

## Does defensive posture increase mimetic fidelity of caterpillars with eyespots to their putative snake models?

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**Abstract** Organisms often evolve behaviours that increase or reinforce the protection from predators afforded by their morphological defences. For example, mimetic animals may adopt postures or locomotory behaviours that emulate a characteristic feature of their model to increase predator deception. Caterpillars with eyespots are thought to mimic snakes, and when threatened many of these caterpillars adopt a posture that appears to enhance this resemblance. Herein we evaluate the quantitative strength of evidence of behavioural mimicry in the caterpillars of 14 species by comparing how closely a series of putative snake-mimicking caterpillars resemble snakes while at rest and when threatened. Specifically, we quantified the head morphology and eye position of a range of snake species, as well as the shape of the apparent head (i.e. anterior body segments) and position of eyespots in caterpillars resting or in their defensive posture. This allowed us to objectively examine evidence for an increased resemblance to either snakes generally, or to Viperidae snakes specifically, upon adopting the defensive posture. Widening the anterior body segments during the defensive posture typically made caterpillars appear more viper-like as opposed to more snake-like in general. Enhanced resemblance to vipers upon mounting the defensive posture was apparent only from the dorsal view. Laterally, caterpillars more closely resembled snakes in the resting posture and shifting to the defensive posture instead reduced mimetic fidelity. Overall we found evidence for behavioural mimicry in all 14 species examined. We highlight that objectively quantifying mimetic fidelity can help identify key features involved in deception [*Current Zoology* 60 (1): 76–89, 2014].

**Keywords** Behaviour, Geometric morphometrics, Protective colouration, Mimicry, Morphology, Vipers

Animals show a variety of predator defences ranging from those which minimize detection (crypsis) to those rendering prey both conspicuous and unprofitable to attack (aposematism) (Edmunds, 1974; Ruxton et al., 2004). Each strategy typically involves trait combinations which mutually reinforce one another. In particular, behaviours frequently evolve to increase the efficacy of an animal's physical traits, such that its overall protection from predators is improved. For example, camouflaged moths often orient themselves on trees to maximize crypsis (Webster et al., 2009; Kang et al., 2012), while noxious newts signal their unpalatability to on-looking predators through a rigid defensive posture that displays their bright ventral colouration (Johnson and Brodie, 1975). Similarly, mimetic animals may employ behaviours to increase their resemblance to dangerous or noxious models. Spectacular examples of this include hoverflies that hold up and wave their dark front legs in front of their head to mimic the conspicuous antennae of wasps (Waldbauer, 1970; Penney et al., in press), and mimetic butterflies that fly slowly and in a

straight line to mimic the nonchalant flight behaviour of their models (Srygley, 1999, 2004). Clearly behavioural mimicry can play a key role in making the discrimination task of the predator more difficult, thereby conferring greater protection to mimetic prey.

While naturalists have long recognized that many lepidopteran caterpillars possess conspicuous eye-like markings ("eyesspots"), many have also noted that when threatened these caterpillars adopt a defensive posture that seems to increase their resemblance to a snake (e.g., Bates, 1862; Weismann, 1882; Poulton, 1890; Cott, 1940). Specifically, when confronted with a perceived threat, many of these caterpillars inflate their anterior body segments and/or pull their head into their body telescopically such that the anterior segments are similarly inflated (Bates, 1862; Weismann, 1882; Poulton, 1890). Fear responses to caterpillars bearing eyespots and displaying their defensive posture have been anecdotally described in taxa ranging from birds to primates (see descriptions from Poulton 1890 and Cott 1940).

Recent work has demonstrated that a fixed defensive

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posture in artificial caterpillars is capable of conferring protection from insect-eating birds in the field (Hossie and Sherratt, 2013). Widening the anterior body segments may function to deter attack for a number of reasons including emphasizing the eyespots, bluffing the potential predator by appearing larger, and enhancing the caterpillar's overall resemblance to snakes. The latter explanation in particular remains speculative without an objective measure of mimetic fidelity in both rest and defensive postures. More fundamentally, despite widespread acceptance that caterpillars with eyespots mimic snakes, we are not aware of any attempt to quantify this resemblance.

Although subjective, inflation of the anterior segments appears to increase the 'head-like' appearance of the anterior body segments (particularly in those species with eyespots, TJH and TNS pers. obs.). This is certainly the case for a range of temperate and tropical caterpillars that we have had the opportunity to observe directly (incl., temperate: *Papilio canadensis*, *P. cresphontes*; tropical: *Eumorpha phorbis*, *Hemeroplanes* sp., *Therinia transversaria*, *Xylophanes cthulhu*). The defensive posture often creates a wider or more triangular-shaped head which seems viper-like on cursory examination, supporting the occasional suggestion that at least some caterpillars with eyespots mimic vipers specifically (Bates, 1962; Valkonen et al., 2011). Yet, the snake families Boidae, Colubridae and Viperidae all contain several species that are important predators of insect-eating birds, and thus snakes from any of these groups pose an imminent mortality threat to insectivorous birds. As such there seems to be little reason to suspect that these caterpillars mimic vipers specifically, as opposed to snake mimicry more generally. Indeed, Janzen et al. (2010) suggested that eyespots function because birds possess a generalized aversion to the eyes of threatening vertebrates in general (i.e., including but not limited to snakes). Venomous snakes may however pose a unique threat in that non-predatory attacks can also result in mortality, and even those snakes too small to consume an insect-eating bird pose considerable risk. Further, large birds and other non-avian insectivores may not be similarly deterred from attacking what appears to be a small snake unless it appears to be venomous. Valkonen et al. (2011) showed that a viper-like head shape reduced predation by raptors on model snakes (compared to models with a "colubrid-like" head shape), and in combination with our work (Hossie and Sherratt, 2013) it seems that birds are generally more cautious when dealing with snake-like prey possessing

wide "heads". Thus, it remains possible that the defensive posture of at least some caterpillars increases their resemblance to Viperidae snakes specifically. Clearly however, the contention that caterpillars with eyespots resemble a Viperidae snake more so than a Colubridae snake requires an objective measure of mimetic fidelity.

Here we have employed a landmark-based shape analysis (i.e., geometric morphometrics, see Zelditch et al., 2004) to quantify the head shape and position of eyes in snakes, to the "head" shape and position of eyespots in putative snake-mimic caterpillars. Specifically, we have attempted to answer two related questions: 1) Does the defensive posture of caterpillars with eyespots increase their resemblance to snakes? and 2) Do these caterpillars resemble Viperidae snakes more so than Colubridae snakes when they adopt their defensive posture?

## 1 Materials and Methods

### 1.1 Specimens

We photographed 10 *Papilio canadensis* (Papilionidae) caterpillars which were hand-reared from eggs laid by wild-caught females collected in Kemptville, Ontario Canada during the summer months of 2011. All *Papilio* caterpillars came from 2 females and were photographed during the final (5<sup>th</sup>) instar in both the rest and defensive posture from both the lateral and dorsal view. Photos of the putative snake mimic *Therina transversaria* (Saturniidae) were taken by TJH of a caterpillar collected by parataxonomists as part of an ongoing inventory project in the Área de Conservación Guanacaste (ACG), Costa Rica (Janzen et al., 2005; Janzen and Hallwachs, 2011). Remaining photos were taken from Janzen and Hallwachs (2013), an online database that catalogues the results of the aforementioned inventory project in the ACG. We searched this database for photos of caterpillars with eyespots that clearly showed the caterpillar from a dorsal or lateral view. Photos were deemed appropriate for this work only if the view of the caterpillar was not rotated, that is, the camera shot was directly over the caterpillars body (dorsal view) or directly revealed the lateral profile of the caterpillar (lateral view). Although this process limited the number of species that could be included in our analysis it was necessary because only these photos could be used to accurately quantify the position of the features of interest (i.e., eyespots, and "head shape") and compare them to their putative models. Further, only those species from which we were able to collect a photo of the caterpillar in both the rest and the defensive

posture were included in our analysis. This was important because it would be difficult otherwise to determine whether the difference in morphology between “rest” and “defensive” photos truly resulted from a change in body posture, and was not simply an artifact of among species variation. Overall, we were able to obtain rest and defensive posture photos for 22 lepidopteran species in total, however only 14 of these species had suitable photos in both lateral and dorsal views. To create shape variables (see below) we used 18 species in the dorsal view and 18 species in lateral view; 4 species in each analysis differed between dorsal and lateral views (see Table S1). The number of caterpillar photographs available (i.e., photos of different individuals) for each species varied from 1–5 (see Table S1), and in cases where multiple images were available we used the average morphology from these photos in our analyses (see below).

Preserved snake specimens from the collections at the Canadian Museum of Nature, Ottawa were photographed from the dorsal and lateral orientations. It seems unlikely that a given caterpillar with eyespots mimics a specific species, but is instead a more general mimic of animals such as snakes that pose an imminent threat to insect-eating birds (Janzen et al., 2010). We therefore collected photos of snake specimens from a range of taxonomic groups that vary in morphology. This approach is in line with our goal which was to characterize the morphospace occupied by snakes in general, as well as colubrid- and viperid-specific morphospaces, such that we could determine the extent of overlap with the caterpillars when adopting their resting and defensive postures. This approach is also conservative in that it minimizes the possibility that failing to select a particular snake species would affect our final conclusions. While we were somewhat limited by availability we were able to photograph 82 preserved snakes, representing 36 species from 19 genera, within six subfamilies (Table S2). Sixteen of these species were from Colubridae, 19 from Viperidae, and one species was from Boidae (Table S2). Dorsal photos required the eye not to be damaged or sunken into the orbit, and lateral photos were only used if the specimen’s mouth was closed or could be closed without distorting the specimen. After close inspection of the snake photos for quality control two species were not included in the dorsal analysis and three species were not included in the lateral analysis because the photos were unsuitable (see Table S2). Overall, the number of photos (of different individuals) for each species of

snake ranged from 1–6, where multiple photos were available the average morphology used in the analyses (see below).

## 1.2 Measurements

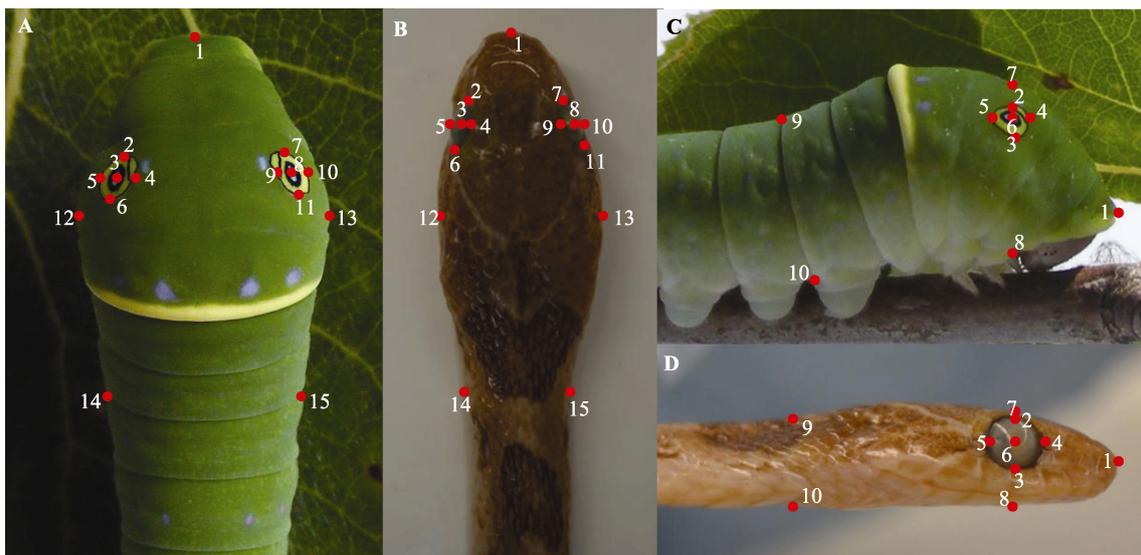
Landmarks were digitized on all photos using tpsDig2 software (Rohlf, 2006) following the landmark placements detailed in Table 1 (see also Fig. 1). We contend that although the landmarks are not placed on anatomically analogous locations between snakes and caterpillars they reflect apparently analogous features in both taxa as seen by a potential predator such as an insect-eating bird (see also Benitez-vieyra et al., 2009 for a similar approach). This landmark data was read into CoordGen7a (Sheets, 2011a) where we conducted a Procrustes transformation to eliminate effects of size, rotation, and translation on shape (Zelditch et al., 2004). In cases where more than one specimen was available within a species (and also within posture for caterpillars) a consensus mean (i.e., a single average set of landmark coordinates for each species) was generated using the reference specification function in CoordGen7a. This process minimized inaccurate assignment of landmark positions within species. We then conducted two principal component analyses (PCAs) using PCAGen7a (Sheets, 2011b) to describe and quantify the variation in shape for both dorsal and lateral views. In each PCA we included landmark data from snakes and from caterpillars in both resting and defensive postures. PCA was selected over other methods, such as canonical variates analysis, because it does not require placing the specimens into pre-defined groups and thereby objectively determines which shape features best describe shape variation in the data set. Principal components (PCs) which described more than 10% of the variation in shape and laid to the left of the “elbow” in the scree plot were then used to describe the morphospace occupied by caterpillars in each posture and snakes, respectively.

## 1.3 Analyses

We determined which of the significant PCs described a change in apparent shape between caterpillars in the resting and defensive posture using matched-pairs *t*-tests (i.e., paired by species). As we were interested in how a change in posture affected resemblance to snakes, only those PCs that showed significant difference in shape between postures were included in subsequent Linear Discriminant Analyses (LDAs) described below. First, we examined whether caterpillars in the defensive posture appear more snake-like than caterpillars in the resting posture by developing a LDA model to discriminate between caterpillars and snakes. To develop

**Table 1** The position of landmarks for geometric morphometric comparison of ‘eyespot’ and body shape of *Papilio* caterpillars and the corresponding landmark positions on snakes

Lateral View		
Landmark	Caterpillar	Snake
1	Center of eyespot	Center of eye
2	Top of eyespot	Top of eye
3	Bottom of eyespot	Bottom of eye
4	Anterior extent of eyespot	Anterior extent of eye
5	Posterior extent of eyespot	Posterior extent of eye
6	Behind 1 <sup>st</sup> segment behind head	Tip of snake nose
7	Top of body above center of eyespot	Top of head above center of eye
8	Bottom of body below center of eyespot	Bottom of head below center of eye
9	Top of body after the 6 <sup>th</sup> body segment	Top of body, where neck meets the head
10	Directly below LM 9	Directly below LM 9
Dorsal View		
Landmark	Caterpillar	Snake
1	Behind 1 <sup>st</sup> segment behind head	Tip of snake nose
2	Anterior extent of left eyespot	Anterior extent of left eye
3	Center of left eyespot	Center of left eye
4	Left eyespot, closest point toward the midline	Left eye, closest point towards center of head
5	Left eyespot, furthest point to the left	Left eyespot, furthest point to the left
6	Posterior extent of left eyespot	Posterior extent of left eye
7	Anterior extent of right eyespot	Anterior extent of right eye
8	Center of right eyespot	Center of right eye
9	Right eyespot, closest point toward the midline	Right eye, closest point towards center of head
10	Right eyespot, furthest point to the left	Right eyespot, furthest point to the left
11	Posterior extent of right eyespot	Posterior extent of right eye
12	Widest point on the left side of body	Widest point on the left side of head
13	Widest point on the right side of body	Widest point on the right side of head
14	After 6 <sup>th</sup> body segment, left extent	Left extent of body after the head
15	After 6 <sup>th</sup> body segment, right extent	Right extent of body after the head

**Fig. 1** Landmark placements for caterpillars and snakes in their dorsal and lateral views

**A.** *Papilio canadensis* (Papilionidae) caterpillar in defensive posture, dorsal view. **B.** *Leptodeira annulata* (Colubridae) snake, dorsal view. **C.** *P. canadensis* caterpillar defensive posture, lateral view. **D.** *L. annulata*, lateral view.

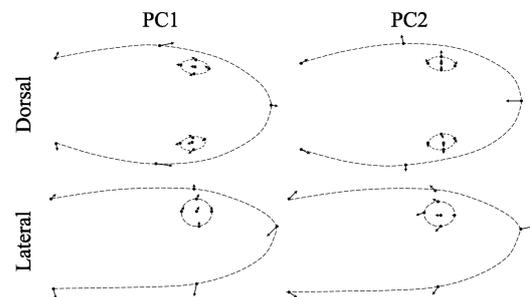
the model we included data from caterpillars in the resting posture and all the snake species sampled, but excluded data from caterpillars in their defensive posture. This model was then used to classify caterpillars in the defensive posture as either caterpillars or snakes (using a posterior probability threshold of  $>0.5$ ). Posterior probabilities for the classification of resting and defensive posture caterpillars were extracted and we used a matched-pairs *t*-test to examine whether the probability of classification as a snake changed with posture.

Next, we created a second LDA model to determine whether caterpillars in the defensive posture look more like vipers than colubrids. Specifically, a model was developed to discriminate among caterpillars, Colubridae snakes, and Viperidae snakes using data from caterpillars in their resting posture and all colubrid and viperid snake species sampled, but excluding data from caterpillars in their defensive posture. The resulting LDA model was then used to classify caterpillars when in their defensive posture (i.e., as a caterpillar, Colubridae snake, or Viperidae snake). Using the posterior probabilities of classification from the LDA model we tested whether the probability of classification of the caterpillars as a caterpillar, Colubridae snake, or Viperidae snake changed between postures with dependent *t*-tests. A final LDA model that included all significant PCs (i.e., including those that did not differ significantly with posture) was developed in the same way to determine the relative importance of each PC in discriminating among groups when all information is available. Differences between snake families (Colubridae and Viperidae) in dorsal and lateral PCs were tested using Welch's *t*-tests. All LDAs and *t*-tests were conducted using R statistical software (R Core Development Team, 2012).

## 2 Results

In quantifying the variation in shape when considering caterpillars in resting and defensive posture, as well as snakes from Colubridae and Viperidae (and one Boiidae species), our PCA revealed that two PCs explained the majority of the variance in shape for the dorsal view (% variance explained: PC1 = 63.6%, PC2 = 19.6%), and similarly two PCs explained the majority of the variance in the lateral view (% variance explained: PC1 = 37.7%, PC2 = 33.4%). A greater dorsal PC1 value indicates a more anterior position for the widest points on the "head", a slight posterior shift of the "eyes", and an anterior lengthening of the "head" (Fig. 1). In con-

trast an increase in dorsal PC2 represents a widening of the "head" with concurrent movement of the "eyes" away from the midline, and the anterior point moving in towards the body shortening the "head" (Fig. 2). As the lateral PC1 value increases the body becomes dorso-ventrally thicker, the "eyes" move dorsally, and the anterior point of the body comes in toward the body (Fig. 2). Finally, an increase in lateral PC2 indicates a dorso-ventral thickening, slight enlargement of the "eye", and a lengthening of the anterior point of the head (Fig. 2). The morphospace occupied by each group in the dorsal and lateral view is depicted in Fig. 3.



**Fig. 2** Vector plots illustrating the shape change described by principal components (PCs) 1 and 2 for both the dorsal and lateral view

Vectors point in the direction of an increasing PC value.

Only two PCs described shape variation that differed significantly between the caterpillars in the resting and defensive posture: dorsal PC2 and lateral PC1 (Table 2, Fig. 3). Yet only dorsal PC2, and not lateral PC1, differed significantly between Colubridae and Viperidae snakes (dorsal PC2:  $t_{23,28} = -4.215$ ,  $P = 0.0003$ , lateral PC1:  $t_{19,89} = -1.414$ ,  $P = 0.17$ ). The first LDA was only able to correctly identify 50% (7/14) of the rest caterpillars and only misclassified 13% (4/32) of snakes as caterpillars. When caterpillars in their defensive posture were classified by this model, an equivalent 50% of the caterpillars were identified as snakes (i.e., had posterior probability of  $>0.5$ , Table S4). Caterpillars from three species shifted from being classified as a caterpillar in the rest posture to a snake when in the defensive posture, and similarly three species classified as snakes in the rest posture were classified as caterpillars in the defensive posture (Table S4). A dependent *t*-test did not indicate a significant change in the posterior probability of classification as a snake when considering all species examined ( $t = -0.41$ ,  $df = 13$ ,  $P = 0.69$ ), although some species clearly became more snake-like (Table S4).

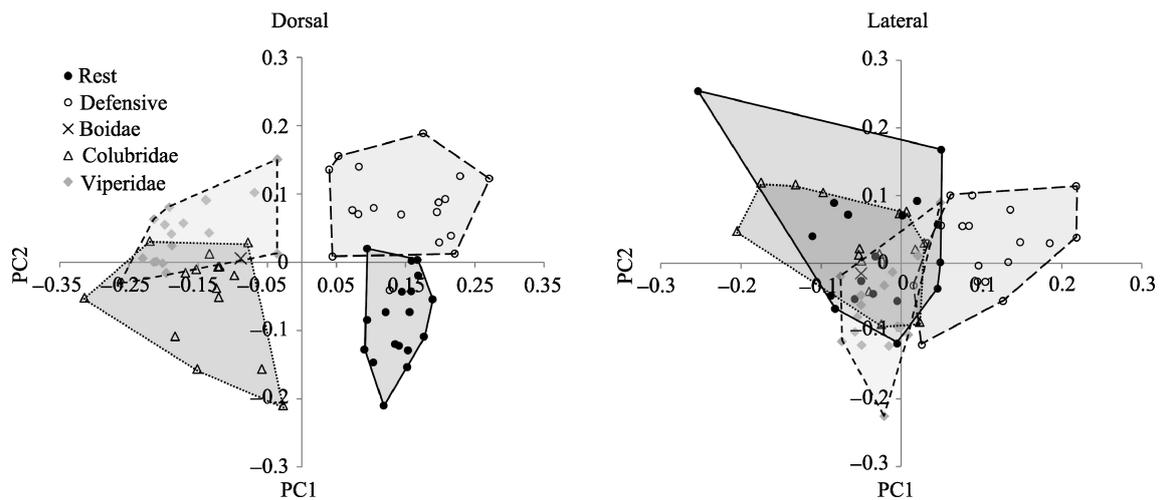
In the second LDA, 57% (8/14) of rest caterpillars were correctly identified as caterpillars (6 were classi-

fied as Colubridae snakes), whereas 71% (22/31) of snakes were correctly assigned to family. Three colubrid snakes were misclassified as vipers, but only two vipers as a colubrid. Four snakes were misclassified as caterpillars (three Colubridae and one Viperidae). This LDA model correctly classified 57% (8/14) of the defensive posture caterpillars as caterpillars, the remaining 43% (6/14) were misclassified as vipers. Of the caterpillars misclassified as vipers, three had been classified as caterpillars in the resting posture and three had been classified as colubrid snakes (Table S4). Dependent *t*-tests revealed that upon adopting the defensive posture caterpillars generally became significantly less caterpillar-like ( $t = 8.09$ ,  $df = 13$ ,  $P < 0.001$ ), significantly more viper-like ( $t = -3.34$ ,  $df = 13$ ,  $P = 0.005$ ), but not significantly more colubrid-like ( $t = -0.67$ ,  $df = 13$ ,  $P = 0.52$ ).

Data inspection revealed that a shift to the defensive posture actually decreased mimetic fidelity in terms of the shape change described by lateral PC1 (Fig. 3). In

addition, only dorsal PC2, but not lateral PC1, differed between colubrid and viperid snakes. Taken together this indicated that mimicry might be operating from the dorsal view only. Thus, we conducted an additional LDA using only dorsal PC2 to examine classification rates under the assumption that predators primarily use this information. Similar to the previous analysis (i.e., LDA 2) we found that 8/14 resting caterpillars were classified as caterpillars (4/14 as colubrids, 2/14 as vipers), but when the model was applied to the defensive posture all 14 species were classified as snakes (1/14 as a colubrid, 13/14 as vipers, Figure 4). Importantly, dependent *t*-tests confirmed that caterpillars were less “caterpillar-like” in the defensive posture ( $t = 9.67$ ,  $df = 13$ ,  $P < 0.001$ ), but also that they were less colubrid-like ( $t = 6.90$ ,  $df = 13$ ,  $P < 0.001$ ) and more viper-like ( $t = -10.63$ ,  $df = 13$ ,  $P < 0.001$ ).

Finally, the overall LDA model which included all four PCs (i.e. PC1 and PC2 from both dorsal and lateral views) had the most accurate assignment rates. All rest



**Fig. 3** The morphospace occupied by caterpillars with eyespots in their resting and defensive postures as compared to Colubridae and Viperidae snakes

Only one Boidae snake was measured and its location is demarked with an X.

**Table 2** Results from matched-pairs *t*-tests comparing the shape of caterpillars in their rest and defensive postures for each of four shape variables (i.e. principal components)

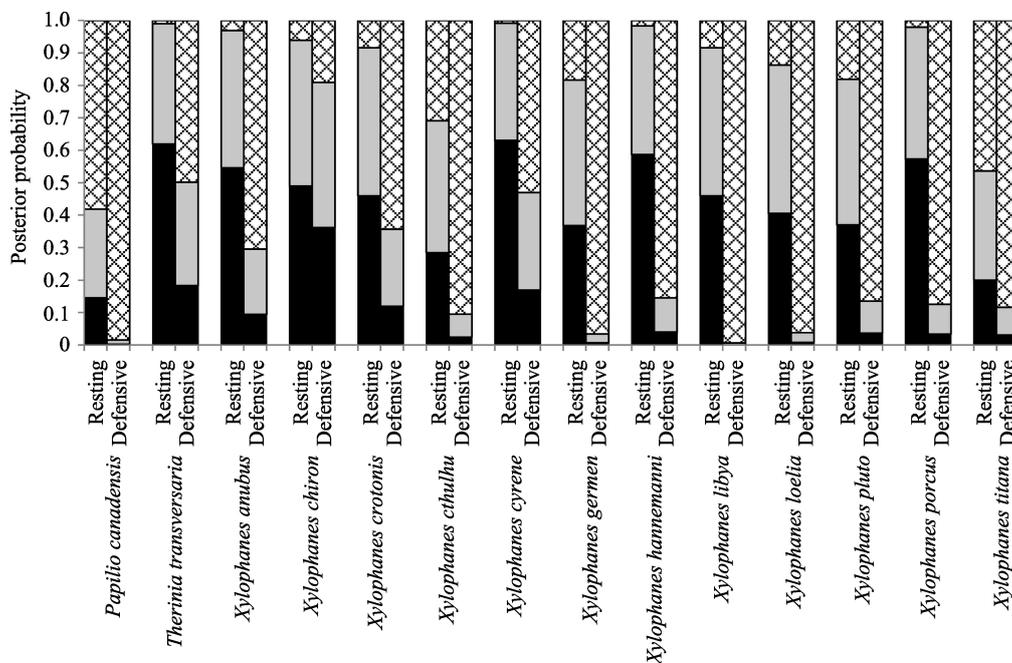
Principal Component	Posture	Mean	SD	<i>n</i>	<i>t</i>	<i>df</i>	<i>P</i> -value
Dorsal PC1	Rest	0.14	0.03	18	-0.04	17	0.63
	Defensive	0.148	0.0733	18			
Dorsal PC2	Rest	-0.082	0.0626	18	-9.734	17	<0.0001
	Defensive	0.082	0.0581	18			
Lateral PC1	Rest	-0.037	0.0751	18	-6.356	17	<0.0001
	Defensive	0.105	0.0606	18			
Lateral PC2	Rest	0.023	0.0927	18	-0.049	17	0.96
	Defensive	0.024	0.0608	18			

caterpillars were correctly assigned as caterpillars (i.e., in both resting and defensive postures), two Colubridae snakes were misclassified as vipers, and one viper was misclassified as a Colubridae snake. The standardized coefficients of the linear discriminants for all LDA models are provided in the electronic supplementary material (Table S3).

### 3 Discussion

We quantified the head morphology of preserved snakes as well as the shape of the anterior body segments (i.e., the apparent head) of 14 caterpillars with eyespots in their resting and defensive postures to test for evidence of behavioural mimicry. Specifically, we tested whether the defensive posture of these caterpillars increases their resemblance to snakes in general, or if it increases their resemblance to vipers. Our first discriminant analysis was developed to distinguish between resting posture caterpillars and snakes, but only assigned 50% of the resting caterpillars correctly. Applying this model to the same caterpillars when in their defensive posture revealed that the change in posture did not significantly increase the probability of classification as a snake. We therefore did not find sufficient evidence to indicate that the defensive posture increases (or reduces) the resemblance of these caterpillars to snakes in general.

The second discriminant analysis, developed to distinguish among caterpillars at rest, Colubridae snakes, and Viperidae snakes, revealed that caterpillars in their defensive posture were more viper-like compared to when in their resting posture. Also, no caterpillar in the defensive posture was misclassified as a colubrid snake, but 43% were misclassified as vipers. As the lateral view reduced mimetic fidelity upon adopting the defensive posture (see Fig. 3), and did not differ between colubrid and viperid snakes, an additional analysis assessed how caterpillars would be classified if only the key dorsal features (i.e., dorsal PC2) were used. This analysis revealed that the classification of caterpillars shifted significantly towards a more viper-like appearance and away from that of a resting caterpillar or colubrid snake (Fig. 4). All 14 caterpillars in the defensive posture were classified as snakes (13/14 as vipers, 1/14 as a colubrid). Our analyses thus provide statistical evidence for behavioural mimicry in all species examined (including species from Papilionidae, Sphingidae, and Saturniidae), and reveal that the shift in posture helps these caterpillars mimic dorsal, but not lateral, features of venomous snakes. Of course, just because the caterpillars happen to look more viper like does not prove that they are adopting this posture in order to improve their mimetic fidelity - the enhanced similarity could be entirely incidental. However, our analysis is consistent



**Fig. 4** Posterior probabilities for the classification of caterpillars from 14 species as a caterpillar (black), colubrid snake (grey), or viperid snake (hatched) when in their resting and defensive posture

Posterior probabilities shown here were extracted from a linear discriminant analysis using only dorsal features that changed with posture (i.e., dorsal PC2 only).

with this theory, as well as repeated anecdotal observations that the caterpillars become more snake like when they adopt their defensive postures.

Our final LDA which included all four shape variables (PCs) did not misclassify any caterpillars as snakes, even when the caterpillars adopted the defensive posture. This indicates that it should be possible for a predator to discriminate between snakes and each of the caterpillars examined here based solely on the features we quantified. Critically, perfect mimicry is not required to yield a selective advantage over non-mimics (Edmunds, 2000; Penney et al., 2012); even small adjustments in mimetic fidelity can result in large differences in the degree of protection, particularly when the model is highly noxious (Duncan and Sheppard, 1965; Ditttrich et al., 1993; Sherratt, 2002). It is therefore likely that the apparent morphological changes resulting from a shift in posture, as quantified here, translate into a significant protective effect. Indeed, we have recently shown such an effect in the field using model caterpillars designed to represent the resting and defensive postures (Hossie and Sherratt, 2013). Predators also face a speed-accuracy trade-off which imposes limits to the amount of information that can be acquired and instead favours rapid decisions based on conspicuous features (Chittka and Osorio, 2007; Abbott and Sherratt, 2013). Insect-eating birds likely adopt a “safety first” strategy in order to balance the benefit of avoiding an imminent mortality threat which far outweighs the cost of losing a meal. Such a strategy would enable caterpillars to gain protection from even relatively poor levels of mimetic fidelity (Ruxton, 2005; Bura et al., 2011; Olofsson et al., 2012). Finally, we note that by adopting a more viper-like “head” shape the caterpillars resemble a snake that is less frequently confused with caterpillars (as judged by our analyses). Therefore increasing resemblance to vipers may simply aid in concealing the caterpillar’s true identity, as opposed to indicating that viper-specific resemblance has arisen because vipers pose a greater threat to attackers.

Although the apparent head shape of caterpillars in the defensive posture increases the caterpillar’s resemblance to Viperidae snakes when viewed dorsally, adopting the defensive posture did not increase resemblance to either snake family (or to snakes in general) from the lateral view. Features visible from above, such as apparent head width, may be under stronger selection to resemble snakes because insect-eating birds often view caterpillars from above, or because dorsal features more reliably distinguish colubrid and viperid snakes.

Constraints relating to caterpillar anatomy may also help explain the lack of similarity of the defensive posture when viewed laterally. For example, inflating the anterior body segments to achieve the goal of widening the apparent head might simultaneously deepen the “head” due to the caterpillar’s soft exoskeleton. This explanation is consistent with our morphometric analysis which illustrated that a change from rest to defensive posture resulted in a wider but shorter apparent head dorsally (dorsal PC2), and deeper but shorter apparent head laterally (lateral PC1). There is however substantial overlap between resting caterpillars and snakes in the lateral morphospace (Fig. 3), indicating that resting caterpillars may effectively mimic snakes while resting so long as they are viewed laterally. Briefly, we highlight that our method of quantifying mimetic fidelity is distinct from other approaches (e.g., Taylor et al., 2013), but such landmark-based approaches are particularly well suited for examining changes in similarity due to behaviour (i.e., behavioural mimicry) and offer a promising tool for future research. Landmark-based methods are useful when analogous features (e.g., eyespots vs. real eyes) are easily denoted among models and mimics (even if such features are not homologous), whereas methods akin to Taylor et al. (2013) are likely to be superior in cases where colour patterns are not immediately analogous (e.g., yellow and black bands on mimetic flies and their hymenopteran models).

Under what conditions should we expect behavioural mimicry to evolve? Does it arise in relatively good mimics reflecting the comparatively strong selection for mimetic perfection or in poor mimics as a means of compensation? Initial evidence in hoverflies suggests that behavioural mimics also tend to be relatively good morphological mimics (Penney et al., in press). Anecdotally, this also seems to be true for caterpillars with eyespots as the most complete case of behavioural mimicry of which we are aware occurs in caterpillars from the *Hemeroplanes* genus (Sphingidae). In the defensive posture these species show an uncanny resemblance to snakes, and further extend the deception by reaching out from the tree in a display that convincingly resembles an arboreal viper outstretched from a branch (TJH, *personal observation*; see photos in Janzen and Hallwachs, 2013). Further, we expect behavioural mimicry in caterpillars with eyespots to be more pronounced in large species for a number of reasons. First, large species are more profitable prey items making predators more inclined to search them out and less easily deterred from attack upon encounter (see also Penney et

al., 2012). Second, large preys are more conspicuous and may therefore be under stronger selection to evolve defences that offer protection post-encounter. Third, behavioural mimicry may be more convincing (and therefore effective) when the caterpillar falls closer to the size range of real snakes. More generally, larger “items” may simply be more likely to pose a significant threat, thereby favoring startle or mimicry defences more strongly in relatively large prey. Finally, large caterpillars may be more readily attacked by non-avian predators that utilize a different set of cues to identify snakes and thereby require more complete mimicry to deceive a wider range of predators.

Although our results provide an important step towards understanding mimicry in this system by quantifying mimetic fidelity of caterpillars with eyespots to their putative models, interpretation of our results should be tempered by the following considerations. First, our analyses only considered snakes as possible models, whereas lizards and other dangerous vertebrates may serve to generate or reinforce the aversion to attacking eyespot caterpillars. We also acknowledge the possibility that the specific snake species used in our analysis may have influenced our results. Specifically, the head morphology of some colubrid snakes not included here may be more similar to that of the “viper-like” head shape described by our analyses. However, we attempted to select species from a range of taxonomic lineages with diverse head morphologies, and thus our results should be robust to the addition or removal of a given species. Unfortunately, we were not able to measure enough Boidae species to compare mimetic fidelity to these snakes directly, although these snakes likely pose an important risk to birds and may represent an important model. Due to a lack of photos we did not characterize the head-on view of caterpillars which may also play an important role in the mimetic resemblance to snakes, particularly for those caterpillars that hide in leaf shelters. Similarly, a lack of available photos limited our investigation to 3 families within Lepidoptera, the majority of which came from one genus (*Xylophanes*). Finally, we note that there are several caterpillars that lack or have poorly developed eyespots which adopt defensive postures similar to those described here, and a mimetic function is suspected in at least some of these species (e.g., *Eumorpha phorbis*, *Papilio cresphontes*).

The evolution of eyespots and coincident behavioural mimicry could have important evolutionary consequences within Lepidoptera, such as influencing the rate

of speciation. There are several examples of species-rich genera within Lepidoptera which have independently evolved eyespots, and the associated behavioural mimicry discussed here, including two that we examined: *Papilio* (Papilionidae) and *Xylophanes* (Sphingidae). Whereas caterpillars that employ crypsis rely on host-specific colour matching for effective concealment, and aposematic caterpillars rely on secondary metabolites from their host plant to gain toxicity, caterpillars with eyespots and deceptive behaviours are diminished in their reliance on a specific host plant for protection from predators possibly facilitating radiation. Ongoing research will examine this possibility that species with caterpillars employing deceptive anti-predator defences (e.g., snake or bird-dropping mimics) radiate more rapidly. The augmented rates of speciation observed in orchids (Orchidaceae) have been similarly explained by the evolution of deception, though within a different context (Cozzolino and Widmer, 2005; Papadopulos et al., 2013). Doubtless, the numerous examples of caterpillars which appear to mimic snakes or other threatening vertebrates indicates that deception has played an important role within Lepidoptera, and has likely influenced each species’ behaviour or life history in ways yet to be discovered.

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## Electronic Supplementary Material

Table S1 Voucher codes for the caterpillar photographs from the Janzen and Hallwachs (2013) database used in this study

Family	Genus	Species	Voucher Code - Dorsal View		Voucher Code - Lateral View	
			Rest	Defensive	Rest	Defensive
Papilionidae	<i>Papilio</i>	<i>canadensis</i>	Our photos (×10)	Our photos (×10)	Our photos (×10)	Our photos (×10)
Saturniidae	<i>Therinia</i>	<i>transversaria</i>	Our photo	Our photo	Our photo	Our photo
Sphingidae	<i>Hemeroplanes</i>	<i>triptolemus</i>	10-SRNP-56098-DHJ478827, 10-SRNP-56277-DHJ478913	02-SRNP-1085-DHJ64470, 99-SRNP-136-DHJ50036	97-SRNP-4423-DHJ42550 97-SRNP-999-DHJ40683	03-SRNP-11366-DHJ75729, 97-SRNP-4423-DHJ42596 97-SRNP-999-DHJ40677
Sphingidae	<i>Xylophanes</i>	<i>acrus</i>				
Sphingidae	<i>Xylophanes</i>	<i>anubus</i>	89-SRNP-45-DHJ10874	84-SRNP-778-DHJ7654, 84-SRNP-781-DHJ7582	10-SRNP-56277-DHJ478914	10-SRNP-56277-DHJ478918
Sphingidae	<i>Xylophanes</i>	<i>ceratomioides</i>			07-SRNP-30429-DHJ419664, 97-SRNP-1330-DHJ41367	07-SRNP-30429-DHJ419665
Sphingidae	<i>Xylophanes</i>	<i>chiron</i>			03-SRNP-11913-DHJ75997, 97-SRNP-1115-DHJ40852, 97-SRNP-1115-DHJ40861	84-SRNP-778-DHJ7652
Sphingidae	<i>Xylophanes</i>	<i>crotonis</i>	88-SRNP-210-DHJ10547, 97-SRNP-1277-DHJ41214	05-SRNP-30799-DHJ403870, 90-SRNP-131-DHJ12359	07-SRNP-36072-DHJ421962, 97-SRNP-1413-DHJ41460	05-SRNP-30799-DHJ403873, 97-SRNP-991-DHJ40663
Sphingidae	<i>Xylophanes</i>	<i>ctulhu</i>	04-SRNP-46796-DHJ85724, 05-SRNP-70564-DHJ409953	04-SRNP-46796-DHJ85713, 04-SRNP-56290-DHJ400264, 05-SRNP-31108-DHJ403970	04-SRNP-46796-DHJ401834	05-SRNP-70564-DHJ409942, 06-SRNP-5738-DHJ411363
Sphingidae	<i>Xylophanes</i>	<i>cyrene</i>	97-SRNP-1186-DHJ41014, 97-SRNP-1308-DHJ41297, 98-SRNP-4167-DHJ45054	03-SRNP-20005-DHJ90017, 04-SRNP-33965-DHJ86617	03-SRNP-6092-DHJ74160, 07-SRNP-30411-DHJ419654, 07-SRNP-33235-DHJ430174, 97-SRNP-1308-DHJ41287	02-SRNP-35532-DHJ67352
Sphingidae	<i>Xylophanes</i>	<i>germen</i>	97-SRNP-759-DHJ40413	98-SRNP-2906-DHJ44485	97-SRNP-759-DHJ40402, 97-SRNP-759-DHJ40408	98-SRNP-2906-DHJ44487
Sphingidae	<i>Xylophanes</i>	<i>hannemanni</i>	05-SRNP-35718-DHJ406592, 97-SRNP-1445-DHJ41503, 98-SRNP-2904-DHJ44482	95-SRNP-8588-DHJ25725, 97-SRNP-1319-DHJ41328	97-SRNP-1187-DHJ41027, 97-SRNP-1189-DHJ41041, 97-SRNP-1297-DHJ41273, 97-SRNP-1446-DHJ41510	05-SRNP-35718-DHJ406600, 89-SRNP-782-DHJ11707, 96-SRNP-7049-DHJ28067
Sphingidae	<i>Xylophanes</i>	<i>jocasta</i>	01-SRNP-2579-DHJ62779	03-SRNP-15009-DHJ76686		
Sphingidae	<i>Xylophanes</i>	<i>juanita</i>	81-SRNP-233-DHJ2260, 84-SRNP-668-DHJ7569, 84-SRNP-1403-DHJ8202	84-SRNP-1403-DHJ8203		
Sphingidae	<i>Xylophanes</i>	<i>libya</i>	01-SRNP-1685-DHJ57768, 06-SRNP-5047-DHJ410874, 08-SRNP-56233-DHJ442748, 84-SRNP-668-DHJ7569, 99-SRNP-12438-DHJ51791	97-SRNP-3065-DHJ42131	01-SRNP-1685-DHJ63211, 99-SRNP-12438-DHJ51793	99-SRNP-12438-DHJ51781
Sphingidae	<i>Xylophanes</i>	<i>loelia</i>	04-SRNP-41581-DHJ85472, 08-SRNP-42461-DHJ449689	08-SRNP-42458-DHJ449660		08-SRNP-42458-DHJ449661
Sphingidae	<i>Xylophanes</i>	<i>maculata</i>	03-SRNP-6093-DHJ74217, 05-SRNP-30849-DHJ403890	84-SRNP-176-DHJ7129		

Continued Table S1

Family	Genus	Species	Voucher Code - Dorsal View		Voucher Code - Lateral View	
			Rest	Defensive	Rest	Defensive
Sphingidae	<i>Xylophanes</i>	<i>pluto</i>	01-SRNP-10544-DHJ1875,	88-SRNP-263-DHJ10610	92-SRNP-1004-DHJ15003,	06-SRNP-55100-DHJ409510,
			81-SRNP-633-DHJ2814,		98-SRNP-4966-DHJ45359	81-SRNP-633-DHJ2817
			92-SRNP-894-DHJ14973,			
			92-SRNP-1004-DHJ15019,			
			98-SRNP-4966-DHJ45363			
Sphingidae	<i>Xylophanes</i>	<i>porcus</i>	06-SRNP-21539-DHJ11902,	97-SRNP-1185-DHJ41007	06-SRNP-21539-DHJ411904,	10-SRNP-56353-DHJ478981
			84-SRNP-367A-DHJ7287,		06-SRNP-21542-DHJ411912,	
			95-SRNP-7691-DHJ24958,		84-SRNP-367A-DHJ7286	
			98-SRNP-3198-DHJ44671			
Sphingidae	<i>Xylophanes</i>	<i>tersa</i>			05-SRNP-34374-DHJ405859,	08-SRNP-40795-DHJ442047,
					97-SRNP-7088-DHJ43706,	97-SRNP-1395-DHJ41417,
					98-SRNP-4176-DHJ45099	97-SRNP-2397-DHJ41875
Sphingidae	<i>Xylophanes</i>	<i>titana</i>	02-SRNP-1570-DHJ87871,	02-SRNP-1567-DHJ67108,	02-SRNP-1567-DHJ67106	02-SRNP-1567-DHJ67131
			06-SRNP-65788-DHJ425756	02-SRNP-1567-DHJ67129		
Sphingidae	<i>Xylophanes</i>	<i>zurcheri</i>	98-SRNP-2996-DHJ44551	02-SRNP-1942-DHJ67139		

Table S2 Voucher codes for snake specimens from the collections at the Canadian Museum of Nature photographed for this study

Family	Subfamily	Genus	Species	Voucher (dorsal)	Voucher (Lateral)	Dorsal	Lateral
Boidae	Boinae	<i>Corallus</i>	<i>caninus</i>	CMNAR 13955, CMNAR 28546	CMNAR 13955, CMNAR 28546, CMNAR 28547	Yes	Yes
Colubridae	Colubrinae	<i>Ahaetulla</i>	<i>nasuta</i>	CMNAR 3160	CMNAR 3160	Yes	Yes
Colubridae	Colubrinae	<i>Boiga</i>	<i>dendrophila</i>	CMNAR 30936, CMNAR 32425, CMNAR 34932, CMNAR 34983	CMNAR 30936, CMNAR 32425, CMNAR 34983	Yes	Yes
Colubridae	Colubrinae	<i>Elaphe</i>	<i>obsoleta</i>	CMNAR 3929, CMNAR 12743, CMNAR 25734, CMNAR 27969, CMNAR 31910	CMNAR 3929, CMNAR 12743, CMNAR 25734, CMNAR 31910	Yes	Yes
Colubridae	Colubrinae	<i>Entechinus</i>	<i>major</i>	CMNAR 35068	CMNAR 35068	Yes	Yes
Colubridae	Colubrinae	<i>Lampropeltis</i>	<i>getulus</i>	CMNAR 1273, CMNAR 10182, CMNAR 12509, CMNAR 12534	CMNAR 1273, CMNAR 10182, CMNAR 12509, CMNAR 12533	Yes	Yes
Colubridae	Colubrinae	<i>Liochlorophis</i>	<i>vernalis</i>	CMNAR 2667, CMNAR 3936, CMNAR 25190 (x4), CMNAR 34014, CMNAR 36004	CMNAR 2667, CMNAR 3936, CMNAR 25190 (x4), CMNAR 34014, CMNAR 36004	Yes	No
Colubridae	Colubrinae	<i>Opheodrys</i>	<i>aestivus</i>	CMNAR 890, CMNAR 1659, CMNAR 10987, CMNAR 17660, CMNAR 29763	CMNAR 890, CMNAR 10987, CMNAR 17660, CMNAR 29763	Yes	Yes
Colubridae	Colubrinae	<i>Opheodrys</i>	<i>vernalis</i>			No	Yes
Colubridae	Colubrinae	<i>Philothamnus</i>	<i>hoplogaster</i>	CMNAR 15830, CMNAR 25672	CMNAR 15830, CMNAR 25672	Yes	Yes
Colubridae	Dipsadinae	<i>Leptodeira</i>	<i>annulata</i>	CMNAR 2172, CMNAR 3212, CMNAR 7625	CMNAR 2172, CMNAR 3212, CMNAR 7625	Yes	Yes

Continued Table S2

Family	Subfamily	Genus	Species	Voucher (dorsal)	Voucher (Lateral)	Dorsal	Lateral
Colubridae	Natricinae	<i>Thamnophis</i>	<i>elegans</i>	CMNAR 621, CMNAR 622, CMNAR 1614, CMNAR 5667, CMNAR 12299, CMNAR 28980	CMNAR 621, CMNAR 622, CMNAR 1614, CMNAR 5667, CMNAR 12299, CMNAR 28980	Yes	Yes
Colubridae	Natricinae	<i>Thamnophis</i>	<i>sirtalis</i>	CMNAR 14415, CMNAR 18796, CMNAR 35932, CMNAR 36177(x4)	CMNAR 14415, CMNAR 18796, CMNAR 35932, CMNAR 36177(x4)	Yes	Yes
Colubridae	Xenodontinae	<i>Heterodon</i>	<i>platyrhinus</i>	CMNAR 14886, CMNAR 15855, CMNAR 19201, CMNAR 29583, CMNAR 34170	CMNAR 14886, CMNAR 15855, CMNAR 19201, CMNAR 29583, CMNAR 34170	Yes	Yes
Colubridae	Xenodontinae	<i>Oxybelis</i>	<i>aeneus</i>	CMNAR 27243	CMNAR 27243	Yes	Yes
Colubridae	Xenodontinae	<i>Oxybelis</i>	<i>fulgidus</i>	CMNAR 34864	CMNAR 34864	Yes	Yes
Colubridae	Xenodontinae	<i>Sibynomorphus</i>	<i>vagus</i>	CMNAR 35191	CMNAR 35191	Yes	Yes
Viperidae	Crotalinae	<i>Agkistrodon</i>	<i>acutus</i>	CMNAR 30966, CMNAR 34908	CMNAR 30966(x2), CMNAR 34908	Yes	Yes
Viperidae	Crotalinae	<i>Agkistrodon</i>	<i>bilineatus</i>	CMNAR 30950		Yes	No
Viperidae	Crotalinae	<i>Agkistrodon</i>	<i>contortrix</i>	CMNAR 12564, CMNAR 34671, CMNAR 34879, CMNAR 34962	CMNAR 12564, CMNAR 34671, CMNAR 34879, CMNAR 34962	Yes	Yes
Viperidae	Crotalinae	<i>Agkistrodon</i>	<i>halys</i>	CMNAR 32423, CMNAR 34960	CMNAR 32423, CMNAR 34960	Yes	Yes
Viperidae	Crotalinae	<i>Agkistrodon</i>	<i>rhodostoma</i>	CMNAR 34959	CMNAR 34959	Yes	Yes
Viperidae	Crotalinae	<i>Bothrops</i>	<i>godmani</i>	CMNAR 13798	CMNAR 13798	Yes	Yes
Viperidae	Crotalinae	<i>Bothrops</i>	<i>lateralis</i>		CMNAR 30949	No	Yes
Viperidae	Crotalinae	<i>Bothrops</i>	<i>nummifer</i>	CMNAR 34915		Yes	No
Viperidae	Crotalinae	<i>Bothrops</i>	<i>schlegelii</i>	CMNAR 32421(x3), CMNAR 34901	CMNAR 32421(x3), CMNAR 34901	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>adamanteus</i>	CMNAR 33995	CMNAR 33995	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>atrox</i>	CMNAR 8304	CMNAR 8304	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>durissus</i>	CMNAR 31654	CMNAR 31654	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>horridus</i>	CMNAR 13954, CMNAR 34319	CMNAR 13954, CMNAR 34319	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>scutulatus</i>	CMNAR 12441, CMNAR 34694	CMNAR 12441, CMNAR 34694	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>tigris</i>	CMNAR 34412, CMNAR 34981	CMNAR 34981	Yes	Yes
Viperidae	Crotalinae	<i>Crotalus</i>	<i>viridis</i>	CMNAR 17663	CMNAR 17663	Yes	Yes
Viperidae	Crotalinae	<i>Lachesis</i>	<i>muta</i>	CMNAR 34902	CMNAR 34902	Yes	Yes
Viperidae	Crotalinae	<i>Sistrurus</i>	<i>catenatus</i>	CMNAR 13786(x4)	CMNAR 13786(x4)	Yes	Yes
Viperidae	Crotalinae	<i>Sistrurus</i>	<i>militarius</i>	CMNAR 1283	CMNAR 1283	Yes	Yes

**Table S3 The standardized coefficients of the linear discriminants**

Principal Component	Caterpillar vs. Snake (LDA1)	Caterpillar, Colubridae, or Viperidae (LDA2)	Caterpillar, Colubridae, or Viperidae (Dorsal PC2 only)	Overall model (LDA3)
Dorsal PC1				21.297
Dorsal PC2	20.717	25.483	17.281	-14.289
Lateral PC1	-20.012	-17.529		13.99
Lateral PC2				-5.514

**Table S4 Classification of caterpillars as predicted by the linear discriminant analyses (LDAs)**

Family	Genus	Species	LDA1		LDA2	
			Rest	Defensive	Rest	Defensive
Papilionidae	<i>Papilio</i>	<i>canadensis</i>	Snake (55%)	Snake (63%)	Caterpillar (46%)	Viperidae (73%)
Saturniidae	<i>Therinia</i>	<i>transversaria</i>	Caterpillar (97%)	Caterpillar (84%)	Caterpillar (95%)	Caterpillar (84%)
Sphingidae	<i>Xylophanes</i>	<i>anubus</i>	Snake (53%)	Caterpillar (85%)	Colubridae (50%)	Caterpillar (86%)
Sphingidae	<i>Xylophanes</i>	<i>chiron</i>	Caterpillar (56%)	Caterpillar (99%)	Caterpillar (57%)	Caterpillar (99%)
Sphingidae	<i>Xylophanes</i>	<i>crotonis</i>	Snake (77%)	Caterpillar (93%)	Colubridae (62%)	Caterpillar (92%)
Sphingidae	<i>Xylophanes</i>	<i>cthulhu</i>	Snake (80%)	Snake (89%)	Colubridae (50%)	Viperidae (83%)
Sphingidae	<i>Xylophanes</i>	<i>cyrene</i>	Caterpillar (88%)	Caterpillar (51%)	Caterpillar (83%)	Caterpillar (54%)
Sphingidae	<i>Xylophanes</i>	<i>germen</i>	Caterpillar (85%)	Snake (80%)	Caterpillar (84%)	Viperidae (81%)
Sphingidae	<i>Xylophanes</i>	<i>hannemanni</i>	Caterpillar (67%)	Snake (54%)	Caterpillar (64%)	Caterpillar (41%)
Sphingidae	<i>Xylophanes</i>	<i>libya</i>	Snake (60%)	Snake (99%)	Colubridae (51%)	Viperidae (99%)
Sphingidae	<i>Xylophanes</i>	<i>loelia</i>	Snake (58%)	Snake (93%)	Colubridae (48%)	Viperidae (93%)
Sphingidae	<i>Xylophanes</i>	<i>pluto</i>	Caterpillar (56%)	Snake (92%)	Caterpillar (58%)	Viperidae (84%)
Sphingidae	<i>Xylophanes</i>	<i>porcus</i>	Snake (59%)	Caterpillar (64%)	Colubridae (56%)	Caterpillar (63%)
Sphingidae	<i>Xylophanes</i>	<i>titana</i>	Caterpillar (56%)	Caterpillar (95%)	Caterpillar (58%)	Caterpillar (95%)

Values in brackets indicate the posterior probability for the assigned classification, expressed as a percentage. LDAs were developed to discriminate between snakes and resting caterpillars (LDA1) or among Colubridae snakes, Viperidae snakes, and resting caterpillars (LDA2) then used to classify the same caterpillars when adopting their defensive posture.