimicry, but also on the ecological and evolutionary dynamics of defensive mimicry in general.

## ACKNOWLEDGMENTS

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