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THE "TRIGON" WING PATTERN VARIANT IN FEMALE *PAPILIO GLAUCUS* (PAPILIONIDAE) IN AN INDIANA POPULATION

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ABSTRACT. A small percentage of adult dark-morph female eastern tiger swallowtails, *Papilio glaucus* L. (Papilionidae), display wing coloration patterns intermediate between those of normal yellow-morph and normal dark-morph females. One of these patterns (which, for the sake of convenience, I refer to in this paper as the "trigon" pattern) involves normal melanization of the scales in the basal portions of the dorsal wing surfaces but incomplete melanization of the scales in the central portions, resulting in the appearance of an inverted triangle (trigon) centered on the insect's body when the wings are outstretched. Between mid-July and mid-August 2010, I observed trigon-type female *P. glaucus* in the Terre Haute (Vigo Co.), Indiana region for the first time since I had begun systematically observing the *P. glaucus* in the area in 2002. Five trigon-type females out of 2,388 females were observed, suggesting that the trigon type comprised about 0.2% of the local female *P. glaucus* population. An examination of photographs of *P. glaucus* posted on an insect/spider identification website by users from throughout *P. glaucus*'s range revealed a notable increase in the percentage of trigon-type females in 2010, suggesting that the Vigo Co. increase was not a localized phenomenon. I concluded that the unusually high temperatures that prevailed in the summer of 2010 affected wing pigment production during pupal development, thereby serving to make the trigon phenotype more prevalent that year. Other evidence further suggests that in general the prevalence of the trigon phenotype is associated with elevated temperatures (e.g. severe heat events). The findings of the present study suggest that if record high temperatures continue to prevail throughout *P. glaucus*'s range during pupal development times, dark female *P. glaucus* expressing the trigon (and other intermediate) color patterns could become more prevalent, potentially altering the dynamics of dark female *P. glaucus*'s mimetic relationship with *Battus philenor* in the most impacted populations.

Additional key words: melanin, papiliochrome, temperature-sensitive phenotypic variation, wing pattern development, climate change

The eastern tiger swallowtail, *Papilio glaucus* L. (Papilionidae), ranges throughout the eastern half of the United States from New England west to the Great Plains and south to northeastern Mexico (Tyler et al. 1994). "Normal" adult females occur in both a yellow morph similar in appearance to the male and a dark morph in which the yellow is replaced with black dorsally and brown ventrally (Fig. 1a–b). In addition, a small percentage of female *P. glaucus* exhibits "intermediate" color patterns, which appear to involve the incomplete melanization of a genetically dark form (Ritland 1986).

In one type of rare dark-morph variant, the scales in the basal areas of the dorsal side of both the forewings and the hindwings are melanized, "filling in" the regions between the thorax and the inner edge of the proximal set of "tiger" stripes. The remaining wing surface, excluding the distal "tiger" stripes and marginal black bands, is generally yellow, although in some individuals it can appear "dusted" with varying proportions of dark scales. Because the proximal one-third of the dorsal wing surface is melanized and the resulting pattern gives the impression of an inverted triangle centered on the body when the outstretched wings are viewed from the dorsal side, I refer, for the sake of convenience, to this otherwise unnamed pattern as the "trigon" pattern. Both naturally occurring and experimentally produced females of this type have been reported in the literature (e.g. Edwards 1884 Fig. 5.2–3; Clark 1932 Fig. 38.2, also figured in Clark & Clark 1951 Fig. 21h; Ehle 1981 Fig. 1.2; Ritland 1986 Fig. 1.4; Scriber et al. 1987 Fig. 3a; Tyler et al. 1994 Fig. 94l) and photographs of these individuals have appeared online. The trigon pattern appears to represent a categorically distinct and consistent intermediate phenotype.

Between mid-July and mid-August 2010, I observed five trigon-type female *P. glaucus* in the Terre Haute (Vigo Co.), Indiana region (Fig. 1d–h). Although other intermediate females displaying an overall "dusting" of yellow and black scales but lacking the trigon pattern were also observed (e.g. Fig. 1c), such females are observed every year at low numbers, usually comprising ~0.5–1.0% of the female population. The sightings of the trigon-type females in 2010 marked the first time that I had observed this type since I had begun systematically observing the *P. glaucus* in the Terre Haute area in 2002. This paper discusses the 2010 observations and possible reasons for the appearance of this phenotypic variant.

METHODS AND MATERIALS

I observed trigon-type female *P. glaucus* while collecting data on the percentages of males, yellow females, and dark females at the J. I. Case Wetland Wildlife Refuge at Hawthorn Park in Terre Haute (39°29′20.0″ N, 87°19′05.0″ W) and at my home in Terre Haute during July and August 2010. I photographed all of these females with a digital camera at 2816 × 2112 pixel resolution on the dorsal side, where the trigon pattern is the most conspicuous, and

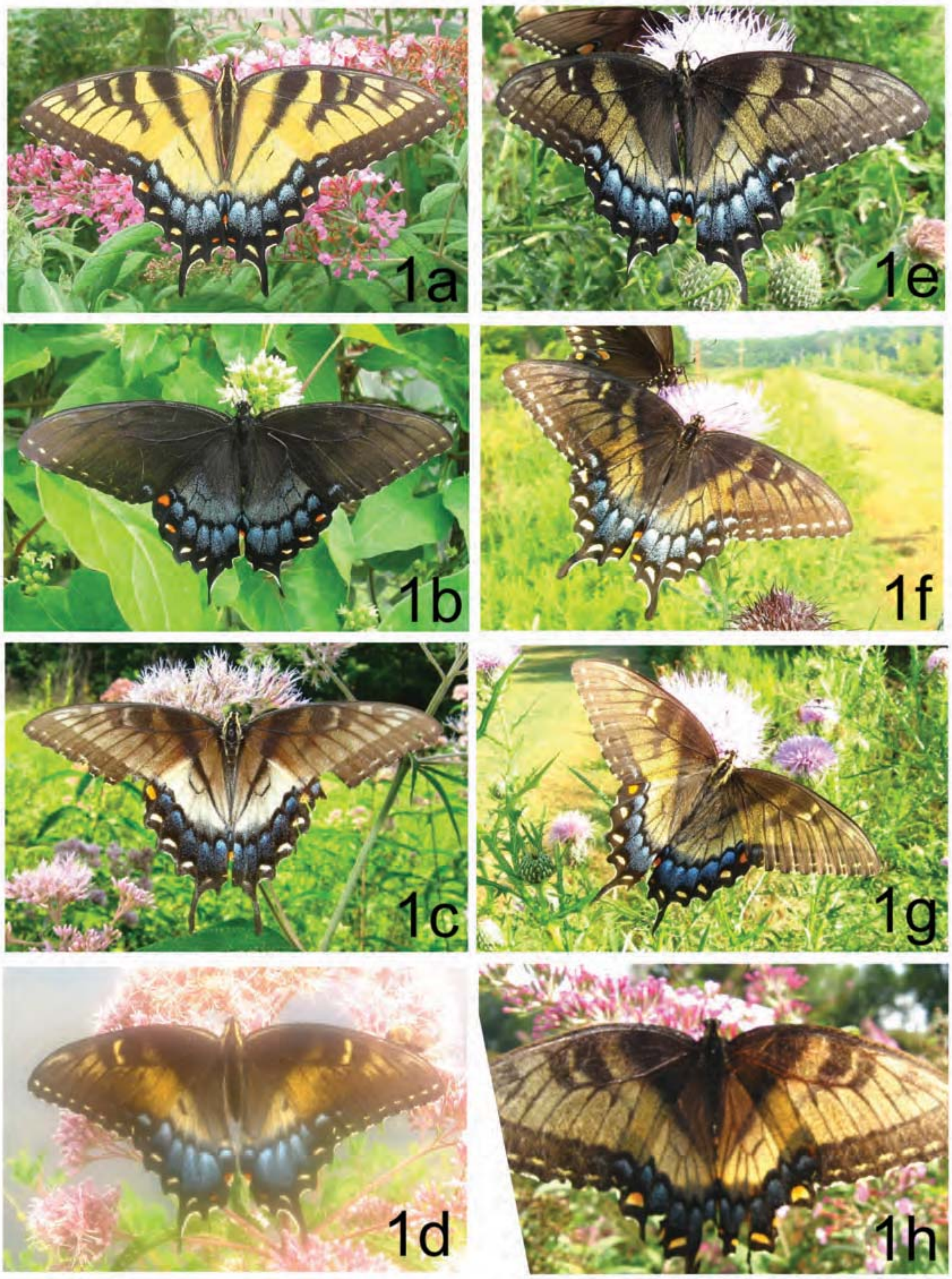

FIG. 1. "Normal" and "trigon"-type adult female *Papilio glaucus* from Vigo Co., Indiana. **(a)** Normal yellow female, 29 July 2006, author's home. **(b)** Normal dark female, 23 July 2004, author's home. **(c)** Intermediate non-trigon-type female, 7 August 2010, J. I. Case Wetland Wildlife Refuge. **(d)** Trigon-type female, 21 July 2010, 1333 h, taking nectar from *Eutrochium fistulosum* (Barratt) Lamont, J. I. Case Wetland Wildlife Refuge near SW corner of lake. FW length: 49.5 ± 3.3 mm. **(e)** Trigon-type female, 17 August 2010, 1400 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge near SE corner of lake. FW length: 50.0 ± 3.3 mm. **(f)** Trigon-type female, 22 August 2010, 0919 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge near SE corner of lake. FW length: 53.9 ± 3.3 mm. **(g)** Trigon-type female, 24 August 2010, 1009 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge near SE corner of lake. FW length: 51.8 ± 3.3 mm. **(h)** Trigon-type female, 19 August 2010, 1303 h, taking nectar from *Buddleja davidii* Franch., author's home. FW length: 55-60 mm. All photographs © Roger Carpenter.

recorded data relevant to each observation (e.g. date, time, location, behavior).

Although I did not obtain morphometric data, I estimated forewing length from photographs in which the wings were positioned parallel to the camera lens and the body was fully visible. Assuming an average body length of 26.7 mm (based on previous sampling of second-brood female *P. glaucus* in Vigo Co.), forewing length in pixels was divided by body length in pixels and the resulting value was multiplied by 26.7 to derive forewing length in millimeters. The confidence interval (95%) was based on the standard deviation derived from the body length data (SD = 1.7 mm; 95% CI ± 3.3 mm).

I estimated the proportions of trigon-type females in both the female and dark female samples (CI = 95%). In addition, I performed z-tests of proportions (two-tailed) to determine 1) if the proportions of trigon-type females observed at the Refuge and at my home, respectively, significantly differed and 2) if the proportions of trigon-type males and that of females, respectively, significantly differed. Statistical analyses were performed using SPSS v20.0 software (IBM Corp. 2011).

Results

At the Refuge, I observed four trigon-type females out of a total sample of 2,325 females (0.17 ± 0.17%). These individuals are illustrated in Fig. 1d–g. At my home, I observed one trigon-type female out of a total sample of 63 females (1.6 ± 3.1%). This individual is illustrated in Fig. 1h. The overall percentage in the combined sample (n = 2,388) was 0.21 ± 0.18%, suggesting that the true population percentage of trigon-type females lay between 0.03% and 0.39%. A z-test of proportions revealed that the difference between the proportion of trigon-type females in the Refuge sample and that in the home sample was significant, $z = -2.425$, $P = .016$. The overall percentage of trigon-type dark females in the combined sample (n = 1,273) was 0.39 ± 0.34%, suggesting that the true population percentage of trigon-type dark females lay between 0.05% and 0.73%.

In my sample, the trigon pattern appeared to be restricted to females. None of the 2,281 males in my Refuge sample or the 55 males in my home sample (total n = 2,336) exhibited this wing pattern. A z-test of proportions revealed that the difference between the proportion of trigon-type males and that of females was significant, $z = 2.213$, $P = 0.027$.

The bodies of all five trigon-type females had the yellow- and black-striped pattern more typical of yellow morphs than of dark morphs. Neither the wings nor the bodies exhibited any obvious structural abnormalities and, apart from the variant wing pattern, appeared normal compared to other female *P. glaucus*.

Discussion

The significant difference in the proportion of trigon-type females at the Refuge and that at my home is probably due to the small number of *P. glaucus* in the home sample as opposed to a non-statistical effect. In addition, the significant difference in the proportion of male and female trigon-type *P. glaucus* reflects the fact that no males of this type were observed. Scriber and Evans (1987) reported a wild-caught partly trigon-type male from Dane Co., Wisconsin (Fig. 6a–b), and Shull (1987) reported a similar male from Nashville (Brown Co.), Indiana (pl. 19), but the trigon patterns in these males were incomplete, appearing more prominently on the dorsal forewings. Scriber and Evans hypothesized that their male may have inherited a translocated melanizing gene from a dark mother or predecessor, and the appearance of Shull's male (whose body is also black) suggests the presence and expression of dark female genes. The facts that none of the 2,300+ males in my 2010 sample (or samples for other years) showed evidence of even a partial trigon pattern and that almost all of the trigon-type *P. glaucus* that have, to my knowledge, been depicted in the literature and elsewhere have been female support the hypothesis that "trigonation" is fundamentally the product of female genetics.

In explaining the occurrence of the trigon-type females observed in 2010, two possibilities can probably be discounted. First, hybridization between *P. glaucus* and other *glaucus*-group species is known to produce variant wing patterns (Clarke & Willig 1977; Scriber & Evans 1988a,b; West & Clarke 1988; Scriber 1990; Scriber et al. 1990; Scriber et al. 2009), but no other *glaucus*-group species occurs within ~350 km of Vigo Co. (*P. canadensis* in central Michigan). In addition, hybridization between *P. glaucus* and other swallowtail species that are sympatric with it in Vigo Co. (*P. troilus*, *P. cresphontes*, *P. polyxenes asterius*, *Battus philenor*, and *Eurytides marcellus*) is doubtful. *P. troilus* is the most common (pers. obs.) and genetically compatible (Caterino et al. 2001), but Scriber and Lederhouse (1988) reported that numerous attempts at hand-pairing *P. glaucus* females with *P. troilus* males produced only one successful pairing and no viable eggs. Such difficulties in producing *glaucus* × *troilus* offspring under controlled laboratory conditions suggests that successful hybridization between these two species is even less likely to occur in nature. In addition, the absence of non-*glaucus* features in the trigon-type females I observed further suggests they were not *glaucus* × *troilus* hybrids.

P. cresphontes is very rare in Vigo Co.; I observed only two in 2010 (and only three between 2002 and 2009), which suggests that even casual encounters between *glaucus* and *cresphontes* in Vigo Co. are highly infrequent. Hereau and Scriber (2003) reported a male *P. polyxenes* and a dark female *P. glaucus* in copulo in the field, but the authors pointed out that *glaucus* and *polyxenes* are separated by the greatest genetic distance of any two papilionid species reported mating in nature (except for a female *B. philenor* and a male *E. marcellus*, Rausher & Berenbaum 1983), making viable offspring from such pairings unlikely. *B. philenor* and *E. marcellus* are genetically even more distant, belonging to entirely different tribes (Troidini and Leptocircini, respectively). Therefore, hybridization between *P. glaucus* and other swallowtail species is improbable.

Second, the possibility that the trigon pattern arose in multiple individuals through random mutation is unlikely because of the uniformity of the pattern. In addition, it seems unlikely that all of the females I observed came from a single mother that passed on a heritable mutation. The first (Fig. 1d) was observed one month before the remaining four, making it unlikely that the former came from the same brood(s) as the latter. Although the remaining four, which were observed within a one-week period, could have come from the same brood, three (Fig. 1e–g) were observed at the Refuge and one (Fig. 1h) at my home, which are several kilometers apart. In addition, the low survival rate of members of a particular brood into adulthood also argues against the possibility that all four came from the same brood. Consequently, at least two (and likely several) mothers carrying the same transmissible mutation would probably have had to be involved. Although possible, it seems unlikely that several such mothers would be clustered in the same area at the same time but not at other times.

The most convincing explanation for the occurrence of the trigon-type females I observed is the unusually high temperatures that prevailed in the Terre Haute area throughout July and August 2010. Ritland (1986) found that the genetically dark female offspring of wild-caught dark female *P. glaucus* reared at higher temperatures were more likely to produce incompletely melanized color patterns than those reared at lower temperatures. For instance, broods reared at 22°C produced normal dark females. Those reared at 25°C, however, produced some females that exhibited an increase in the proportion of yellow scales relative to that found in normal dark females. Those reared at 28°C produced some females that displayed the most dramatic lack of melanization. One of these females (Fig. 1.4) is prototypical of the trigon phenotype. Ritland speculated that heightened temperatures interfered with the melanization process during pupal development, thereby producing incompletely melanized dark females.

In July 2010, the mean temperature in Vigo Co. was 25.3°C (SD = 2.3°C), while in August, the mean temperature was 24.9°C (SD = 3.0°C). For both months combined, the mean temperature was 25.1°C (SD = 2.7°C). The mean high temperature for July and August combined was 31.3°C (SD = 2.3°C). The summer of 2010 was, in fact, the hottest summer in Vigo Co. since 1995. Since all of the trigon-type females I observed would have pupated between mid-July and mid-August, when the mean temperature was 26.3°C (SD = 2.2°C) and the mean high temperature was 31.8°C (SD = 2.4°C), conditions would have been ideal for producing incompletely melanized dark females, if temperature were in fact the main determining factor.

To obtain a rough measure of the situation in other parts of *P. glaucus*'s range in 2010, I examined photographs of *P. glaucus* that users of the insect/spider identification website *Bug Guide* (2013) had taken between 2002 and 2012. The results of this analysis are presented in Table 1. In the 2010 sample (n = 26), at least five females displayed the trigon pattern (19.2%). In addition, a sixth female that did not display the trigon pattern was strongly intermediate in coloration, displaying a heavy "dusting" of black scaling on a predominately yellow surface. By contrast, the data for only two other years (2006 and 2007) revealed trigon-type females. In the 2006 sample (n = 22), only one female was of the trigon type (4.5%), while in the 2007 sample (n = 19), only one was of this type (5.3%). None of the females from these two years displayed a non-trigon intermediate pattern. The samples for the remaining years revealed no trigon-type or intermediate females. Although the *Bug Guide* data should be interpreted with caution, given their unsystematic nature and small sample sizes for some years, between-year comparisons nonetheless suggest that trigon-type female *P. glaucus* were more common in 2010 than in other years.

Given that the 2010 observations took place over an area of >500,000 km², it is clear that the relative abundance of trigon-type female *P. glaucus* in 2010 was a consequence not of local factors, but of a widespread phenomenon that affected *P. glaucus* throughout a substantial portion of its range (e.g. temperature).

The observation dates for the 2010 trigon-type female *P. glaucus* displayed on *Bug Guide* (23 July–26 August) overlap those in my sample (21 July–24 August), suggesting that all of these females pupated sometime between mid-July and mid-August. Perhaps

TABLE 1. Percentages of Photographs of Trigon-Type Female *Papilio glaucus* Posted on the *Bug Guide* Website (http://bugguide.net), 2002–2012.

Year	Female	Intermediate	Trigon	Trigon %
2002	0	0	0	0.0%
2003	4	0	0	0.0%
2004	0	0	0	0.0%
2005	10	0	0	0.0%
2006	22	0	1	4.5%
2007	19	0	1	5.3%
2008	17	0	0	0.0%
2009	7	0	0	0.0%
2010	26	1	5	19.2%
2011	9	0	0	0.0%
2012	6	0	0	0.0%
Total	120	1	7	5.8%

NOTE. Lighter versions of the 2010 trigon-type females were photographed in Waterloo Park, Elkridge (Howard Co.), MD (28 July, http://bugguide.net/node/view/433902), Danville (Hendricks Co.), IN (22 August, http://bugguide.net/node/view/445641), and Mt. Olive Cemetery near Knoxville (Knox Co.), TN (26 August, http://bugguide.net/node/view/447462). Darker versions of these females were photographed in Montgomery Co., PA (23 July, http://bugguide.net/node/view/432146) and Whitewright (Grayson Co.), TX (31 July, http://bugguide.net/node/view/600454). The 2010 intermediate female was photographed in Avery Co., NC (29 August, http://bugguide.net/node/view/463111).

significantly, the highest mean July–August temperature that occurred between 2002 and 2010 for the five *Bug Guide* locations combined that reported trigon-type females in 2010 occurred in 2010. For three locations (Danville, IN; Knoxville, TN; Elkridge, MD), the highest mean July–August temperature occurred in 2010, while for the remaining two (Montgomery, PA; Whitewright, TX), the second highest occurred in 2010.

Trigon-type *P. glaucus* appear to have become more abundant in other years with unusually hot summers. For example, James Wiker, who has collected Lepidoptera in Illinois since the 1960s and has co-authored field guides on the skippers and the sphinx moths of Illinois (Bouseman et al. 2006; Wiker et al. 2010), has acquired a number of specimens of *P. glaucus* displaying variant wing patterns. Of these that I have examined, at least three are trigon types (Randolph Co., 27 July 1980; Menard Co., 21 August 1995; Alexander Co., 28 August 2007). Although these specimens were not collected in 2010, they nonetheless pupated during periods when especially severe heat events affected their pupation sites (e.g. the Chicago heat wave of 1995). In addition, the trigon type depicted in Ehle (1981 Fig. 1.2) was also collected during the heat wave year of 1980.

Interestingly, the wild-caught partly trigon-type male figured in Scriber and Evans (1987 Fig. 6a–b) was collected on 10 August 1983, and the previous one-month period (at some point during which it would have pupated) was the hottest mid-July to mid-August period in Dane Co., Wisconsin since 1955 (mean = 24.1°C, mean high = 30.6°C). The male depicted in Shull (1987), which was collected on 21 August 1984, pupated under similar temperatures (mean = 24.1°C, mean high = 29.2°C). If these males did in fact inherit translocated melanizing genes, then the expression of these genes might have been susceptible to the effects of heightened temperatures, as they appear to be in certain dark females.

Finally, the non-trigon-type intermediate females I observed in 2010 (e.g. Fig. 1c) tended to be lighter than the ones I had observed in the previous eight and subsequent two years, again suggesting that elevated temperatures have an increased demelanizing effect in dark female *P. glaucus*.

My findings not only lend support to Ritland's hypothesis that high temperatures can produce incompletely melanized dark female *P. glaucus*, but also suggest that temperature is an influencing factor not only in the laboratory but also in nature. (In addition, my findings suggest that inbreeding, which occurred in Ritland's studies, probably does not contribute to the production of the trigon form in nature, since inbreeding is unlikely to occur in the highly mobile naturally occurring *P. glaucus* population.)

The pathways that lead to the production of the yellow and black scales that dominate the *glaucus* color pattern are relatively well understood (Koch et al. 1998; Koch et al. 2000a,b; ffrench-Constant & Koch 2003), and this understanding suggests how intermediate phenotypes, including the trigon phenotype, can occur. In particular, during the wing pigmentation process, each wing cell appears to behave autonomously, having a unique threshold of responsiveness to the signal to initiate melanin synthesis; above this threshold, the cell will undergo papiliochrome synthesis and become pigmented yellow, while below this threshold, the cell will undergo melanin synthesis and become pigmented black (ffrench-Constant & Koch 2003). Ritland's (1986) findings strongly suggest that at higher levels, temperature can affect this threshold, causing biochemical changes (see ffrench-Constant & Koch 2003 for details) that lead to papiliochrome synthesis in cells that would normally undergo melanin synthesis and resulting in atypical mixtures of yellow and black scales.

In addition, the incompletely melanized dark females illustrated in Ritland (1986 Fig. 1) suggest that in dark females there is a positive relationship between the distance that a "background" (i.e. non-stripe, non-margin) wing scale lies from the body and the likelihood that the scale will fail to melanize. Scales in the more distal areas of the wing appear to fail to melanize more frequently than those in the more proximal areas, suggesting that in dark females, the more proximal the scale is, the more resistant to papiliochrome synthesis it is. This would explain why "dusted" forms are more common than trigon forms, since the conditions required to produce the heightened demelanization seen in the latter are more extreme (i.e. less common) than those required to produce the lessened demelanization seen in the former. In addition, this would explain why "reverse" trigon patterns (i.e. yellow basally and black distally) are not observed in dark female *P. glaucus*.

Otherwise, the fact that Ritland did not produce a totally yellow-appearing dark female suggests that in dark female *P. glaucus*, the trigon (i.e. least melanized) pattern may represent the upper limit of temperature-sensitive demelanization. Of course, if completely demelanized dark females can and do exist in nature, then some seemingly "yellow" females are in fact dark females "in disguise" and go unrecognized for what they really are.

In Vigo Co., the 2011 July-August mean and mean high temperatures were comparable to those for 2010 (mean = 25.0°C, SD = 3.0°C; mean high = 31.5°C, SD = 2.6°C), while the 2012 July–August mean and mean high temperatures were higher than those for the previous two years (mean = 26.4°C, SD = 3.7°C; mean high = 34.2°C, SD = 3.9°C). Even so, I did not observe trigon-type female *P. glaucus* during the summers of 2011 and 2012. The apparent lack of trigon types during these two years, however, may be the result less of environmental factors than of sampling deficiencies. The number of *P. glaucus* present at the Refuge before mid-July is too low to permit adequate sampling before this time, which means that almost all of the individuals in my Refuge samples (>99%) are observed after mid-July. Unfortunately, changes in the schedule and pattern of mowing activity at the Refuge in 2011 and 2012, which destroyed the majority of larval and imaginal hosts by mid-July, virtually eliminated the *P. glaucus* population there and made adequate sampling impossible for those two years. In addition, the *Bug Guide* samples of female *P. glaucus* for 2011 and 2012 were comparatively small (9 and 6, respectively), providing limited examples. Even so, the facts that I had not observed a trigon type before 2010 among the thousands of female *P. glaucus* that I had previously encountered in the Vigo Co. area and that the trigon types posted on *Bug Guide* clustered in 2010 suggest that in 2010, conditions favored the production of the trigon phenotype.

If the idea proposed here that elevated temperatures were responsible for the increase in the occurrence of trigon-type female *P. glaucus* in 2010 is correct, then this raises the interesting possibility that if record high temperatures continue to prevail throughout *P. glaucus*'s range during pupal development times, genetically dark female *P. glaucus* expressing the trigon (and other demelanized) color patterns could become more prevalent. If so, such an increase in incompletely melanized forms could potentially alter the dynamics of dark female *P. glaucus*'s mimetic relationship with *Battus philenor* in the most impacted populations.

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LITERATURE CITED

BOUSEMAN, J. K., J. G. STERNBURG & J. R. WIKER. 2006. Field guide to the skipper butterflies of Illinois. Ill. Nat. Hist. Surv. Manual 11. 200 pp.

BUG GUIDE. 2013. Identification, images, and information for insects, spiders and their kin for the United States and Canada. Available from: http://bugguide.net/ (9 March 2013).

CATERINO, M. S., R. D. REED, M. M. KUO & F. A. H. SPERLING. 2001. A partitioned likelihood analysis of swallowtail butterfly phylogeny (Lepidoptera: Papilionidae). Syst. Biol. 50(1):106–127.

CLARK, A. H. 1932. The butterflies of the District of Columbia and vicinity. Bull. USNM 157:172–199.

——— & L. F. CLARK. 1951. Butterflies of Virginia. Smithson. Inst. Misc. Coll. 116(7):124–144.

CLARKE, C. A. & A. WILLIG. 1977. The use of α-ecdysone to break permanent diapause of female hybrids between *Papilio glaucus* L. female and *Papilio rutulus* Lucas male. J. Res. Lepid. 16(4):245–248.

EDWARDS, W. H. 1884. The butterflies of North America. Vol. II. Houghton Mifflin Co., Boston. 357 pp.

Ehle, G. 1981. Ripples. News Lepid. Soc. 23(5):63.

FFRENCH-CONSTANT, R. & P. B. KOCH. 2003. Mimicry and melanism in swallowtail butterflies: Toward a molecular understanding, pp. 259–279. *In* Boggs, C. L., W. B. Watt & P. R. Ehrlich (eds.), Butterflies: Ecology and evolution taking flight. Univ. Chicago Press, Chicago, Illinois. 739 pp.

HEREAU, H. & J. M. SCRIBER. 2003. Interspecific copulation of a dark morph *Papilio glaucus* female and a male *P. polyxenes* (Papilionidae): Observation and significance. J. Lepid. Soc. 57(1):71–74.

IBM CORP. 2011. IBM SPSS Statistics for Windows, version 20.0. Armonk, NY.

KOCH, P. B., B. BEHNECKE & R. H. FFRENCH-CONSTANT. 2000a. The molecular basis of melanism and mimicry in a swallowtail butterfly. Curr. Biol. 10:591–594.

———, ———, M. WEIGMANN-LENZ & R. H. FFRENCH-CONSTANT. 2000b. Insect pigmentation: Activities of β-alanyldopamine synthase in wing color patterns of wild-type and melanic mutant swallowtail butterfly *Papilio glaucus*. Pigment Cell Res. 13(s8):54–58.

———, D. N. KEYS, T. ROCHELEAU, K. ARONSTEIN, M. BLACKBURN, S. B. CARROLL & R. H. FFRENCH-CONSTANT. 1998. Regulation of dopa decarboxylase expression during colour pattern formation in wild-type and melanic tiger swallowtail butterflies. Development 125:2303–2313.

RAUSHER, M. D. & M. R. BERENBAUM. 1983. A natural occurrence of inter-tribal copulation in the Papilionidae. J. Lepid. Soc. 37(1):81–82.

RITLAND, D. B. 1986. The effect of temperature on the expression of the dark phenotype in *Papilio glaucus* (Papilionidae). J. Res. Lepid. 25(3):179–187.

SCRIBER, J. M. 1990. Two new aberrant forms of tiger swallowtail butterfly from the Great Lakes hybrid/transition zone (Lepidoptera: Papilionidae). Great Lakes Entomol. 23(3):121–126.

———, R. V. DOWELL, R. C. LEDERHOUSE & R. H. HAGEN. 1990. Female color and sex ratio in hybrids between *Papilio glaucus glaucus* and *P. eurymedon, P. rutulus*, and *P. multicaudatus* (Papilionidae). J. Lepid. Soc. 44(4):229–244.

——— & M. H. EVANS. 1987. An exceptional case of paternal transmission of the dark form female trait in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae). J. Res. Lepid. 25(2):110–120.

——— &———. 1988a. A new heritable color aberration in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae). J. Res. Lepid. 26(1–4):32–38.

——— &———. 1988b. Bilateral gynadromorphs, sexual and/or color mosaics in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae). J. Res. Lepid. 26(1–4):39–57.

———, M. H. EVANS & D. B. RITLAND. 1987. Hybridization as a causal mechanism of mixed color broods and unusual color morphs of female offspring in the eastern tiger swallowtail butterflies, *Papilio glaucus*, pp. 119–134. *In* Huettel, M. (ed.), Evolutionary genetics of invertebrate behavior: Progress and prospects. Plenum Press, New York. 346 pp.

——— & R. C. LEDERHOUSE. 1988. Hand-pairing of *Papilio glaucus glaucus* and *Papilio pilumnus* (Papilionidae) and hybrid survival on various food plants. J. Res. Lepid. 27(2):96–103.

———, H. ROMACK & M. D. DEERING. 2009. Aberrant color patterns in the *Papilio* and an update on the semi-melanic *"fletcheri"* variants, including females (Lepidoptera: Papilionidae). J. Lepid. Soc. 63(2):118–126.

SHULL, E. M. 1987. The butterflies of Indiana. Ind. Acad. Sci., Indianapolis, Indiana. 262 pp.

TYLER, H. A., K. S. BROWN & K. H. WILSON. 1994. Swallowtail butterflies of the Americas: A study in biological dynamics, ecological diversity, biosystematics, and conservation. Scientific Publ., Gainesville, Florida. 376 pp.

WEST, D. A & C. A. CLARKE. 1988. Suppression of the black phenotype in females of the *P. glaucus* group (Papilionidae). J. Res. Lepid. 26(1–4):187–200.

WIKER, J. R., J. G. STERNBURG & J. K. BOUSEMAN. 2010. Field guide to the sphinx moths of Illinois. Ill. Nat. Hist. Surv. Manual 13. 155 pp.

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