Are there caterpillars on butterfly wings?

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The wings of insects predate those of other animals. They have had 400 million years to adapt to changing conditions and diversify to bear the vast array of patterns we see today. The great naturalist Henry Walter Bates famously noted that butterfly wing patterns provide a window to the past, writing more than a century ago: "... on these expanded membranes Nature writes, as on a tablet, the story of the modifications of species, so truly do all changes of the organization register themselves thereon...". Duke University zoologist Fred Nijhout brought some order to our understanding of a broad assortment of wing patterns among the 18,000 or so species of butterflies in his book, *The Development and Evolution of Butterfly Wing Patterns* (1991). He continues to study the evolution and development of pigment patterns in butterflies, and many others are active in butterfly evo-devo research (e.g., Paul Brakefield, Patrícia Beldade, Chris Jiggins, Marcus Kronforst, Jim Mallet, W. Owen McMillan, Antónia Monteiro, and Robert Reed).

In a recent conversation, DW (an artist who has worked with butterflies and birds and has been involved in encouraging partnerships between scientists and artists) pointed out to PE (who has also been involved in encouraging such collaborations) that certain butterfly wing-pattern elements seem to resemble larvae. We decided to take a closer look. Here we consider the connection between the patterns of some larvae and adults, and ask if the apparent resemblances are coincidental, especially given the amount of variation in patterns, or adaptive. Examples you might consider appear in Figures 2 - 5 (page 183):

Dorsal or ventral hindwing pattern that resembles a larva of the same species:

* *Parides photinus* (Pink-spotted Cattleheart)
* *Papilio glaucus* (Tiger Swallowtail)
* *Emesis mandana* (Variable Emesis)

Dorsal forewing and/or hindwing margins that resemble a larva of a different species:

* *Danaus plexippus* (Monarch) and a larva of *Battus philenor* (Pipevine Swallowtail)

In the winter and spring of 2015 we surveyed numerous "expanded membranes", comparing photographs of pinned specimens and larvae in the *Butterflies of America* website (Warren, et al., 2012), for resemblances. Tendencies emerged. Nijhout had identified a ground plan comprising three bands that extend vertically from forewing to hindwing, which he called the basal, central and border symmetry systems. We found that most resemblances appear on the ventral hindwing portion of Nijhout's border symmetry system (Fig. 1), in an area we coin as the "larval band". Why there? Many butterflies hold their wings closed while resting, leaving their ventral hindwings exposed, so it is possible that the patterns comprise signals to predators. Future research should be able to confirm if ventral larval bands displaying resemblances are evenly distributed among toxic and palatable adults and larvae. In some cases, resemblances were located on the dorsal hindwing larval band, such as those in *Papilio*, whose larvae may be chemically protected by their osmeteria, and patterns that occasionally extend to the lower portion of the forewing (Fig. 3), or on wing margins featuring likely chemically protected larvae of another species (Fig. 5). Only in a few cases did we find resemblances on the dorsal surface closer to the body.

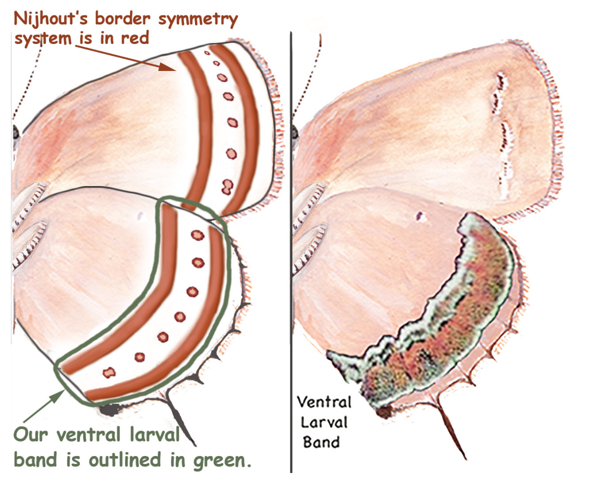

Fig. 1. Left: modified drawing by DW, with computer generated overlay, after Nijhout (1991); right: drawing by DW, with photographic overlay of modified larval band.

We know that complexities arise when identifying similarities. The process is, of course, subjective and the perception of similarities may vary from individual to individual observer as it did between the authors, one of whom, as noted, is an artist and the other a red-green colorblind scientist! Color perception in *Homo sapiens* even varies from season to season (Welbourne et al., 2015). We also know that the avian visual system is very different from the human visual system as is that of lizards and other predators. And we know that perception of similarities may vary from individual to individual predator and from a variety of conditions, each of which adds complications. (For an insightful discussion of the avian visual system, defensive

Four Examples of Apparent Resemblances

Fig. 2. Adult and aposematic larva thought to be chemically protected. The pink markings of the adult male *Parides photinus* (Pink-spotted Cattleheart) are limited to the body and the larval band. The larvae feed on *Aristolochia grandiflora* and *A. asclepiadifolia* (Pelican Flower). It is reported that consuming terpenes in *A. grandiflora* makes the larvae unpalatable. The plant also contains the poisonous compound aristolochic acid. Note that the larva in the photograph has been extracted from the background and modified into a shape similar to the marks on the hindwing (lower right). [Left and upper right] © 2007, 2009 Luc Legal, Jerome Albre and Oscar Dorado.

Fig. 3. Adult and larva with chemically protective osmeteria and false eyespots. Under perceived threat the larvae of *Papilio* spp (swallowtail butterflies) may assume a warning posture and evert their fleshy osmeteria. Here a *P. glaucus* (Tiger Swallowtail) larva has partially everted its osmeteria. The bluish-greenish dorsal hindwing larval band with its large terminal orange spot seems to resemble a larva with osmeteria partially everted (a second orange spot is concealed by the forewing.). Note that the larva in the photograph has been extracted from the background, modified (lower right) and superimposed over the left hindwing. The blue-green coloration of the overlay has been adjusted for effect. [Left] © Jeff Pippen; [Upper right] © Michael Singer.

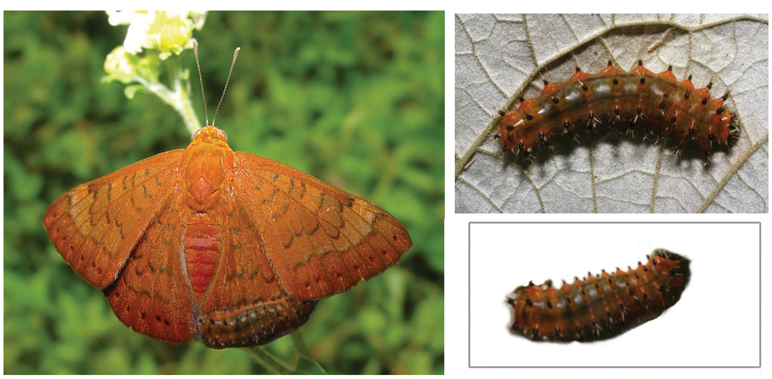

Fig. 4. Adult and edible mimic of urticating larva (those with defensive bristles that cause itching and irritation). *Emesis mandana* (Variable Emesis) larvae are among hundreds of possible mimics of urticating caterpillars, which visually hunting predators apparently learn to avoid. Might predators be warned off adult Variable Emesis, too? Note that the larva (penultimate instar) has been extracted from the background, modified (lower right) and superimposed over the right hindwing. [Left] © Kim Garwood, **www.neotropicalbutterflies.com** [Upper right] © D. Janzen and W. Hallwachs, voucher code: 05-SRNP-63174 **http://janzen.bio.upenn.edu/caterpillars/database.lasso**

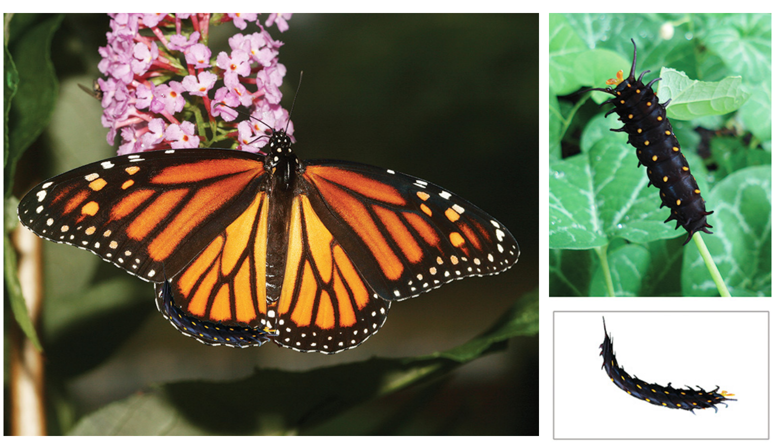

Fig. 5. Adult and co-occurring but unrelated chemically protected larva. The wings of *Danaus plexippus* (Monarch) do not include elements that resemble the often chemically protected Monarch larva, but in some geographic areas adults typically migrate beyond the range of predators that could have learned to avoid the larval pattern. Monarch adults might, however, benefit from the dot pattern on their wing margin if predators learn to avoid dot-patterned larvae like those of *Battus philenor* (Pipevine Swallowtail) (upper right) that feed on toxic pipevine species, sequestering poisonous aristolochic acid. Note that the larva in the photograph has been isolated, modified (lower right) and superimposed over the left hindwing. Also note that while the dots on the pipevine larva are orange and those on the Monarch are generally white, if viewed in low light—when birds are apt to forage—the color mismatch may go undetected. [Left] © Bill Bouton; [Upper right] © 2008 Wanda Smith.

visual mimicry and examples of how well mimics match models see Stoddard 2012.).

We also know that complexities arise when assessing predator avoidance and determining whether a potential butterfly prey was avoided or got away. For example, as noted in the caption for the Monarch (Fig. 5), a number of chemically protected larvae have a dot-like pattern (e.g., *B. philenor* [Pipevine Swallowtail]) that might deter predators and a number of adults have a dot pattern along the wing margin that might also deter predators. In some cases, however, a dot pattern along wing margins may attract rather than deter predators, encouraging them to snap at the periphery, not the body, leaving the adult with little more than a torn wing or beak mark, as evidenced by numerous torn or marked specimens in collections. In Appendix 2 we present photographs of 17 butterfly specimens showing a dot pattern on the wing margins. There are, of course, many other patterns along the wing margins. In his aforementioned book, Nijhout provides a figure cataloging 36 forms found in the border ocelli in nymphalids and the frequency of their occurrence (See Nijhout, 1991, Fig. 2, page 89.).

John Hessel, in correspondence with us, raised an essential issue noting that the precision in eyespot mimicry found on butterfly wings, which may include pupillary highlights and reflections, is often lacking in larval resemblances. We think those differences in precision might be explained by predator reaction time: Ideally, perceiving eyespots would lead a predator to act immediately, often as a hard-wired reaction as Janzen, Hallwachs, and Burns discuss in their excellent and persuasively-illustrated paper on eyespots in Costa Rican larvae (Janzen et al., 2010), or as an immediate, experience-based decision, both of which may save the butterfly. In contrast, perceiving a larva presents a less pressing choice, and the resemblance would only need to be sufficiently similar to a toxic, unpalatable, or urticating (producing a nettle-like stinging) prey for the predator to choose to avoid sampling it.

The first step in determining if adult-larval resemblances are sufficiently widespread and not merely coincidences requires a broader survey of species that evaluates similarities between adults and as many larval instars as possible. (See, e.g., *News of the Lep Soc.,* 56:3, p. 109-110, and compare Fig. 24 with the margin of Fig. 33.) In our preliminary online search we found what we believe to be resemblances in all six butterfly families, although examples among pierids were very sparse and may well be coincidental. Appendix 1 presents photographs of 25 larval/adult pairs.

There are, however, many gaps in the online pictorial record that will constrain a resemblance survey. In our inspection, for example, the larval band on a number of adults looked promising, (e.g., *Magnastigma hirsuta* [Hirsuta Hairstreak], *Perisama alicia*, and *Zaretis pythagoras*), but images of larvae were unavailable. Considering the growing interest in butterfly photography and the ease of using smart phone cameras this seems an ideal time and a resemblance survey seems an ideal project for observational "citizen science."[1] Butterfly collectors and photographers, nature photographers, science artists, other naturalists and students around the world could dramatically expand the pictorial archive. They could compare larval and adult patterns in species they photograph in the field or find in online databases and submit image, foodplant and location information of promising examples to a central online "resemblance" database that is curated, maintained and linked to key organizations such as the North American Butterfly Association (NABA).

Some Benefits of a Citizen Science Larva/Adult Resemblance Project

***increase our knowledge of butterfly life-histories** (by focusing more attention on immatures and foodplants; the emphasis now is still disproportionately on adults)

***increase our knowledge of butterfly behavior** (by comparing larval foraging patterns, pupation site selection, etc., Do aposematic larvae feed in more exposed positions than cryptic ones?; Are aposematic pupae attached to more exposed positions than cryptic ones?)

***increase our knowledge of butterfly population dynamics** (by comparing abundances related to proportions of mimics and models)

***increase our knowledge of predator memory and behavior** (by assessing how much avoidance behavior is learned and how much is hard-wired)

***provide citizen scientists opportunities to interact with scientists in the field** and experience how careful observation, note-taking and data analysis can reveal patterns that provide answers as they "do" science

***provide citizen scientists opportunities to help educate others about how science is done.**

For information on the Citizen Science project, see: **http://web.stanford.edu/group/stanfordbirds/cit_sci/Resemblances.html**

If resemblances prove widespread, an extensive area for future research would open up, investigating such things as the frequency of geographic co-occurrence of adult-larval resemblance; opportunities for exposure of both larval

[1]Online databases include, for example, BOLD <http://www.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxid=162755>; Butterflies of America <http://www.butterfliesofamerica.com/>; EOL (Encyclopedia of Life) <http://eol.org/pages/29472815/overview> and MCZBase - Harvard University <http://mczbase.mcz.harvard.edu/TaxonomySearch.cfm >

and adult patterns to the same predators; differences and similarities in the presence of defensive compounds; the possible influence of interspecies inter-stage resemblances, and so forth. The questions raised would be open-ended. Educators could gain new examples to convey the intricacy of evolution, and conservationists could show how the protection or the loss of a population of one species could influence the conservation status of another in ways not previously recognized.

Some important issues have been raised in correspondence with us by University of South Carolina evolutionary biologist Ward Watt, including the question of comparing the real segmentation in larvae with the appearance of segmentation in wing patterns. Even taking this into consideration the aposematic warning cues in adults that had been present in chemically protected larvae seem more likely adaptive than circumstantial, since adults and larvae share their genome and their available pigment pathways are correlated. That the larval "mimics" on the wings are not just carry-overs from larval segmental patterns is also suggested by their discrete shapes and restricted positions on the wings. Notice, for example, how the terminal larval segment in *P. glaucus* (Tiger Swallowtail) appears separately, but perfectly aligned, on the forewing (Fig.3).

Raising the visibility of butterflies through a citizen science program is apt to raise the visibility of conservation efforts, and that increased attention is apt to be a key to the success of both. In this regard, collaboration among scientists and artists will help artists provide faithful—and inspired—renderings while providing scientists with access to skilled visual observers and communicators, whose depictions can, among other things, help expand the corps of citizen scientists and the reach of their findings. Scientifically accurate artwork, when evocative and presented as Science Art (that is, when accompanied by a caption that provides a science lens), can help convey time-sensitive information. While photography is essential for resemblance comparisons, in the case of suboptimal photographs, photo-realistic artwork can reduce or eliminate distracting imperfections and be used in displays, presentations and publications especially when local projects require community involvement. Access to time-sensitive visual resources is also important when public debate lingers at the fringe, as it does, for instance, in discussions of evolutionary biology and climate change where science remains under constant assault by anti-evolutionists and climate change deniers.

As the photographic record expands to include the instars of more larvae it will become easier to select species that are good candidates for assessing predator reactions and other behaviors that will allow evolutionary biologists to test whether any given inter-stage resemblance is adaptive or merely an eye-catching "spandrel." (Gould and Lewontin, 1979)

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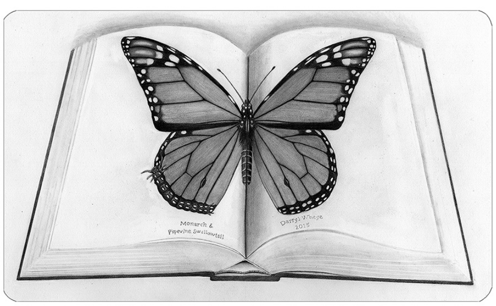


MONARCH II ©2015 Darryl Wheye, pencil, Private collection. A Pipevine Swallowtail larva overlays the left hindwing margin.

Lep Soc members and others:

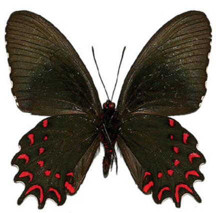
Any examples of larval/adult resemblances in your collection? Have you seen any in other collections, online or in photos taken in the field? It would be wonderful if you could send jpgs to the resemblance database.

It would also be wonderful if you could help lead and/or advise the citizen science resemblance program. Please let us know.

Links to the appendices (and image enlargements), contact information and a query/registration/image submission form are here: **http://web.stanford.edu/group/stanfordbirds/cit_sci/Resemblances.html**

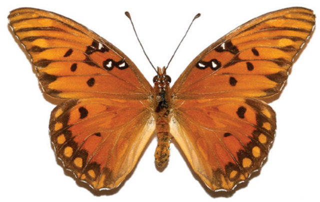
Appendix 1. Twenty-five Examples of Larva/Adult Resemblances

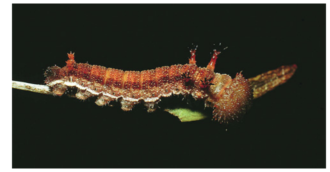
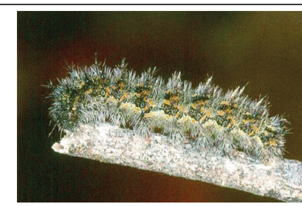
A yellow and/or black outline highlights the resemblance in the "Outlined Resemblance" column. The "Adult Caption" column notes the resemblance. The "Larva Caption" column provides available instar and foodplant information.

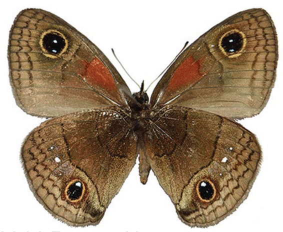
#		Adult	Outlined Resemblance	Adult Caption	Larva	Larva Caption
Papilionidae (3)						
1	*Heraclides anchisiades idaeus* ♀ (Ruby-spotted Swallowtail)	 © 2007 Andrew Warren		The pink and black dorsal hindwing larval band resembles early instar larvae, which are gregarious.	 © 2007 Dan Hardy	The instar is not noted on the photograph. Later instars are darker.
2	*Papilio glaucous* ♀ (Eastern Tiger Swallowtail)	 © 2008 Kim Davis, Mike Stangeland, and Andrew Warren		This example is from our text. The lower end of the pale blue green dorsal hindwing larval band has an orange spot that resembles the partially ever-ted orange osmiteria that lar-vae display defensively. When alive, forewings cover the upper hindwing orange spot and complete the larval resemblance.	 © Michael Singer	This photo is from a study of herbivore diet breadth vs. bird predation. Read more at: http://phys.org/news/2014-07-eaters-eaten.html#j. The instar is not noted on the photograph.
3	*Parides photinus* ♀ (Pink-spotted Cattleheart)	 © 2008 David Robacker		This example is from our text. The pink marks on the ventral hindwing larval band and white marks on the wing edge resemble, to a degree, the pink and white larval spines.	 © 2009 Luc Legal, Jerome Labre & Oscar Dorado	The foodplant is Aristolochia *splendens*. The instar is not noted on the photograph.
Pieridae (1)						
4	*Anthocharis sara thoosa* ♀ (Sara Orangetip)	 © 2009 Jim P. Brock		The pale orange "tip" of the dorsal forewing and the black mark on the discal cell edge seems to parallel pairing of the orange larva and its black eyes.	 © 2010 Jim P. Brock	First instar is orange with a few bristles.

Lycaenidae (4)						
5	*Theritas mavors* ♂ (Deep-green Hairstreak)	 © 2010 D.H. Janzen and W. Hallwachs voucher code 09-SRNP-71199, http://janzen.bio.upenn.edu/caterpillars/database.lasso		There is a fairly strong resemblance between the color and shape of the larva and the ventral hindwing "larval band."	 © 2010 D.H. Janzen and W. Hallwachs voucher code 04-SRNP-41639, http://janzen.bio.upenn.edu/caterpillars/database.lasso	Last Instar. The food-plant is *Conostegia xalapensis*.
6	Callophrys mcfarlandi ♀ (Sandia Hairstreak)	 © 2009 Jim P. Brock		The pale yellowish-greenish ventral hindwing "larval band" resembles a larva.	 © 2010 Jim P. Brock	The instar is not noted on the photograph. Coloration might be influenced by camera and available light (note the black background).
7	*Euphilotes ellisii ellisii* ♀ (Ellis' Blue)	 © 2008 Kim Davis, Mike Stangeland and Andrew Warren		The orange-pink ventral hindwing "larval band" resembles the larva, but some photos the larvae are very pale.	 © 2011 Nicky Davis	The larva is on *Eriogonum corymbosum*. The instar is not noted on the photograph.
8	*Euphilo euphilotes spaldingi* ♀ (Spalding's Blue)	 © 2008 Todd Stout		The orange ventral hindwing "larval band" resembles, to a degree, prediapause a 4th instar larva.	 © 2008 Todd Stout	The 4th instar, pre-diapause larva is pale orangish-pinkish-reddish with darker marks.

Riodinidae (5)						
9	*Euselasia pellonia pellonia* ♂ (Red-rimmed Euselasia)	 © 2014 Jim P Brock		The aposematic orange-red ventral hindwing "larval band" with black spots and white marks resembles, to a degree, a black-spotted, greenish-orange larva.	 © 2010D.H. Janzen and W. Hallwachs voucher code 04-SRNP-2598, http://janzen.bio.upenn.edu/caterpillars/database.lasso	This instar is greenish-orange with black spots and pale bristles. The foodplant is *Vochysia guatemalensis.*
10	*Hades noctula* ♂ (White-rayed Metalmark)	 © 2010 D.H. Janzen and W. Hallwachs voucher code 01-SRNP-2576.03, http://janzen.bio.upenn.edu/caterpillars/database.lasso		The outer half of the black and white "ray" patterned ventral hindwing resembles, to a degree, a last instar larva. This pattern seems consistent with Nijout's "intervenous stripe system".	 © 2010 D.H. Janzen and W. Hallwachs voucher code 01-SRNP-2576, http://janzen.bio.upenn.edu/caterpillars/database.lasso	The last instar has long bristles and black/whitish-greenish "rays". The foodplant is *Tapirira mexicana*.
11	*Esthemopsis pherephatte pherephatte* ♂ (Godart's Metalmark)	 © 2010 D.H. Janzen and W. Hallwachs voucher code 01-SRNP-2685, http://janzen.bio.upenn.edu/caterpillars/database.lasso		The aposematic yellow patch on the blackish blue ventral forewing resembles a last instar larva, minus the black dots.	 © 2010 D.H. Janzen and W. Hallwachs voucher code 01-SRNP-2685, http://janzen.bio.upenn.edu/caterpillars/database.lasso	Last instar larvae are yellow with black bristles (that look like dots from above) and long pale bristles along the edge. The foodplant is *Trichospermum grewiifolium.*
12	*Pirascca tyriotes* ♂ (Golden-banded Metalmark)	 © 2010 D.H. Janzen and W. Hallwachs voucher code 08-SRNP-72467, http://janzen.bio.upenn.edu/caterpillars/database.lasso		The aposematic orange patch on the black dorsal hindwing resembles a penultimate instar larva.	 © 2011 D.H. Janzen and W. Hallwachs voucher code 08-SRNP-72573, http://janzen.bio.upenn.edu/caterpillars/database.lasso	The penultimate instar is orange with long pale bristles along the edge. The foodplant is *Miconia argentea*.

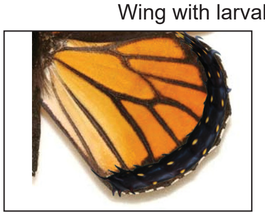
13	*Emesis mandana* ♂ (Variable emesis)	 © 2010 Kim Davis, Mike Stangeland and Andrew Warren		This example is from our text. The resemblance is seen along both dorsal wing margins.	 © 2011 Daniel Janzen and W. Hallwachs voucher code 05-SRNP-63174, http://janzen.bio.upenn.edu/caterpillars/database.lasso	Penultimate instar is greenish orange with irritating bristles growing from short black spines that resemble the black dots on the wing margins. The foodplant is *Croton yucatanensis*.
Nymphalidae (9)						
14	*Agraulis vanillae incarnata* ♀ (Gulf Fritillary)	 © 2009 Jim P. Brock		The orange and dark brown dorsal hindwing "larval band" resembles, to a degree, a last instar larva.	 © 2010 D.H. Janzen and W. Hallwachs voucher code 00-SRNP-16240, http://janzen.bio.upenn.edu/caterpillars/database.lasso	The last instar of this orange and black larva has long black spines with black bristles. The foodplant is *Passiflora foetida*.
15	*Dione juno huascuma* (Juno Longwing)	 © 2005 Kim Davis and Mike Stangeland <kimandmikeontheroad.com>		The orange and black dorsal hindwing "larval band" resembles, to a degree, a last instar larva. This is more evident in some photographs than in others.	 © 2011 Kenji Nishida	The last instar is orange and purplish-brown with black spines and bristles. The larva is on *Passiflora edulis*.
16	*Heliconius sara theudela* ♀ (Sara Longwing)	 © 2009 Kim Davis, Mike Stangeland and Andrew Warren		The brown ventral hindwing has red dots near the body. The dark segmentation lines on the white "larval band" resembles, to a degree, the segmentation pattern and might even call to mind the long black spines of a third instar larva.	 © 2011 Rudy Dodero	Third instar larvae are whitish with black spines.

17	*Adelpha tracta* (Tracta Sister)	 © 2011 D.H. Janzen and W. Hallwachs voucher code 05-SRNP-35693, http://janzen.bio.upenn.edu/caterpillars/database.lasso		The rusty pinkish-mauve patterned ventral hindwing "larval band" resembles a penultimate instar larva.	 © 2010 D.H. Janzen and W. Hallwachs voucher code 02-SRNP-23504, http://janzen.bio.upenn.edu/caterpillars/database.lasso	The penultimate instar matches the adult relatively well. The foodplant is *Viburnum venustum*.
18	*Hamadryas guatemalena marmarice* ♀ (Guatamalan Cracker)	 © 2011 Andrew D. Warren		The black and white patterned ventral hindwing margin is probably aposematic and, to a degree, resembles the larva.	 © 2010 Jim P. Brock	This white, black and yellow -- and presumably aposematic -- larva has black spines and black bristles. The instar is not noted on the photograph. It was photographed on *Dalechampia*.
19	*Vanessa annabella* ♀ (West Coast Lady)	 © 2009 Andrew Warren		The complex beige, bright and pale orange, pale blue, black, light and dark brown pattern on the ventral hindwing "larval band" resembles, to a degree, the complex pattern of the larva.	 © 2009 Jim P. Brock	The instar of this bright and pale orange and black larva with grey bristles is not noted on the photograph.
20	*Chlosyne fulvia coronado* ♀ (Fulvia Checkerspot)	 © 2009 Jim P. Brock		The dark brown, orange, pale orange, and white dorsal hindwing "larval band" resembles the larva.	 © 2009 Kim Davis and Mike Stangeland <kimandmikeontheroad.com>	This blackish-brown, pale orange and white larva has black-spines and black-bristles. The instar is not noted on the photograph.

21	*Poladryas minuta minuta* ♂ (Dotted Checkerspot)	 © 2010 Andrew D. Warren		The basically orange ventral hindwing "larval band" has some dark dots and resembles the black-dotted, black-spined larva.	 © 2011 Jim P. Brock	The instar is not noted on the photograph.
22	*Calisto muripetens* ♂ (Muripetens Calisto)	 © 2014 Rayner Nuñez		Except for the rust-ringed false eye, the pale brown ventral hindwing "larval band" with black, cream, and beige marks resemble, to a degree, the brown-patterned larva.	 © 2014 Rayner Nuñez	The instar is not noted on the photograph.
Hesperiidae (3)						
23	*Aguna asander asander* ♀ (Gold-spotted Aguna)	 © 2009 Kim Davis, Mike Stangeland and Andrew Warren		The light mauve, rust, white, cream and beige ventral hindwing "larval band" is bordered on one end by a rust-colored triangle and resembles, to a degree, a last instar larva	 © 2011 D.H. Janzen and W. Hallwachs voucher code 06-SRNP-56548, http://janzen.bio.upenn.edu/caterpillars/database.lasso	The last instar larva has rust-colored eyes and a cream-colored body. It was photographed on *Bauhinia ungulata*.
24	*Zestusa dorus* ♂ (Short-tailed Skipper) (Northern Zestusa)	 © 2009 Andrew D. Warren		The light grey and creamy-grey ventral hindwing "larval band" resembles a penultimate instar larva.	 © 2010 Jim P. Brock	The penultimate instar is creamy-grey with pale yellow stripes. A greenish cast—the color of the leaf--seems to show through the skin.
25	*Eantis papinianus* ♂ (Cuban Sicklewing)	 © 2009 Kim Davis, Mike Stangeland and Andrew Warren		The whitish pale bluish ventral hindwing "larval band" resembles the fifth instar larva.	 © 2010 Andrei Sourakov	The fifth instar has a pale bluish-green cast showing through the skin. The pale yellow stripes and cream-colored head seem similar to the pale patch on the ventral hindwing. First instar larvae have a dark head. Larva photographed on Citrus.

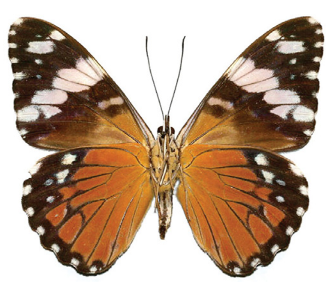
Appendix 2. Seventeen Examples of Dot Patterns on Wing Margins

In some cases a wing margin dot pattern might deter a predator by resembling a larva it considers unpalatable, chemically protected or capable of shedding irritating hairs. In others, the pattern might attract a predator that does not associate the pattern with a warning.

1	*Danaus plexippus plexippus* ♀ (Monarch)	 © 2011 Andrew D. Warren	This example is from our text. The resemblance is not with a Monarch larva, but with a *Battus philenor* (Pipevine Swallowtail) larva. Note the double dotted pattern is seen on both fore- and hindwings.	 © 2008 Wanda Smith
		Wing with larval overlay  	The larva was isolated from the background in the photograph (right) and modified to show the resemblance with the wing margin pattern (left).	

Papilionidae			**Pieridae**		
2	Papilio victorinus victorinus ♀ (Victorine Swallowtail)	 © 2008 Kim Davis, Mike Stangeland and Andrew Warren	3	Catasticta nimbice nimbice ♀ (Mexican Dartwhite)	 © 2010 Kim Davis, Mike Stangeland and Andrew Warren

Nymphalidae					
4	Danaus eresimus Montezuma ♂ (Soldier)	 © 2011 Andrew D. Warren	5	Danaus gilippus thersippus ♂ (Queen)	 © 2009 Jim P. Brock
6	Lycorea halia atergatis ♂ (Tiger Mimic-Queen)	 © 2011 Andrew D. Warren	7	Olyras theon ♀ (Rusty Tigerwing)	 © 2009 Kim Davis, Mike Stangeland and Andrew Warren

8	Scada zibia xanthine ♀ (Zibia Tigerwing)	 © 2009 Kim Davis, Mike Stangeland and Andrew Warren	9	Mechanitis lysimnia labotas ♀ (Lysimnia Tigerwing)	 Image courtesy of Smithsonian Institution and Nick V. Grishin
10	Godyris zavaleta caesiopicta (Variegated Clearwing)	 © 2009 Kim Davis, Mike Stangeland and Andrew Warren	11	Dryadula phaetusa (Banded Longwing)	 © 2009 Jim P. Brock
12	Eueides procula asidia ♂ (Darkened Longwing)	 © 2009 David Robacker	13	Eueides tales pythagoras	 © 2011 Kim Garwood Specimen courtesy of Universidade Federal do Paraná, Curitiba, Brasil (UFPR)
14	Speyeria idalia occidentalis ♀ (Regal Frittilary)	 © 2011 Andrew D. Warren	15	*Limenitis archippus watsoni* ♂ (Viceroy)	 © 2008 Jim P. Brock
16	Hamadryas amphinome mazai ♂ (Red Cracker)	 © 2008 Jim P. Brock	17	Eresia ithomioides poecilina ♀ (Variable Crescent)	 © 2010 Kim Davis, Mike Stangeland and Andrew Warren