The "Converse to Bergmann's Rule" in Tiger Swallowtail Butterflies:

Boundaries of Species and Subspecies Wing Traits are Independent of Thermal and Host-Plant Induction

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Size is an important fitness trait of adult insects, affecting territoriality, the ability to store energy or nutrients, mating attractiveness, ability to withstand temperature extremes, phenological timing of emergence, mating flights, and pollinator effectiveness; and variation in body size of insects has many causes (Chown and Gaston 2010). A widely recognized geographic pattern in the size of many insect groups is the "Converse to Bergmann's Rule," in which individuals have a smaller size at higher (cooler) latitudes (Mousseau 1997, Blanckenhorn and Demont 2004). While Bergmann's rule (animals tend to be larger at higher latitudes/altitudes) is commonly observed in endotherms and probably reflects responses to temperature (in that larger individuals have smaller surface-to-volume ratios), the converse of the rule seems to be mediated in insects by constraints on season length for organisms with one or two generations per year and limited time available for foraging, growth, and diapause (Nylin 1988, Scriber and Lederhouse 1992, Blanckenhorn and Dement 2004). Generation time relative to season length is a critical factor in determining whether Bergmann's rule or its converse applies (Scriber and Lederhouse 1992, Blanckenhorn and Demont 2004, Chown and Gaston 2010).

Tiger swallowtail butterflies are found throughout most of North America (Brower 1959, Scriber 1988, 1996a; Scriber et al. 1991, 1995), and the size of adults (measured by forewing length) represents an example of the "Converse to Bergmann's Rule" (Scriber 1994). The eastern tiger swallowtail, *Papilio glaucus* L. (Lepidoptera: Papilionidae), and its sister species, the Canadian tiger swallowtail, *P. canadensis* (Rothschild and Jordan) (Hagen et al. 1991) represent species of differing sizes that collectively range from Alaska to Florida (Ritland and Scriber 1985, Scriber 1988). A well-described hybrid zone between these species is located in the Northeastern-Central Suture Zone (Remington 1968, Scriber et al. 2003, 2008; Scriber 2011: Fig. 1), a region with multiple hybrid zones likely influenced by secondary contact of populations in expanding glacier refugia during the Pleistocene Epoch (Hewitt 1996, 2001; Swenson and Howard 2005).

A previously described inverse latitudinal trend with female body size (indexed as forewing length and correlated with pupal size; Scriber 1994, Ayres and Scriber 1994) showed that *P. canadensis* populations from central Alaska to the Great Lakes/New England hybrid zone ranged from mean forewing lengths of 43 mm to 48 mm, where there is a demarcation with *P. glaucus* populations. Average forewing lengths of populations of *P. glaucus* ranged from 50 mm in the North to 59 mm in Georgia, north of the Northern-Florida Suture Zone (Fig. 1); a region with multiple hybrid zones possibly influenced by the fluctuating sea levels of the Pleistocene Epoch (Lane 1994). Although characterized by unique morphometrics and
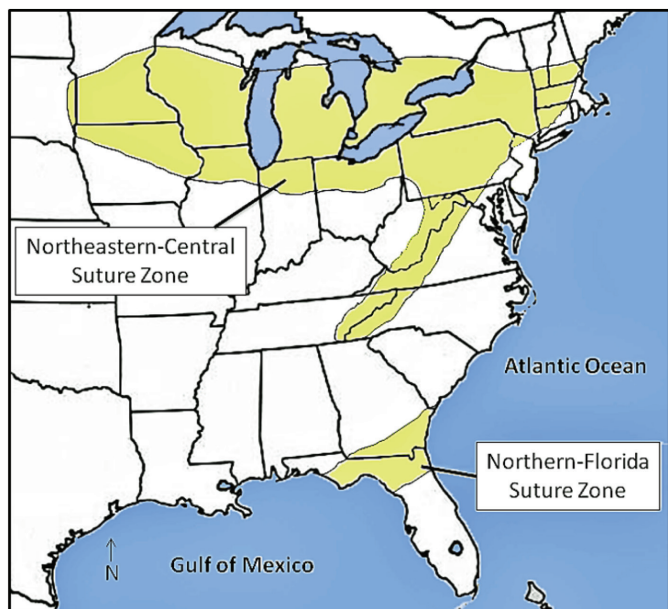
Fig. 1. Map of two suture zones that overlap regions where there are transitions in tiger swallowtail butterfly species or subspecies. The *P. canadensis* and *P. glaucus* hybrid zone resides within the Northeastern-Central Suture Zone. The transition zone of *P. glaucus* subspecies overlaps the Northern-Florida Suture Zone. Maps of suture zones are based on those presented by Remington (1968).

ecological adaptations, studies of the populations of *P. glaucus* south of the Northern-Florida Suture Zone (i.e. Florida populations of the putative *P. g. maynardi* (= *australis*) Gauthier subspecies) are lacking.

Individuals of *P. g. maynardi* have the largest reported forewing lengths for this species (e.g. "Converse to Bergmann's Rule") with mean spring flight females at 62-63 mm and late summer flights at 65-67mm (Scriber 1994), and an orange hue or ochraceous color on the wings (Maynard 1891, Lehnert et al. 2011), in contrast to the smaller yellow individuals of the northern *P. glaucus* subspecies (Fig. 2). The dark female morph of *P. glaucus*, a suggested mimic of
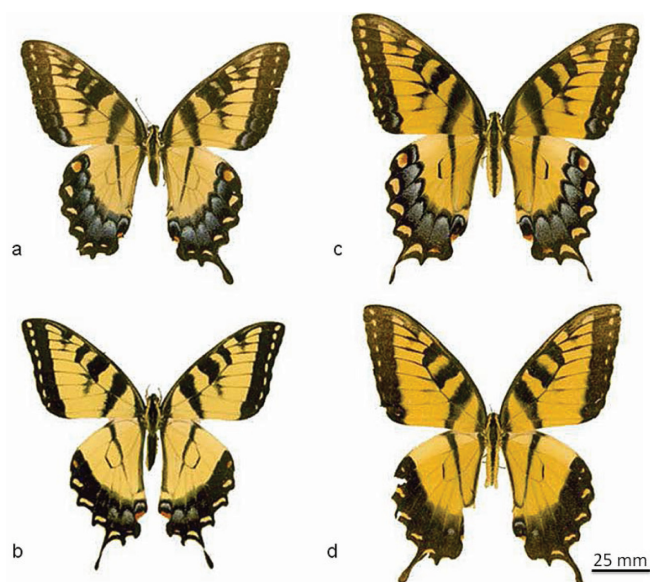

Fig. 2. Color-calibrated photographs of both subspecies of eastern tiger swallowtail. (A) and (B) represent female and male *Papilio g. glaucus*, respectively (captured from Vicksburg, MS, and La Fayette, GA, respectively). (C) and (D) represent female and male *P. g. maynardi*, respectively, from Cedar Key, Florida. Images were taken at the same magnification and color-calibrated according to methods described by Lehnert et al. (2011).

the Aristolochiaceae-feeding pipevine swallowtail, *Battus philenor* L. (Brower 1958), has been reported within the range of both *P. glaucus* subspecies (Lederhouse and Scriber 1987, Scriber et al. 1996).

Although dozens of host plant species are available throughout the range of *P. glaucus*, sweetbay (*Magnolia virginiana* L. [Magnoliaceae]) (Fig. 3) is the only host plant in the range of the monophagous southern Florida populations, and they prefer this plant in laboratory choice tests with a range of hosts (Scriber 1986, Bossart and Scriber 1995a,b; Scriber et al. 1998). Larval survival bioassays of Florida populations of *P. glaucus* suggest an ability to detoxify plants in the Salicaceae family (Lehnert and Scriber 2011), an ancestral trait not exhibited by the northern subspecies *P. g. glaucus* (Scriber 1988). The ability to detoxify both Salicaceae and Magnoliaceae are unique among 570 species of Papilionidae, occurring only in *P. canadensis*, *P. rutulus*, lab-paired hybrids, and the hybrid species *P. appalachiensis* Pavulaan and Wright (Scriber 1984 a,b; Scriber et al. 1995, Scriber and Ording 2005).
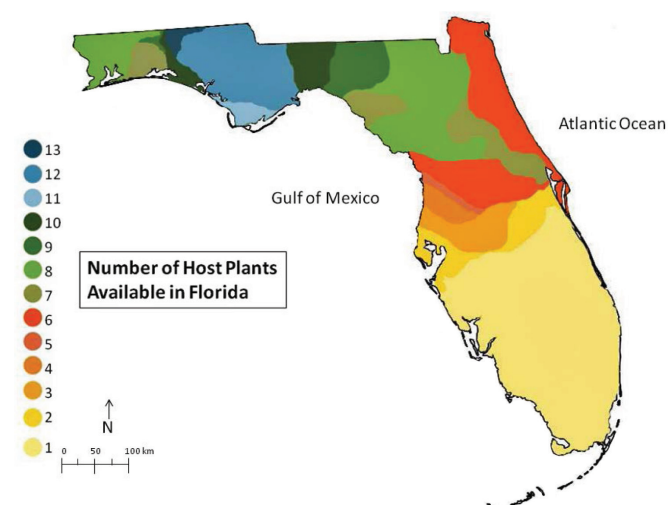

Fig. 3. Number of host-plant species available for populations of *P. glaucus* in Florida. The number of host plants decreases southward, and only one host plant, sweetbay (*Magnolia virginiana*), is available in southern Florida. Image is based on the number of reported host plants per county (after Scriber, 1986).

The putative transition zone between the two subspecies of eastern tiger swallowtail near the GA-FL border might overlap a transition in the number of potential host plant species (Fig. 3; Scriber 1986). This dual transition suggests a link between host-plant availability and unique wing traits (forewing length and color). Previous studies have demonstrated a correlation in forewing length and host plant choice and quality (Rodrigues and Moreira 2002). Here, we examine the influence of warmer temperatures (characterizing lower latitudes) and different host plants used during larval feeding stages to determine if the distinctive wing traits and "Converse to Bergmann's Rule" of these putative subspecies populations of *P. g. maynardi* (south of the transition zone; Fig. 1) are an example of environmentally induced phenotypic plasticity. Considering the location of the Northern-Florida Suture Zone and the putative transition in *P. glaucus* subspecies, we hypothesized that the diagnostic wing traits of the *maynardi* subspecies are not completely dependent on environmental cues, and are instead genetically controlled and possibly associated with the geological factors that influenced the formation of the suture zone.

In order to determine the role of temperature on wing traits (simulating spring versus late summer conditions), we also conducted

experimental split brood studies of pupae of both *P. glaucus* and *P. canadensis* for comparison. We hypothesized that temperature would have little effect on the diagnostic wing traits of northern populations of *P. glaucus* and *P. canadensis* based on results of a previous study (Scriber and Sonke 2011). We report on three decades of sampling female forewing sizes of dark and yellow morphs to see if they show the same patterns (including the larger wing size in the late summer flight season versus the spring flight; Scriber 1994) across the latitudinal geographic range for the bivoltine and trivoltine *P. g. glaucus* and *P. g. maynardi*.

Experimental Evaluation of Temperature Effects

We studied the impact of various spring emergence temperatures upon post-diapause development and wing traits using *P. canadensis* collected in Washington Co., NY and Bennington Co., VT (43° N latitude) and *P. glaucus* collected in Lancaster Co., PA (40° N latitude). Pupae were obtained from field-reared offspring of wild females of *P. canadensis* from the early flight in late May and June and similarly from *P. glaucus*; eggs of 12–25 females of each species were laid and larvae fed on black cherry branches sleeved with silk cloth. The pupae of both species were maintained in field sleeves for several weeks after pupation and were then shipped to Michigan State University in late August or early September. After an additional week at ambient temperatures of 17–20° C to detect any potential natural non-diapausing emergers, pupae were moved to winter below-snow simulation conditions (3–4° C in darkness) to assure that diapause was completely induced. Six months later, pupae were removed from the below-snow simulation, individually weighed, and placed inside individually screened cylinders (150 mm diameter) with Petri-dish lids and bottoms. Pupae were allocated to controlled-environment chambers (Percival Scientific, Perry, IA) at 14, 18, 22, and 26° C in long-day conditions (18L: 6D). Each chamber contained 30 or 31 *P. glaucus* or 29 *P. canadensis*. Survival of *P. glaucus* ranged from 97–100% for all temperature regimes except 14°, in which survival was 73.3%. Survival was also high for *P. canadensis* (86–100%) at all temperatures. The forewing lengths (mm) and hindwing band widths (%) were evaluated to determine the impact of spring emergence temperatures (see Luebke et al. 1988, Scriber 2002a, Scriber and Sonke 2011).

The responses of male and female pupae to cooler post-diapause spring conditions show that forewing length shortens for males and females of *P. glaucus* (a total range of 49–55 mm, Fig. 4), which might be due to greater use of energy reserves (Scriber et al. 2012). However, only females of *P. canadensis* showed a similar trend, and only at the coldest temperatures (14° C; a total range of 42–47 mm, Fig. 4). At cooler emergence temperatures, the hindwing band widths widened slightly in both sexes of *P. glaucus* (total range of 28–35%) but not in male or female *P. canadensis* (total range of 61–69%) when compared to warmer emergence temperatures (Fig. 4). In any case, this variable morphological plasticity in hindwing band width and forewing length does not alter their value as species diagnostic traits, since the interspecific differences between all *P. canadensis* and *P. glaucus* remain distinct. The phenotypic differences induced by adult emergence temperature regimes might explain some of the long-recognized latitudinal trend (and the late-season increases) in intraspecific wing lengths across eastern North America (i.e., "Converse to Bergmann's Rule") (Fig. 5, Scriber 1994), including populations of *P. appalachiensis* (Pavulaan and Wright 2002, Scriber et al. 2008, Ording et al. 2010). These results support our hypoth-
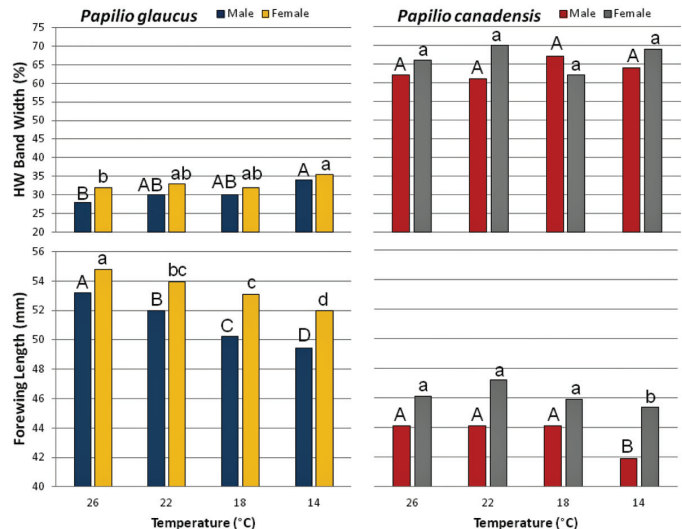
Fig. 4. The mean *P. glaucus* and *P. canadensis* hindwing black band widths (%) and forewing lengths (mm) as a function of spring emergence temperatures. Males are on the left and females on the right within each species for each treatment. Wing measurements were evaluated by analysis of variance (ANOVA, p = 0.05) for significant differences and a Tukey-Kramer Honestly Significant Difference (HSD) test (p = 0.05) was used to separate and compare means between treatments (females, small letters; males, capital letters).

esis that temperature would have little effect on the morphological dissimilarities between these genetically distinct *P. glaucus* and *P. canadensis* populations, and provides an example of the maintenance of species diagnostic traits in closely related species when exposed to different temperature regimes. However, Florida populations of *P. g. maynardi* populations apparently lack strong reproductive isolating mechanisms from the northern *glaucus* subspecies (Bossart and Scriber, 1995b).

Morphological Wing Traits

Wild individuals of both sexes of *P. g. maynardi* were collected during July–October 2007 and March–October 2008 from the southeastern U.S. and categorized as either north, within, or south of the
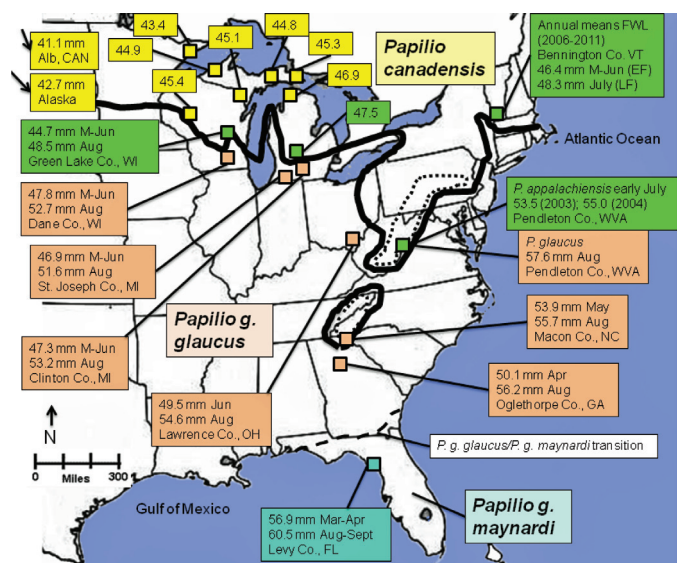
Fig. 5. The mean forewing lengths (mm) of males for populations of *P. canadensis* (yellow), *P. g. glaucus* (red), *P. g. maynardi* (blue), and hybrid populations (green) showing latitudinal trends and the differences between the spring and late summer flights. Forewing length is larger in the summer flights for all populations sampled.
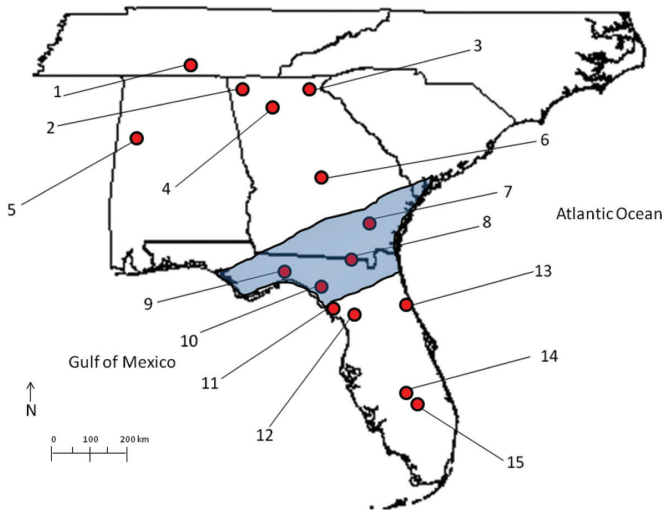
Fig. 6. Map of southeastern U.S. depicting *P. glaucus* collecting sites in relation to the Northern-Florida Suture Zone. North of the suture zone (blue), *P. glaucus* was collected from Elkton, TN (1), La Fayette, GA (2), Cooper's Creek, GA (3), Fairmount, GA (4), Fayette, AL (5), and Horse Creek, GA (6). In the suture zone, *P. glaucus* was collected from Waycross, GA (7), Florida/Georgia border (8), Wakulla, FL (9), and Perry, FL (10). South of the suture zone, specimens were collected from Cedar Key, FL (11), near Goethe State Park, FL (12), Barberville, FL (13), Sebring, FL (14), and Lake Placid, FL (15).

Northern-Florida Suture Zone (Remington 1968; Fig. 6) because the transition of subspecies possibly overlaps the suture zone. We also grouped butterflies as either a spring/early summer group (March–June, Time Period I) or a late summer/fall group (July–October, Time Period II) to detect a possible shift in wing traits of *P. glaucus* from the spring to fall broods. No females were collected north of the Northern-Florida Suture Zone in Time Period I. To assess differences in wing color, we isolated three regions with orange and/or yellow hues on wings of captured butterflies (n = 384 wild collected) and quantified them with the use of a lightbox, a color standard, a digital camera, and Adobe Photoshop 6.0 and LensEye® computer software according to Lehnert et al. 2011 (Fig. 7a-c). We recorded six wing measurements from each captured butterfly (Fig. 7d) based on obser-

vations of pinned specimens at the McGuire Center for Lepidoptera and Biodiversity (Florida Museum of Natural History, University of Florida) and a previous study (Luebke et al. 1988).

Wing traits were significantly different among the regions sampled (ANOVA, p = 0.05). Both sexes of *P. glaucus* collected south of the Northern-Florida Suture Zone had significantly larger forewing lengths and higher a* color values (more orange) than those collected north of the suture zone (Fig. 8). A linear discriminant analysis revealed a distinct classification distinguishing *P. glaucus* captured north of the suture zone (i.e., *glaucus* subspecies) from those captured in the other regions (i.e., *maynardi* subspecies) for both sexes, which was verified by cross-validation (Table 1). For instance, males of *P. glaucus* collected north of the suture zone in Time Period I (n = 28) were approximately 80% correctly classified, and the remaining individuals were classified as within the suture zone. Females from this region in Time Period II were 100% (n = 8) correctly classified; males from the same time period showed similar results (n = 46). These data were validated by the principal components biplots (Fig. 9), as these assemblages (females, NII; males, NI and NII) were positioned relatively distant from the other assemblages. These results suggest that the *glaucus* and *maynardi* subspecies have distinct wing traits and that the southern subspecies is most common in Florida.

The similarity of wing measurements and color values of populations within and south of the suture zone in both time periods (Table 1; Figs 9, 10) suggests that the *P. g. maynardi* subspecies occupies both of these regions (Fig. 9). Our results illustrate the existence of significant differences in orange coloration (higher a* and b* values for red and yellow, respectively) and forewing lengths (FWL) for populations within and south of the suture zone (Figs. 6, 7) compared to those farther north. Both of these traits (large wing size and orange hues) previously have been considered indicative of the *maynardi* subspecies (Maynard 1891; Lehnert et al. 2011), but this study verifies these characters as diagnostic traits. Color values and wing measurements shifted from Time Period I to Time Period II (Fig. 8 and 9) in populations of *P. g. maynardi*; they became more orange and larger throughout the season. Populations of *P. g. glaucus* also displayed a positive shift in color values and wing measurements,
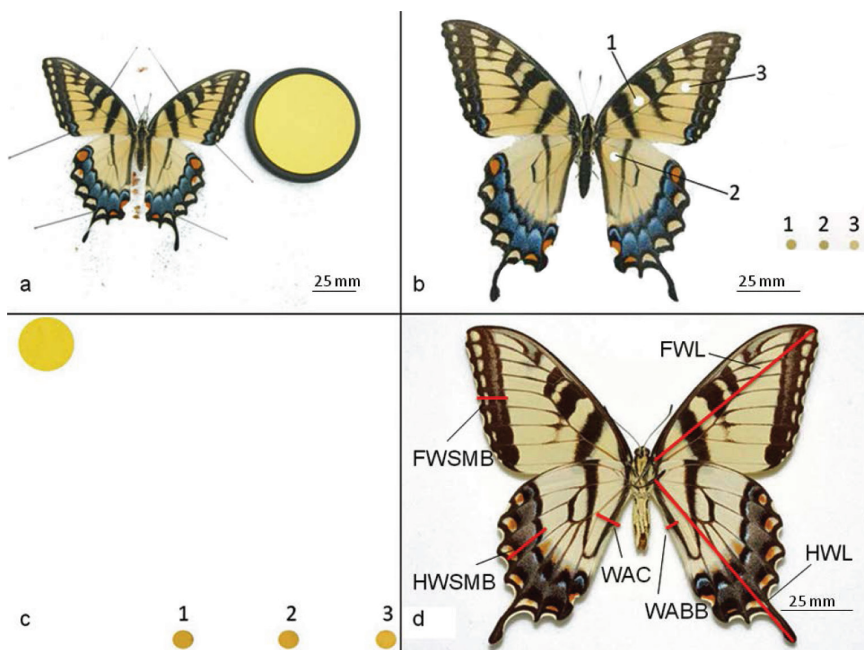

Fig. 7. Regions of wings of *P. glaucus* analyzed to study color values and morphometrics. (A) Raw image of female of *P. glaucus* with a Labsphere® yellow-color standard with known L* (lightness, scale: 0 – 100), a* (green to red, scale: -120 – 120), and b* (blue to yellow, scale: -120 -120) values of 90.17, -3.27, and 74.30, respectively. (B) Areas analyzed to obtain color values were (1) the forewing discal cell between the two proximal black stripes, (2) the discal cell of the hindwing between the stripe and the black anal margin, and (3) within the M2 cell of the forewing. The regions of interest and a yellow circle in the color standard were isolated in Adobe Photoshop 6.0 and moved to a new file and saved as a Bitmap image (24 bit). The image was opened in LensEye software and calibrated (C) to receive the L*, a*, and b* values used for color analysis. (D) The six wing measurements (red lines) recorded from the ventral side of each *P. glaucus* were forewing length (FWL), width of black band within anal cell of hindwing (WABB), width of anal cell of hindwing (WAC), hindwing length (HWL), width of hindwing black submarginal band (HWSMB), and width of forewing black submarginal band (FWSMB). Photograph in (D) copyright of Kim Davis, Mike Stangeland, and Andrew Warren 2008, Butterfliesofamerica.com.
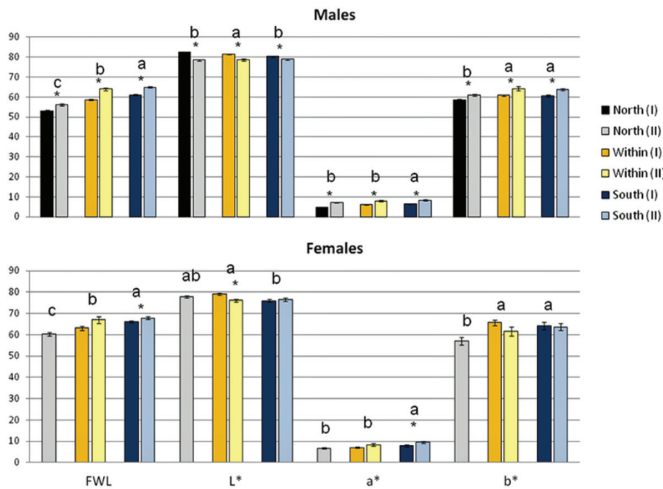
Fig. 8. Forewing length and color value summaries for populations of *P. glaucus* north, within, and south of the Northern-Florida Suture Zone. Forewing length (FWL, mm) and color values (L*, a*, and b*) are expressed as the mean ± SE of all sampled populations per time period (I, II) of each region (males, n = 37, 46 (north); 146, 18 (within); 64, 57 (south); females, n = 0, 15 (north); 15, 6 (within); 23, 25 (south), captured in Time Periods I and II, respectively). An ANOVA (p = 0.05) was used to test for significant differences (*) of values between each time period, and a Tukey's HSD (p = 0.05) was used to apply rankings to the means of the time periods within groups, as shown with letters above bars; bars within groups with the same letter are not significantly different. Sexes were separately analyzed to account for possible differences in wing-color values and morphometrics, and because no females were collected north of the suture zone in Time Period I. As seen here, both sexes of *P. glaucus* collected north of the suture zone had significantly different forewing lengths and a* and b* color values (represent orange hues) than those collected within and south of the suture zone.

but these butterflies always lacked the orange color values and large wing measurements diagnostic of the southern populations, implying that these subspecies' traits remain distinguishable in time and space.

Host Plant and Temperature Effects

We used offspring from females of *P. glaucus* collected in 2008 to study the impact of temperatures and host plants on wing traits. Eggs were collected from females placed in revolving plastic arenas in front of a light-bank (Scriber 1993; as modified by Lehnert and Scriber 2011). The eggs were removed from host-plant leaves and kept in a Petri dish at long-day conditions (18:6h photoperiod) at 22°–25° C until hatching. Neonates from females collected in Time Period I were randomly placed on one of four different aqua-picked host plants inside plastic dishes with lids (Rubbermaid TakeAlongs, Atlanta, GA) and kept at the same environmental conditions as the eggs. The four host-plant treatments were sweetbay (SB); black cherry (BC), *Prunus serotina* Ehrh (Rosaceae); green ash (GA), *Fraxinus pennsylvanica* Marshall (Oleaceae); and Carolina willow (W), *Salix caroliniana* Michx. (Salicaceae). Tulip tree, *Liriodendron tulipifera* L. (TT) (Magnoliaceae), was added as a fifth host plant to Time Period II.

Second-instar larvae and their assigned host plants were placed in controlled-environment chambers (Florida Reach-In Chambers, University of Florida) set at various temperatures, with a 15:9h photoperiod. Larvae from females collected during Time Period I were placed in chambers with a constant temperature of 22, 24, or 27° C, or a fluctuating temperature of 22–32 or 17–30° C, representing the average daily summer temperatures of Naples, FL, and La Fayette, GA, respectively. Larvae from Time Period II were placed in chambers with a constant temperature of 24° C or average daily

summer temperatures of Naples, FL or Lansing, MI (14–27° C). At least three environmental chambers were used for each temperature. Temperatures from these locations were chosen because Naples, FL hosts southern populations of *P. g. maynardi*, and the other two locations host *P. g. glaucus*. The chosen temperatures also represented the average summer temperatures (June–August, acquired from the National Oceanic and Atmospheric Administration, www.noaa.com) of nearly the most northern (Lansing, MI) and southern (Naples, FL) range limits of *P. glaucus*. If temperature and/or host ~~plant availability~~ is responsible for the wing traits diagnostic of the southern subspecies, these temperatures and host-plant regimes were expected to induce the response. Reared adults (n = 274) were passed through color analysis and morphometric measurement procedures to determine the effects of temperature and host plant on phenotypes.

Despite our different temperature and host-plant rearing regimes, the standardized linear discriminant analysis revealed a classification system similar to the wild-collected *P. glaucus* (Table 1). The standardized linear discriminant analysis, however, made some mistakes when classifying offspring reared from mothers collected south of the suture zone; for instance, almost 75% (n = 51) of males from south of the suture zone were incorrectly classified as collected within the suture zone, apparently due to temperature or host plant having a small effect on the color values and wing measurements. The main effects of temperature and host plant were significant (ANOVA, p = 0.05) for FWL for both sexes of offspring reared from mothers captured south of the suture zone. Host plant had significant effects on a* values for females and L* and b* color values for male and female offspring from south of the suture zone, and temperature had significant effects on the a* values of males.

The results from these temperature and host plant regimes, however, are the opposite of what would be expected between subspecies under natural conditions. Larvae fed tulip tree or black cherry, for instance, produced larger adults with more orange than those fed sweetbay, the only host plant available to southern Florida populations (Fig. 3), which have diagnostically larger wing sizes and more orange hues than northern populations (Scriber 1986, Bossart and Scriber 1995a,b; Lehnert and Scriber 2011). We found no significant host-plant and temperature interactions for FWL or L*, a, and b*
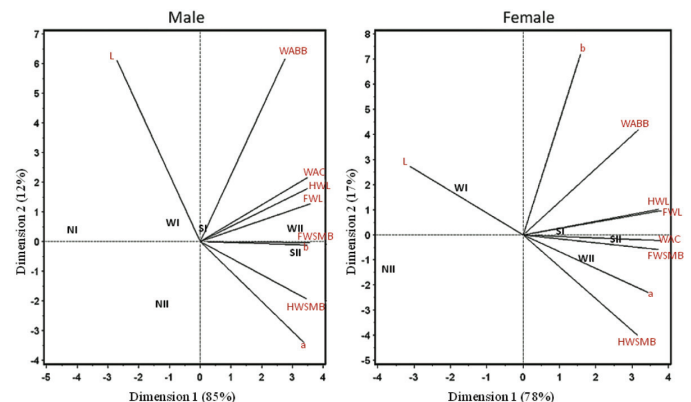

Fig. 9. Principal components biplot depicting the correlation between color values and wing morphometrics for each sex of *P. glaucus* between regions and time periods. Each assemblage represents the region where the butterfly was collected (north = N, within = W, south = S) in relation to the Northern-Florida Suture Zone, and the time period (I or II). For instance, males and females collected north of the suture zone for both time periods (NI and NII, but representation for NI by females) were distinct from individuals collected within and south of the suture zone of both time periods (WI and WII, SI and SII, respectively). Each vector represents a color value or wing measurement.
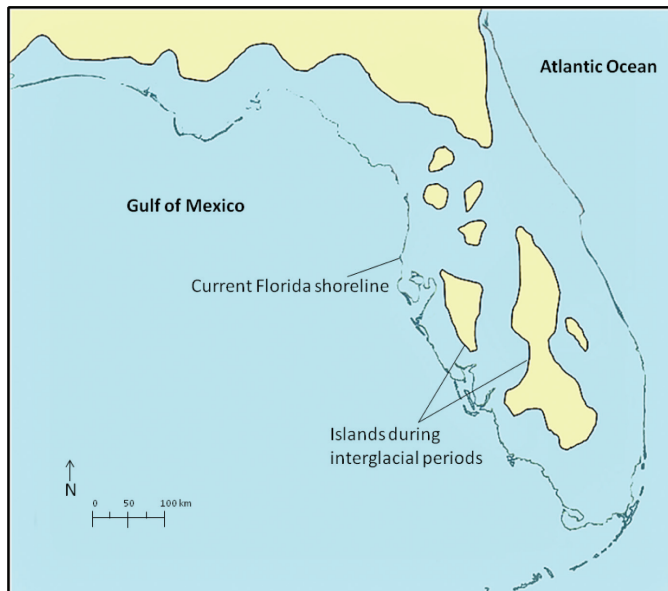
Fig. 10. Terrestrial Florida during interglacial periods of the Pleistocene Epoch. We suggest that isolated populations residing on Florida islands diverged from mainland populations and created the Northern-Florida Suture Zone after sea levels receded. An outline of present-day Florida has been provided for reference. Image is based on previously reported maps (Lane 1994).

color values (ANOVA; P = 0.05) of males and females from mothers collected south of the suture zone; the other zones were not tested because of smaller sample sizes. This study provides evidence that for *P. canadensis*, *P. g. glaucus*, and *P. g. maynardi*, the temperatures during adult eclosion can have a direct impact on the wing traits of emerging adults (but not so much as to reduce the species/subspecies diagnostic value of these traits [see below and Figs. 4 and 5]), and are perhaps responsible for the latitudinal trends observed within species and subspecies. The "Converse to Bergmann's Rule" apparently applies to wing traits (forewing size) within tiger swallowtail species and subspecies, and also to the entire tiger swallowtail complex in eastern North America, with significant and abrupt increases in forewing length across species and subspecies boundaries.

We recognize that other environmental factors during larval feed-ing periods (e.g. humidity, water content in leaves, host-plant quality) could also influence color values, size, and wing measurements of wild specimens. For example, size of some genotypes of the northern *P. canadensis* can also be affected by diurnal temperature variation. A previous study of adult emergences with the same average daily temperatures and identical degree-day accumulations (but with variable diurnal temperature extremes) showed that the variation itself might differentially affect wing traits such as forewing length and hindwing band widths (Scriber and Sonke 2011). Here we saw that thermal vacillation (variability) of cooler temperatures (as in Lansing, MI) and the warmest temperatures (simulating Naples in southern Florida) also resulted in more orange coloration on *P. glaucus* wings.

We were also interested in examining how the genetically controlled dark morph phenotype of females of *P. glaucus* in Florida compares to the size of the yellow morph females (if there is a similar transition in size across the Northern-Florida Suture Zone, i.e., "Converse to Bergmann's Rule"). Three decades of sampling females of both color morphs (dark and yellow) from Michigan to Florida have shown remarkable similarity in their forewing lengths, both during the first generation (spring) emergences and also for late summer; the late summer females were larger (Table 2 with more than 2,300 total female specimens; see also Scriber 1994). It is also interesting that the daily fluctuations over the 2-week flight period in Levy County, FL also remain minimal, with the dark and yellow females of the same size throughout (Table 3). The similar size of dark and yellow morph females across space and time also suggests minimal physiological costs for possessing the Z-linked mimetic melanism trait and the W-linked enabler (Scriber et al. 1996; True 2003; Kunte 2009). Such phenotypic consistency, even with the environmentally induced differences in thermal and host plant regimes we reported here, suggests a strong genetic basis for the unique wing traits (size and color) of the Florida subspecies. The relative frequencies of dark morph and yellow morph females of *P. glaucus* remains remarkably consistent in Levy Co., FL (Table 4) and also across latitudes from 27° to 42° N (Scriber et al. 1996; Table 2; but see Lederhouse and Scriber 1987) The various potential selection pressures on dark versus yellow morphs have not been fully evaluated to date, but mimicry, sexual preferences, thermoregulation, and costs of melanism might be involved (True 2003; Kunte 2009; Aardema and Scriber 2012).

Table 1. Linear discriminant analysis classification of *P. glaucus* north, within, and south of the suture zone by time period (I: March–June; II: July–October) with cross-validation. The data from offspring (Lab-reared) were standardized because of the possible effects of rearing in captivity and were then subjected to the classification rule established from the wild-collected butterflies. Standardization had no impact on the classification results for the wild butterflies.

Sex	Time Period	Region	Wild-collected				Lab-reared (standardized)			
			n	North	Within	South	n	North	Within	South
Female	I	North	0	-	-	-	0	-	-	-
		Within	16	-	25	75	20	-	65	35
		South	23	-	69.57	30.43	56	-	25	75
	II	North	8	100	0	0	1	100	0	0
		Within	4	0	0	100	13	30.77	0	69.23
		South	15	6.67	0	93.33	30	26.67	0	73.33
Male	I	North	28	78.57	21.43	0	0	-	-	-
		Within	124	4.03	87.9	8.06	22	13.64	86.36	o
		South	45	0	64.44	35.56	51	15.69	74.51	9.8
	II	North	46	97.83	0	2.17	7	42.86	0	57.14
		Within	18	11.11	0	88.89	21	28.57	0	71.43
		South	57	1.75	0	98.25	53	30.19	0	69.81

Table 2. Forewing lengths (mm) of yellow and dark morph females of *P. glaucus* from different locations in eastern North America (presented as mean ± sd). Spring flights (first generation in March or April) and late summer flights (late July–early September) are indicated in bold.

Location	Year	N	Yellow	n	Dark
Michigan	1999 July-August	23	54.3 ± 1.8	15	57.1 ± 2.7
(St. Joseph Co.)	2003 August	2	57.0 ± 4.2	2	55.5 ± 3.5
	2003 May	4	49.0 ± 0.8	3	50.7 ± 2.1
Georgia	1993 August	57	57.8 ± 2.8	166	58.2 ± 2.2
(Clark Co.)	1994 August	52	58.4 ± 3.5	105	57.9 ± 3.0
	1995 August	56	59.4 ± 2.9	152	59.1 ± 2.8
	1996 August	8	57.3 ± 2.5	38	57.4 ± 2.8
	1997 August	17	59.5 ± 2.3	68	58.0 ± 2.4
	1998 August	48	57.2 ± 2.8	101	58.0 ± 2.8
	2008 August 1-10	16	59.5 ± 1.4	15	59.3 ± 2.6
	2008 August 12-21	23	59.0 ± 2.0	22	59.1 ± 2.1
	2009 August	21	58.3 ± 1.8	16	59.5 ± 2.9
	2010 August	17	57.5 ± 2.1	16	58.6 ± 2.7
	2011 August	8	57.3 ± 1.9	3	57.0 ± 2.6
	1989 August	15	59.5 ± 2.6	44	58.7 ± 3.1
	1989 March-April	43	52.0 ± 2.3	92	51.7 ± 3.6
	2006 April	26	52.7 ± 2.7	34	54.2 ± 2.7
Florida	**1994 March-April**	37	62.2 ± 3.6	18	62.8 ± 2.5
(Highlands Co.)	**1995 March-April**	14	61.7 ± 1.6	3	61.3 ± 1.5
	1995 September	6	66.3 ± 2.6	8	68.1 ± 1.7
	2008 March-April	12	63.2 ± 3.2	4	63.8 ± 1.7
Florida	**2000 March-Aprl**	46	64.9 ± 2.6	73	65.5 ± 2.6
(Levy Co.)	**2002 April 1**	49	63.0 ± 0.3	49	63.8 ± 0.4
	2002 April 2	31	63.0 ± 0.6	32	63.6 ± 0.4
	2002 April 5	13	64.1 ± 0.6	34	64.6 ± 0.5
	2002 April 9	16	64.3 ± 0.5	28	64.5 ± 0.4
	2004 March-April	14	64.4 ± 3.1	20	64.1 ± 1.9
	2006 March-April	56	62.9 ± 3.1	75	63.1 ± 2.8
	2007 March-April	18	62.1 ± 2.3	34	63.3 ± 2.5
	2008 March-April	132	64.2 ± 2.1	166	64.8 ± 2.2
	2009 March-April	25	63.0 ± 2.0	26	62.2 ± 1.9
	2010 March-April	20	62.5 ± 2.7	20	63.3 ± 1.9
	2003 March-April	6	62.5 ± 3.6	4	63.8 ± 1.7
	2003 September	8	68.6 ± 3.2	3	68.7 ± 2.9

Also see 2008 FL Levy Co. daily variation shown in Table 3

Size impacts the fitness traits of insect adults (Chown and Gaston 2010), and the size (forewing length) of adult tiger swallowtail butterflies tends to decrease with increasing latitude (from 70 mm forewing lengths in Florida to 35 mm in Alaska; Scriber 1994). This pattern of smaller size at higher (cooler) latitudes reflects the "Converse of Bergmann's Rule" (as is often seen in ectotherms; Mousseau 1997; Blanckenhorn and Demont 2004). While trait size is not always a simple readout of body size (Shingleton et al. 2009), a saw-toothed pattern in forewing lengths where these *Papilio* transition from bivoltine to univoltine has been documented (Scriber 1994), and for other butterflies (Nylin and Svärd 1991) and crickets (Masaki 1978). Various trade-offs in adult size (Scriber 1994) and progeny size (Ayres and Scriber 1994; Fox and Czesak 2000) have often been invoked to explain these patterns, and the temperature versus seasonal constraints hypotheses are not mutually exclusive (Nylin and Gotthard 1998, Chown and Klok 2003, Pörtner et al. 2006, Deutsch et al. 2008).

The strong selection for smaller pupal sizes of tiger swallowtail butterflies in Alaska (Ayres and Scriber 1994) and in climatic cold pockets of northern Michigan and Wisconsin (Scriber 1996b, 2002b) permits completion of a single generation, especially if combined with female choice of the best host plants for rapid growth. Relaxed

selection for choosing these fast-growing plant species has been reported in warmer areas for *P. canadensis* and also for *P. glaucus* areas (as in southern Ohio) where two generations are possible on many plant species (even poorer hosts; Scriber 2002b). This phenomenon (abiotic thermal influence on biotic host-plant selection

Table 3. Dark and yellow female frequencies and forewing lengths (mm) at Levy Co. Florida from March 20–April 8, 2008.

Date	N	Dark	N	Yellow
20-March	10	64.1 ±1.6	4	64.0 ± 2.1
21-March	18	64.2 ±2.9	15	63.8 ± 2.2
25-March	22	64.7 ±1.8	19	64.5 ± 2.1
26-March	14	66.2 ±1.8	13	64.7 ± 1.8
27-March	27	65.3 ±2.6	27	64.2 ± 1.8
28-March	8	64.6 ±2.3	5	63.8 ± 1.3
30-March	11	64.3 ±1.3	12	64.3 ± 2.2
31-March	11	64.8 ±1.9	6	64.7 ± 1.9
2-April	6	63.3 ±2.1	4	65.5 ± 2.4
3-April	15	65.5 ±3.2	13	63.5 ± 2.2
4-April	9	64.7 ±1.7	7	64.0 ± 3.0
5-April	7	63.4 ±2.9	3	64.7 ± 0.6
8-April	8	64.1 ±1.6	4	63.0 ± 2.8

No significant differences between dark and yellow means (Tukey-HSD; p = 0.05)

Table 4. Frequencies (captures & sighted) of dark morph females near the southern edge of the range of *P. glaucus* in Levy Co. Florida. (All collections were between mid-March and mid-April).

Year	Total females (dark and yellow)	% dark
2011	16	50
2010	40	50
2009	83	53
2008	729	57.9
2007	133	60.9
2006	132	56.8
2005	55	56.4
2004	45	60
2003	14	42.8
2002	454	58.8
2001	18	44.4
2000	135	60
1995	50	68
1993	26	65.4

patterns) has been called the "voltinism-suitability hypothesis" (see Scriber 2010 for a review). In most of Florida, there are sufficient degree-days each year for three generations. However, sweetbay is the only reported host plant in the southern half of the state. While these *Papilio* populations are adapted to survive better on and process these leaves more rapidly and efficiently than other allopatric populations (Scriber 1986), they are not the best hosts for large size, as we have shown here, and are not responsible for the "Converse of Bergmann's Rule" demonstrated by these *Papilio*.

A suite of morphological (e.g. unique wing traits) and ecological characters (sweetbay specialization, Scriber 1986, Bossart and Scriber 1995a,b; Salicaceae detoxification, Lehnert and Scriber 2011) distinguish the *maynardi* subspecies from northern *glaucus* populations. Molecular studies between *P. g. glaucus* and *P. g. maynardi*, however, have been confined to allozyme studies (Hagen & Scriber, 1991; Bossart & Scriber, 1995b; but see Kunte et al. 2011). Regardless of the lack of molecular data, the accumulation of morphometric and ecological data provides evidence that historical geographic factors might have contributed to the uniqueness of these populations.

As demonstrated here, the transition from the *maynardi* subspecies to *glaucus* subspecies apparently overlaps the Northern-Florida Suture Zone, which suggests that the evolutionary history of these butterflies might be tied to the geological events that also impacted the other hybrid zones here (Remington 1968). The lack of climatic (Remington 1968) or geological change in landforms (e.g. mountains) along a north-south transect of the Northern-Florida Suture Zone indicates that vicariance events might be attributable to rising sea levels during the Pleistocene, which acted as a geographic barrier preventing gene flow between Florida islands and mainland populations (Fig. 10) .

The shape of terrestrial Florida has been dynamic, with at least four great glaciations recognized during the Pleistocene (Lane, 1994), and sea level fluctuations have produced at least five distinct shorelines above the current sea level (Webb, 1990). Florida shorelines have ranged from 130 m below the current sea level during glacial maximum periods (which increased the land area of Florida and likely served as a large refugium for populations moving southward to escape encroaching glaciers and cool temperatures) to more than 30 m above present sea level during warm interglacial periods. During the warmest interglacial periods, the rising sea levels submerged portions of Florida and created a large island refugium in central

Florida, with various small islands northward (Neill 1957, Ellsworth et al. 1994, Lane 1994, Fig. 10). Higher sea levels from earlier periods (Eocene or Miocene) might have created large geographic separations between Florida islands and the mainland (e.g., the Suwanee strait, Webb, 1990).

We suggest that *P. glaucus* and other lepidopteran species, as well as vertebrate species (Swift et al. 1986, Ellsworth et al. 1994, Smith and Farrell 2005), were isolated in Florida during the warm interglacial periods. Some genetic divergence might have occurred among these isolated populations compared to mainland populations, indicated by the unique host-plant detoxification abilities (Bossart and Scriber 1995a,b; Lehnert and Scriber 2011) and morphology of the *maynardi* subspecies (possible holdovers from the Pleistocene). We suggest that reproductive isolation of island populations from mainland populations was relatively short-lived or only reduced to rare gene-flow events due to high dispersal abilities of Lepidoptera; thus, full speciation did not occur, but resulted in multiple hybrid zones of subspecies (listed by Remington 1968) when sea levels receded. These dynamics differ from the vertebrates with fewer dispersal abilities, where those hybrid zones probably have stronger pre- and post-zygotic reproductive isolating mechanisms (Ellsworth et al. 1994; Hill et al. 2011) than *Papilio* (Deering and Scriber 2002).

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