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Geographic Variation in Philippine Mimicry System: Hypothesized Widespread Coral Snake (*Hemibungarus calligaster*) Mimicry by Lepidopteran Larvae (*Bracca* sp.) on Luzon Island, Philippines

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Aposematic Batesian mimicry of elapine coral snakes has been widely documented, with the most well-known and highly referenced phenomena occurring between the highly venomous coral snakes of the New World (*Leptomicrurus*, *Micruroides*, and *Micrurus*) and a number of relatively harmless colubrine snakes (e.g., *Lampropeltis triangulum* ssp.; Brodie 1993; Greene and McDiarmid 1981; Greene and McDiarmid 2005). Less common are similar cases of mimicry of the Old World coral snakes (*Hemibungarus*, *Calliophis*). A number of experimental studies have documented apparent increased fitness of relatively harmless species that, even to varying degrees, mimic the aposematic coloration of the highly venomous model species (Brodie 1993; Brodie and Janzen 1995). In such studies, correlations between the model species' abundance and the quality of mimicry indicate an underlying geographic variation in a given mimic's level of similarity to the model species (Harper and Pfennig 2007). Although this system of mimicry has been documented and studied with colubrine mimics, general Aposematic Batesian mimicry systems involving arthropods are much more common (Greene and McDiarmid 1981; Brodie and Moore 1995).

Brown (2006) reported a potential case of mimicry involving the larvae of a species of lepidopteran in the genus *Bracca* and the Philippine coral snake *Hemibungarus calligaster calligaster*. The larva possessed banding and color patterns highly similar to the coral snake where they are sympatric on two distinct mountain ranges of the Bicol Peninsula of southeast Luzon Island, Philippines (Fig. 1). Upon closer inspection of the *Hemibungarus* from the collection of Brown (2006), it is clear that the Bicol Peninsula subspecies is morphologically most similar to *H. c. mcclungi*, formerly believed to be endemic to Polillo Island (Leviton 1963). Brown (2006) questioned whether this example of mimicry was widespread across the Philippines, and whether morphological differences in banding patterns among subspecies of Philippine *H. calligaster* were mirrored in changes in banding pattern of sympatric lepidopteran larvae. In this note, we question the hypothesis of a widespread case of mimicry, report on additional observations of the sympatric association of *Bracca* and *Hemibungarus*, and compare banding and color patterns between two subspecies of *Hemibungarus* and the sympatric lepidopteran from Luzon Island, Philippines.

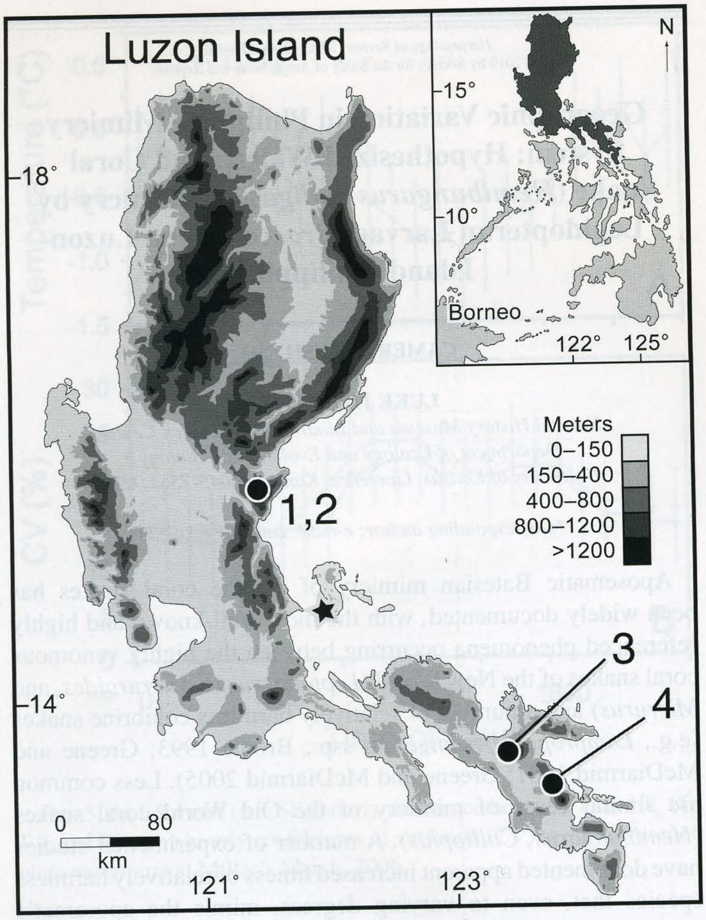

FIG. 1. Localities of observed occurrences of *Hemibungarus calligaster* cf. *mcclungi*, *H. c. calligaster*, *H. c. mcclungi*, and the lepidopteran larvae (genus *Bracca*) on Luzon Island, Philippines. Localities 1 and 2 represent sampling localities from this study, 3 and 4 represent sampling localities from Brown (2006), and the type locality of *H. c. mcclungi* marked with a star. The inset shows the location of Luzon Island (colored black) within the Philippines.

Methods.—In June 2009 we conducted herpetological field surveys at two sites in Aurora Province, Luzon Island: Site 1, mid-elevation forest of Barangay Lipimiental, Municipality of San Luis (15.65366°N, 121.50734°E; WGS 84; Fig. 1); Site 2, mid-elevation forest of Mt. Dayap, Aurora Memorial National Park, local area "Siete," Barangay Villa Aurora, Municipality of Maria Aurora (15.680°N, 121.336°E; WGS 84; Fig. 1). Specimens were deposited in the Philippine National Museum and the University of Kansas Natural History Museum. We measured relative lengths of the color bands of *Bracca* larvae and *Hemibungarus* coral snakes from alcohol-preserved specimens using digital calipers to the nearest 0.1 mm and follow Brown (2006). Bands were measured from their anterior to posterior edges, with all measurements scored by LJW. The coral snake was keyed to species with reference to Leviton (1963), and genus-level identification of the lepidopteran larvae was provided by Brown (2006) and Holloway (1991, 1993).

Results and Discussion.—At Site 1, one individual of the coral snake, *H. c. calligaster* (KU 323337), and two *Bracca* sp. larvae were observed (one collected, deposited in the KU teaching collection). Both *Bracca* sp. larvae were observed suspended 0.5 meter above the ground from a thread of silk. The coral snake

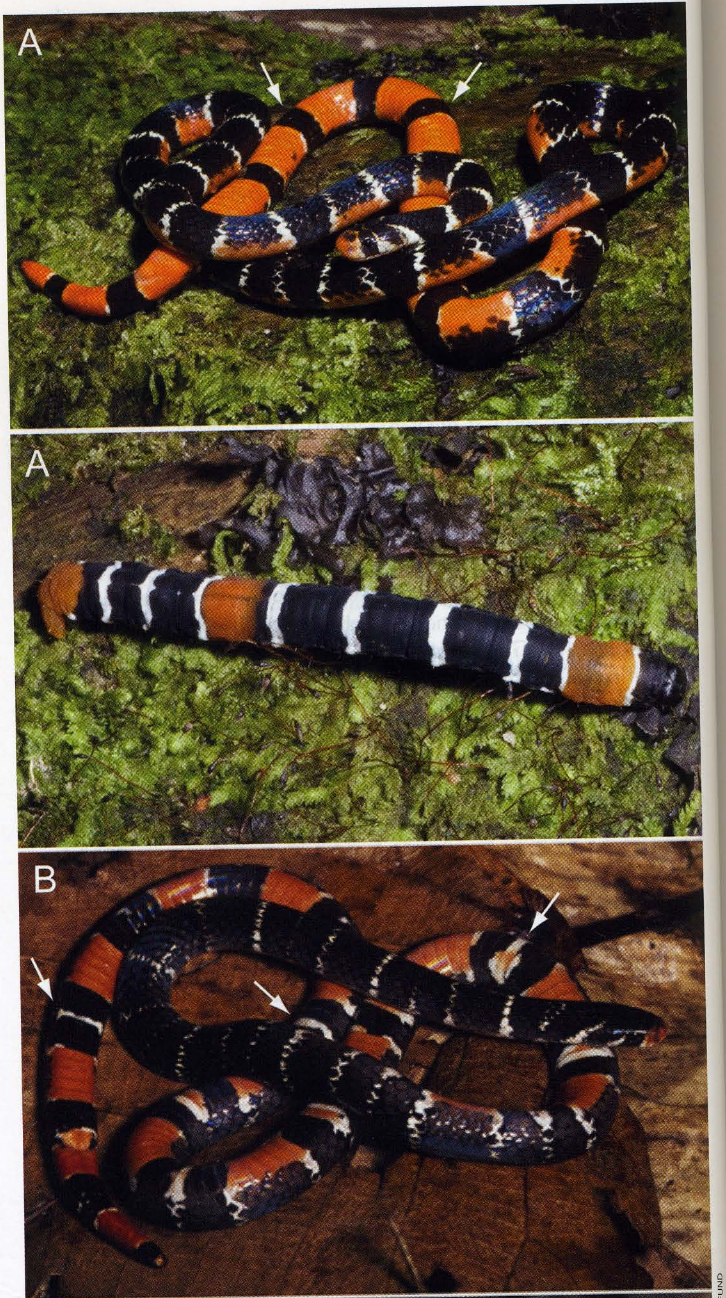

FIG. 2. (A) *Hemibungarus calligaster calligaster* (KU 323337) in life and unidentified species of *Bracca* moth larvae (RMB 10649, deposited in the KU teaching collection) in life. (B) *Hemibungarus calligaster* cf. *mcclungi* (TNHC 62483; Brown 2006) in life and unidentified species of *Bracca* moth larvae (not collected; Brown, 2006) in life. Arrows highlighting ventral banding differences between specimens collected by Brown (2006) and those from this study. Photographs by CDS and R. M. Brown.

COLOR REPRODUCTION SUPPORTED BY THE THOMAS BEAUVAIS FUND

Table 1. Summary of body and banding pattern measurements in *Hemibungarus calligaster calligaster* and *H. c.* cf. *mcclungi*, and the associated *Bracca* sp. from this study and Brown (2006). Sample size for each species and study are included for reference, and all measurements given as the range followed by mean ± standard deviation.

	Hemibungarus c. cf. *mcclungi* (N = 4; Brown 2006)	*Hemibungarus c. calligaster* (N = 2; this study)	*Bracca* sp. (N = 5; Brown 2006)	*Bracca* sp. (N = 1; this study)
Total body length	479–510 (498.5 ± 14.5)	525, 554	71–92 (78.8 ± 8.1)	56.2
Body width at midbody	9.0–17.0 (14.0 ± 0.2)	9.0, 9.1	7.0–11.0 (9.0 ± 0.2)	6
White annuli width	9.0–13.0 (11.0 ± 0.2)	2.8, 2.9	7.0–11.0 (9.0 ± 0.2)	1.5
Black band width	13.1–18.2 (15.8 ± 0.9)	6.6, 6.9	6.0–10.3 (7.5 ± 0.2)	5.9
Red band width	13.8–17.0 (15.8 ± 1.7)	10.7, 10.8	7.4–11.5 (9.2 ± 1.3)	5.1

was found under rocks near a stream. A second coral snake (KU 323337) was collected at Site 2 under rocks near a stream. No *Bracca* sp. larvae were observed at Site 2. When disturbed, both snake and caterpillar exhibited jerky movements, including body twisting and flipping, similar to the observations of Brown (2006).

Both subspecies of coral snake and the lepidopteran larvae possess brightly colored banding patterns (Fig. 2), as observed by Brown (2006). However, the order of colored bands and location of white annuli in the *Bracca* specimens most closely matches those of *H. c.* cf. *mcclungi* in the Bicol Peninsula of Luzon Island (Fig. 2B). In *H. c.* cf. *mcclungi*, the white annuli are clearly defined and divide the black bands into a pattern of black band-white annuli-black band. This pattern is bordered by red bands, and closely resembles the color and banding pattern of the lepidopteran larvae in the Bicol Peninsula as well as those observed in this study. In contrast, white annuli are absent or broken and indistinct ventrally with no division of black bands across the ventral surface in *H. c. calligaster* specimens from mainland Luzon (Fig. 2A). This results in the pattern of red and black bands separated by narrow or indistinct white annuli, dissimilar to the *Bracca* larvae and the Bicol Peninsula coral snake.

Other color patterns differences are also observed in *H. c. calligaster*, *H. c.* cf. *mcclungi*, and the *Bracca* sp. The lepidopteran larvae possess a greater number of black bands between red bands than either coral snake subspecies. Additionally, the red bands of the caterpillar encircle the entire body, whereas they are restricted to the ventral surface of the coral snakes. However, observed defensive movements of both snakes and caterpillars resulted in the flashing of the brightly colored red bands (Brown 2006; this study).

These observations suggest that a mismatch in color and pattern exists between the model (snake) and potential mimic (lepidopteran larvae) across their range of sympatry in the northern Philippines. While the lepidopteran larvae shares a general resemblance to both subspecies of *H. calligaster* on Luzon Island, its banding pattern is more similar to *H. c. mcclungi* than it is to *H. c. calligaster*. This may indicate that the model/mimic system evolved between a single subspecies of Philippine coral snake (*H. c. mcclungi*) and that the lepidopteran does not vary geographically in correspondence with separate subspecies of coral snake as was proposed as a possibility in Brown (2006). Despite the observed differences, the caterpillar's aposematic coloration may be similar enough to coral snakes on Luzon Island to reduce avian predation pressures. An innate prey avoidance behavior in the Bicol Peninsula may extend well past the range of close correspondence between the model and the mimic banding patterns.

Although experimental studies of coral snake mimicry have been successfully conducted (e.g., Brodie 1993; Brodie and Janzen 1995; Brodie and Moore 1995), no experimental confirmation of a model/mimic system has been made for these two species. The sympatric occurrence and striking morphological similarity between snakes and caterpillars seems to be restricted to the Bicol Peninsula of Luzon Island (Fig. 1). If the color pattern is in fact reducing avian predation on the caterpillar, it would be interesting to experimentally determine how quickly the learned avoidance behavior dissipates as geographic distance increases from regions of sympatry. Assuming the close resemblance of caterpillar to *H. c. mcclungi* is a case of mimicry, toxicity analysis should be conducted to determine whether *Bracca* sp. larvae are toxic, or if the caterpillar is a palatable mimic. It remains unknown whether a species of *Bracca* sharing similar color patterns co-occurs with the other Philippine coral snake subspecies, *H. c. gemiannulis* from Cebu, Negros, and Panay Island (Brown 2006; Leviton 1963).

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Australian Freshwater Crocodile (*Crocodylus johnstoni*) Attacks on Humans

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Both *Crocodylus johnstoni* (Australian Freshwater Crocodile) and *C. porosus* (Australian Saltwater or Estuarine Crocodile) occur in northern Australia. *Crocodylus porosus* is accepted as being dangerous, known to attack humans and responsible for at least 25 fatalities in Australia between 1971 and 2009 (Caldicott et al. 2005; C. Manolis, pers. comm.). *Crocodylus johnstoni*, on the other hand, is widely considered harmless to humans (e.g., Crocodile Specialist Group 2008; Webb and Manolis 2007). There are no recorded human fatalities from *C. johnstoni* (C. Manolis, pers. comm.) and locals frequently swim with this species, believing that it does not bite people (pers. obs.). Although it is acknowledged that *C. johnstoni* is capable of inflicting injury, both local people and experts are reluctant to believe they attack humans (Anonymous 2006; Caldicott et al. 2005; Crocodile Specialist Group 2008).

In September 2008, two *Crocodylus johnstoni* attacked one of the authors (KNH) in the Throssell River of the Kimberley Region of Western Australia in the presence of the second author (AS). This experience provides evidence contrary to the prevailing opinion that this species is harmless to humans. We have found additional accounts of *C. johnstoni* attacks on humans in northern Australia, but the difficulty we had in acquiring this information suggests that the widespread belief that *C. johnstoni* is harmless may in part be perpetuated by a lack of reporting, reluctance to lend credence to such accounts, and consequently a lack of media attention. These factors impede a full understanding of this species' behavior and jeopardize public safety. We discuss these issues further using our case study and compiled accounts of additional *C. johnstoni* attacks on humans in northern Australia.

Methods.—We compiled accounts of *C. johnstoni* attacks that were reported in northern Australia. Accounts were gathered between September 2008 and June 2010 from personal narratives brought to our attention, scientific literature, the internet (primarily online newspapers), and the Crocodile Attack Database (CAD) that was begun in 1971 and is maintained by Wildlife Management International in Darwin, Northern Territory of Australia (C. Manolis, pers. comm.). We included accounts where the attacking species was clearly identified as *C. johnstoni* and where there was no obvious human harassment of the animal prior to attack.

Results.—In addition to our encounter involving two *C. johnstoni*, we recorded ten other accounts of *C. johnstoni* attacks on humans in northern Australia between 1971 and 2009 (Table 1). This total is likely an underestimate given that three of the attack accounts were collected through chance personal communications (two relayed to the authors and one acquired by C. Manolis second hand [C. Manolis, pers. comm.]) and another two through personal experience, meaning that nearly half of the accounts were collected opportunistically rather than being available in the scientific literature or from news sources.

There was an average of 0.3 *C. johnstoni* attacks on humans reported annually in northern Australia between 1971 and 2009 (Table 1). The first reported attack was in 1988 and the annual number of reported attacks increased to 0.9 between 2000 and 2009. In all cases, the victims were engaged in water activities–swimming, treading water, or floating in an inner tube or on an inflatable mat—at the time of attack. Where gender of the victims was known, numbers were evenly divided between males and females. Crocodile size was estimated in five of the accounts and attacking crocodiles were reported as 1–2 m total length, with 2 m crocodiles being reported as responsible for three of those attacks. Attacks ranged from a quick bite and release to varying degrees of biting persistence until the victim escaped or resisted further bites. Most injuries were restricted to puncture wounds or cuts made directly by the teeth.

Case Study

The authors' *C. johnstoni* attacks occurred on 17 September 2008, along a remote section of the Throssell River in the Kimberley Region of Western Australia (17.43°S, 126.05°E). September is the dry season and the river was divided into a series of water holes. There was a high density of *C. johnstoni* along the river, but the water hole where the attack occurred had no visible individuals on the bank or at the surface of the water. The water hole was ca. 100 m x 20 m and contained deep, murky water. The bank was steep on both sides with boulders on one end of the river bed and a shallow bank adjoining the river bed on the other end. There was dense vegetation and a steep bank along the side of the hole where the authors entered the water.

Around noon KNH entered the water with a splash and was