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More than mimicry? Evaluating scope for flicker-fusion as a defensive strategy in coral snake mimics

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Abstract Coral snakes and their mimics often have brightly colored banded patterns, generally associated with warning coloration or mimicry. However, such color patterns have also been hypothesized to aid snakes in escaping predators through a "flicker-fusion" effect. According to this hypothesis, banded color patterns confuse potential predators when a snake transitions from resting to moving because its bands blur together to form a different color. To produce this motion blur, a moving snake's bands must transition faster than the critical flicker-fusion rate at which a predator's photoreceptors can refresh. It is unknown if coral snakes or their mimics meet this requirement. We tested this hypothesis by measuring the movement speed and color patterns of two coral snake mimics, *Lampropeltis triangulum campbelli* and *L. elapsoides*, and comparing the frequency of color transitions to the photoreceptor activity of the avian eye. We found that snakes often produced a motion blur, but moving snakes created a blurring effect more often in darker conditions, such as sunrise, sunset, and nighttime when these snakes are often active. Thus, at least two species of coral snake mimics are capable of achieving flicker-fusion, indicating that their color patterns may confer an additional defense aside from mimicry [*Current Zoology* 60 (1): 123–130, 2014].

Keywords Coral snake mimicry, Flicker-fusion effect, CFF, Kingsnake, Defensive strategy

Color patterns of snakes are varied and often stunning. They typically function in helping snakes to avoid predators, either through crypsis (King, 1987), aposematism (Brodie, 1993; Madsen, 1987; Wüster et al., 2004), or mimicry (Brodie and Brodie, 2004; Greene and McDiarmid, 2005; Wallace, 1867). Many color patterns associated with aposematism and mimicry consist of bright bands or rings that alternate along the body. Numerous experiments have demonstrated the aposematic or mimetic function of these color patterns (reviewed in Brodie and Brodie, 2004). It has been hypothesized, however, that bright bands or rings of alternating colors may also serve an additional defensive function by blurring together when snakes move (Pough, 1976). This blurring phenomenon occurs when a banded object moves quickly enough that its colors alternate faster than the eye's photoreceptor cells can fire, also known as the critical flicker-fusion (CFF) rate. For this reason, we refer to this hypothesis as the "flicker- fusion hypothesis" (reviewed in Ruxton et al., 2004; Stevens, 2007).

The flicker-fusion hypothesis was initially based on human observation of northern water snakes (Pough, 1976). Pough (1976) proposed that stationary snakes that suddenly sprinted would instantly appear to have a single color, and then assume their original banded pattern once they stopped. This change in appearance would confuse predators, perhaps by causing them to lose track of their targets. The critical predictions of the flicker-fusion hypothesis are therefore that: (1) banded snakes sprint at speeds that make their color patterns alternate faster than the CFF frequency of their predators, and (2) banded snakes that display such sprinting behavior evade predators more frequently than unbanded ones. However, only a few studies have invoked the flicker-fusion hypothesis to explain color patterns in snakes, and they have only presented indirect evidence for it based on differential survival of snakes with different color patterns (e.g., see Lindell and Forsman, 1996; Shine and Madsen, 1994). Moving banded patterns in a computer simulation experiment had higher survival rates and more missed attack attempts than other color patterns, including camouflage (Stevens et al., 2011). Explicit tests of the flicker-fusion hypothesis' critical predictions have not been performed.

In the present study, we sought to test the first prediction of the flicker-fusion hypothesis: namely, that banded snakes sprint at speeds that make their color patterns alternate faster than the CFF frequency of their predators. To conduct such a test, several elements must

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be considered, including environmental conditions, predator visual abilities, and physical and behavioral characteristics of the prey (in Table 1 we list parameters that could influence a snake's ability to produce a flicker-fusion effect).

We specifically quantified the temporal acuity of avian vision (birds are common predators of snakes), daylight luminance, snake band width and contrast, escape velocity, and escape movement on flicker-fusion achievement; thus addressing many, but not all, of the factors contributing to the illusion. We found that during daylight conditions, high predator temporal acuity could be overcome at maximum sprint velocities and narrow band widths. Sunset and moonlight conditions decreased the CFF of predators such that flicker-fusion could be achieved at slower sprint velocities, complementing the crepuscular behavior of mimics. Finally, the undulating sprint behavior employed by the snakes coincided with alternating patterns of flicker-fusion, particularly in brighter conditions, suggesting another, heretofore unconsidered dimension of the flicker-fusion illusion. These results suggest that flicker-fusion may indeed be a defensive strategy in banded snakes with predators having high temporal acuity, and that in the case of mimics, coloration serves a double function of mimicry while stationary and crypsis in motion.

1 Materials and Methods

1.1 Flicker-fusion and the avian eye

It is important to consider the perceptual system of the predator in any investigation of the defensive benefits of coloration (Endler, 1990). The CFF frequency of the eye determines the critical velocity snakes much achieve to produce a blurring effect. Using human observations as evidence of flicker-fusion is not sufficient, as humans have a maximum temporal acuity significantly lower than that of avian predators (60 Hz as opposed to approximately 87–100 Hz) (Jarvis et al., 2002). A thorough evaluation of the flicker-fusion hypothesis requires that we take into account the physiology of the visual system. We chose to focus on the avian visual system in this study. Birds are highly visual predators, and have been documented preying on coral snakes and their mimics (Brodie, 1993; Brugger, 1989; DuVal et al., 2006; Hinman et al., 1997; Smith, 1975; Smith, 1977) . Furthermore, due to the extensive cultivation of poultry, the avian visual system has been well studied (e.g., see Lisney et al., 2011).

Avian retinas consist of six different photoreceptors: one type of rod, four types of cone, and one type of double-cone, each of which functions at different levels under different lighting conditions (Hart and Hunt, 2007). Rods are very sensitive to light, but refresh very slowly. Cones are less sensitive to light, but refresh much more quickly. Thus, in dim lighting conditions, vision is primarily due to rod function, but in brighter lighting conditions the signal from the cones predominates (Linsey et al., 2011). As a result of the differing refresh rates of rods and cones, as the available light increases, CFF increases because more fast-refreshing

Table 1 Summary of various factors that can impact the efficacy of flicker-fusion

Factors that affect the efficacy of flicker-fusion	
Factor	Impact
Environmental conditions	
†Brightness	Only low luminance levels (twilight and moonlight) significantly lower the flicker-fusion threshold: we found that cloudy and bright daylight conditions produce an equal resulting likelihood of flicker-fusion.
Temperature	A significant decrease in sprint speed is seen at lower temperatures (Brodie and Russell, 1999; Heckrotte, 1967); therefore, flicker-fusion may be more difficult to achieve in cooler conditions.
Predator vision	
†Temporal acuity	The temporal acuity of the predator will allow it to resolve distinct bands at certain frequencies. Avian species with superior vision may have CFFs up to 100 Hz, while nocturnal birds may have CFFs as low as 35 Hz (Ault and House, 1987).
Tracking behavior	If predators track the motion of the snake such that its background becomes blurred, then flicker-fusion at the focal point is less likely. However, tracking behavior is also subject to disruption by varying sprint velocities.
Snake characteristics	
†Velocity of movement	The faster a snake moves, the higher the frequency of its bands, thus achieving flicker-fusion when viewed by predators having a wide range of temporal acuities.
†Width of bands	Wider bands reduce color transition frequency in relation to velocity, thus significantly impacting the sprint speed necessary to achieve flicker-fusion. Snakes with narrow bands are able move at significantly slower critical velocities than those with wide bands.
Discreteness of bands	The distinctiveness of adjacent bands is important in terms of their luminance difference. Colors of similar brightness will blend together more easily than those of wide-ranging luminance (Kalloniatus and Luu, 2007).

Daggers represent specific elements tested in our experiment.

cones are involved in vision (Linsey et al., 2011). The relationship between luminance and CFF is approximately logarithmic: as luminance increases, CFF increases dramatically at low light levels, reaching a maximum CFF that remains relatively constant and independent of further luminance increases. Once light levels are sufficiently high, CFF is limited by the maximum temporal acuity of the cones. Figure 1 (based on data from Table 1 in Linsey et al., 2011) illustrates this effect. Studies in various species of non-predatory birds have indicated that maximum CFF thresholds may range from 87–100 Hz in chickens, budgerigars, starlings, and pigeons (Bornshein and Tansley, 1961; Ginsburg and Nilsson, 1971; Maddocks et al., 2001; Nuboer, 1993[1]); however, no quantitative studies are available on CFF flicker-fusion in raptors or other groups of birds most commonly assumed to prey on snakes. Nevertheless, the rapid flight and hunting methods of raptors suggest that their temporal acuity is comparable to those of other diurnal birds, as CFF in wedge-tailed eagles has been predicted to fall in the range of 90–100 Hz (Olsen, 2005). By contrast, night predators such as owls have much lower CFFs (35–45 Hz) due to the higher proportion of rods in their retinas (Ault and House, 1987). We used data from Lisney et al. (2011) on CFF in chickens to represent diurnal birds as a whole, as data from poultry is available for a wide range of lighting conditions, but is not for other groups. In using this data we sought to show the comparative likelihood of a successful illusion under different light conditions. By also focusing on the visual systems of diurnal birds, we are being conservative in testing the feasibility of the flicker-fusion hypothesis, for whatever exceeds the CFF of diurnal birds will also exceed that of animals with lower temporal acuity, as is predicted for mammalian predators (Coile et al., 1989; Loop and Berkley, 1975).

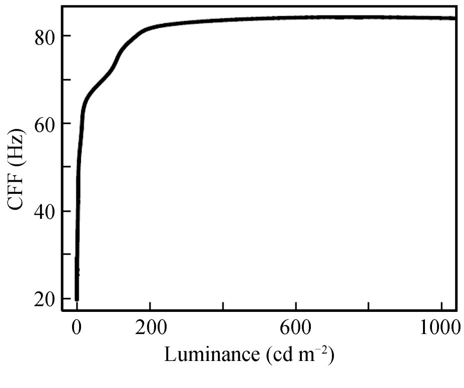

Fig. 1 The logarithmic relationship between the luminance of snakes in different daylight conditions and avian CFF holds until maximum CFF is reached

This suggests that only low luminance values may significantly change CFF. Most daytime spectra yield CFF values at or near the maximum.

1.2 Experimental methods

We measured the widths of the colored rings on two scarlet kingsnakes *Lampropeltis elapsoides* and six juvenile Pueblan milksnakes *L.triangulum campbelli*. We then measured the snakes' sprinting speeds in a laboratory arena that we constructed expressly for this purpose. The arena was a 0.6 m × 1.8 m × 0.5 m enclosure filled with sand approximately 2 cm in depth to provide traction and to emulate the natural habitat of the test subjects. For each trial the snake was gently placed into the arena without excessive handling, covered by a small bucket, and allowed to acclimatize for three minutes. Upon removal of the bucket, we touched the snake with a paintbrush to motivate sprinting (Llewelyn et al., 2010). We recorded all trials at 30 frames per second using a high-definition digital camera (Panasonic G2) that was positioned directly above the center of the enclosure with the lens parallel to the ground. Aegisub 3.0.2 video software was used to calculate sprint velocities by plotting the coordinates of the tip of each snake's head for every frame during a sprint. Because snakes rapidly transitioned from stationary to sprinting states, trials were measured from the last stationary frame before movement began to the first stationary frame following the sprint. Sprints consisted of at least 0.6 seconds of rapid movement. All snakes were tested 2 days after feeding, and only one trial was conducted per day to maximize sprint speed and to avoid conditioning to the testing conditions. Snakes were housed and tested in a climate-controlled animal care room with temperatures that ranged from 22–25 degrees C. The natural habitat temperature of *L.t. campbelli* is of a similar range, with mean daily temperatures of 20–25 degrees C year-round. During summer months when snakes are most active, daily temperatures rarely drop below 16 degrees C (retrieved from the National Meteorological Service of Mexico database entry for Cuernavaca). Animal care was conducted under UNC-IACUC protocol 11-108.

Using the morphometric measurements of our snakes, we calculated the mean width of the colored bands on each snake, i.e. the anterior-posterior distance occupied by each color band along the snake's dorsal axis. This

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[1] Nuboer JFW, 1993. Visual ecology in poultry houses. Proceedings of the Fourth Symposium of Poultry Welfare: 39–44.

corrects for the effects of size, speed, and distance between snake and observer on flicker rate. We then divided the velocity of the snake (as measured from our video footage) by its mean band width to obtain the frequency of color transitions in Hz. We then sought to compare the frequency of color transitions achieved by each snake to the critical flicker-fusion rate for the avian eye. However, because critical flicker-fusion frequency depends on the amount of light available to the eye, we calculated different flicker-fusion rates for each snake under different lighting conditions.

To accomplish this, we measured the reflectance of each snake's colored bands from 200–800 nm using a JAZ-PX spectrophotometer with pulsed xenon light source (Ocean Optics, Dunedin, FL). A reflectance probe held perpendicular at a constant distance of 2 mm (calibrated on a Spectralon diffuse white standard; Labsphere, Inc., North Sutton, NH, USA) was used to take the measurements. The recorded spectra were the average of four 50 millisecond scans. We recorded two spectra of each color per snake and calculated the mean of these to find an average reflectance spectrum of each color for each snake. We then calculated the luminance of each colored band type for each snake under different natural light spectra (Kohonen et al., 2006). We chose to work with "sunset" and "half-cloudy" spectra, as there was such similarity between the shape and intensity of the various spectra in the database of Kohonen et al. (2006) recorded during daytime, that they produced very similar results in our final calculations of avian CFF (even though there can be large variations in the brightness of daylight, most such spectra are bright enough to elicit maximal avian CFF). We used the mean of spectra labeled "sunset" or "half-cloudy," as there were multiple spectra for each condition.

Once we calculated the luminance of each snake's colored bands, we found their mean within each snake to obtain an average luminance value for the snake. We chose to do this because it indicates the general amount of light entering the eye as a bird looks at a snake. The luminance values that we obtained were then related to CFF at different light levels in domestic chickens (Lisney et al., 2011). To determine the light level from Lisney et al. (2011) that corresponded to a particular luminance, we used the equation: light level = 1.6879 ln(luminance) + 3.424. To translate the light levels from Lisney et al. (2011) to obtain CFF values, we used equations that the authors provide therein. We were then able to compare the velocities of difference snakes to avian CFF under different lighting conditions.

1.3 Analyses

We sought to establish whether the flicker-fusion hypothesis was more likely to apply during some lighting conditions than others. To test this, we constructed two Bayesian models using JAGS 3.4 (Plummer, 2003[2]) and called it from R 3.02 (R Development Core Team, 2010) using the package R2jags (Su and Yajima, 2012). The first model was a null model of proportion time spent moving above avian CFF with snake identity as a random effect. The second model also included lighting condition as an independent predictor. Our response variable was a continuous proportion bounded by zero and one, and we modeled it using a beta distribution with a logit link function. We addressed boundary values (those of zero and one) using minimal additions and subtractions so that they would fall within the distribution's range. For both models, we used normally distributed priors with very low precision parameters to reflect minimal prior assumptions. We ran three chains for 10,000 iterations each, discarding the first 5,000.

2 Results

We found that all of the snakes measured were capable of creating a flicker-fusion effect, although individuals varied in their tendency to do so, with some only achieving flicker-fusion for a small portion of the duration of their sprint, and doing this inconsistently. Other snakes consistently exceeded avian CFF. Although there were too few *L. elapsoides* in our sample to meaningfully discriminate their behavior statistically, their sprinting behavior appeared to fall in a similar range of variation as *L. t. campbelli* (Fig. 2). Snakes achieved mean velocities of 47 ± 8 cm/s during their sprints. This indicates that their mean color transition frequencies were 108 ± 26 Hz. This is well above our calculated maximum poultry CFF of 84 Hz, as determined using data from Lisney and others (2011), and slightly above the predicted CFF of 90–100 Hz in raptors (Olson 2005). Although not all trials resulted in mean color transition frequencies in excess of 84 Hz, all snakes exceeded that threshold at least once. Furthermore, sprints varied considerably in direction and speed, which may serve to confuse predators even more. Snakes often crossed the CFF threshold several times during trials, which could cause them to change appearance mid-sprint (Fig. 3).

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[2] Plummer M, 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, 20-22.

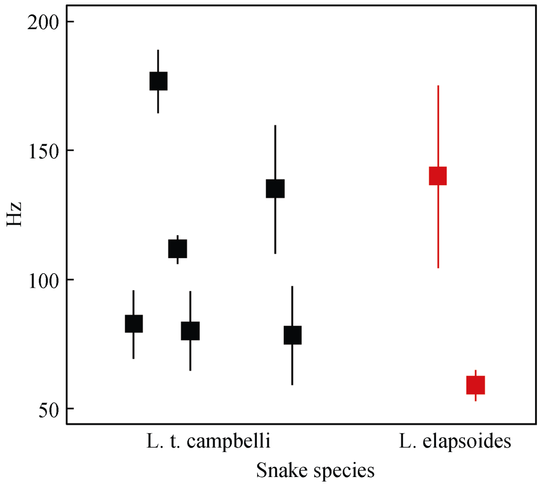

Fig. 2 Frequencies of color band transitions for *L. t. campbelli* and *L. elapsoides*

Each individual ran three trials; we display transition frequency for each individual and 95% confidence intervals. *Lampropeltis elapsoides* individuals fall within the range of variation exhibited by *L. t. campbelli*.

We wanted to determine the effect of lighting conditions and snake brightness on CFF rates because CFF depends on the relative stimulation of rods and cones, and thus in turn the amount of light entering the eye. We found that snakes spent a greater proportion of their time above the avian CFF during dark conditions than light ones. Indeed, our second beta regression model estimated that snakes were above CCF 78.5% (95% credible interval 56.6%–96.6%) of time sprinting in light representative of sunset, but only 57.5% (95% credible interval 27.8%–86.5%) of the time sprinting under half-cloudy daylight conditions. This model outperformed the null model by a large margin ($\mathrm{DIC}_{\text{null model}} = -70.8$, $\mathrm{DIC}_{\text{second model}} = -87.3$; lower is better).

3 Discussion

Our finding that the frequency of colored bands induced by sprint behavior can exceed the temporal acuity of avian predators in a range of conditions indicates that flicker-fusion is a plausible defense mechanism for coral snake mimics. The two mimetic species in our study are both crepuscular in behavior; therefore, the impact of sunset conditions on critical velocities is of particular interest. We found that critical velocities were significantly lower in light conditions such as sunset that are characterized by low luminance levels, indicating that crepuscular activity enhances the likelihood of flicker-fusion. Although the effect of low light levels on raptor CFF is not known, it almost certainly changes in a similar manner to that shown in the chicken. Sprinting by mimics in daylight conditions may cause predators to perceive alternating impressions of blurred and discrete bands, while movement at the same velocity at sunset induces flicker-fusion along the length of the snake. While the alteration of fused and discrete bands produced during daytime may be beneficial in its unpredictability, complete flicker-fusion such as that produced at sunset could also be desirable. Bright aposematic coloration of mimics is only fully perceptible under phototopic conditions when a predator's retinal cones are stimulated, since birds perceive color with their cones (Hart and Hunt, 2007). Therefore, precisely mimicking aposematic hues may be less necessary during twilight hours (when mimics are active). In darker conditions, flicker-fusion of distinctive bright and dark bands may afford a more valuable secondary defense.

Other predators of coral snake mimics include mammals, whose visual systems differ from avian sight with

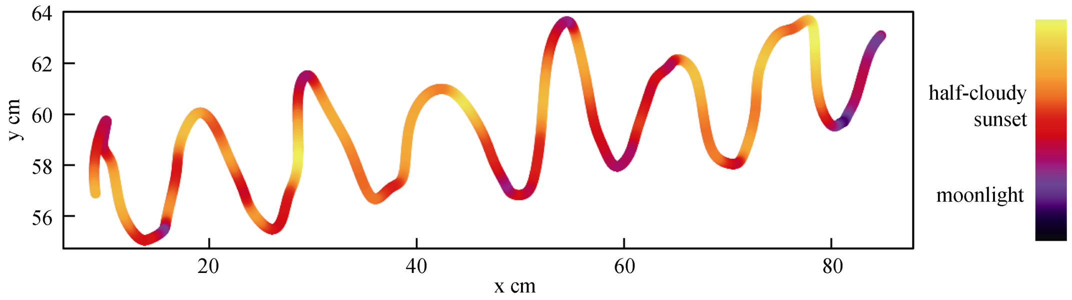

Fig. 3 Variability in the flicker rate of an individual *L. t. campbelli* as it sprints

The x- and y-axes indicate spatial movement of the snake's head over time, while the color of its movement path indicates the mean frequency of its transitions between band colors in Hz. The labels "half-cloudy," "sunset," and "moonlight" indicate the colors which correspond to critical avian flicker-fusion rates under those light conditions (we estimate moonlight as 1 lux for illustrative purposes; CFF rates are 84 Hz, 68 Hz, and 25 Hz, respectively). Hence, all areas of the snake's movement path that have colors which fall above "moonlight" on the color ramp indicate that during those sprint stretches, the snake's bands may be perceived as flicker-fusion by an avian observer on a moonlit night. However, lighting conditions will vary on a small spatial scale and can change quickly over time, so this figure should be viewed as an approximation.

respect to both color and temporal acuity (Jacobs, 2009). Flicker-fusion is likely to be more effective as a defensive strategy against mammalian predators, whose CFF values generally fall below those of birds. Although no studies of flicker-fusion have been conducted in the specific species known to prey on kingsnakes (such as raccoons, coyotes, skunks, and foxes), dogs and cats have CFFs of 80 Hz and 55 Hz, respectively (Coile et al., 1989; Loop and Berkley, 1975). Considering their lower CFFs and typically nocturnal behavior, a flicker-fusion effect will be more apparent to these animals than to birds, especially in dark conditions. For an image of how such animals might perceive a moving snake, see Fig. 4.

Fig. 4 Flicker-fusion in a sprinting *vs.* stationary *L. t. campbelli*

Due to different parts of the snake moving at different speeds, this image shows less blurring towards the head of the snake (red bands are more apparent). The camera shutter speed used to capture these images was 1/50 sec.

Although our study does show that snakes can move quickly enough to induce flicker-fusion, a number of additional factors must be considered when applying the hypothesis to these snakes in their natural habitats. First, our test only measured sprint speeds in a limited sample size of juvenile milksnakes and kingsnakes that had grown to approximately 50%–75 % of their adult lengths. We suggest that further testing in a wide range of species and sizes would demonstrate the likelihood of flicker-fusion for banded snake species as a whole. Presuming an isometric relationship between band width and snake length during ontogeny, adult snake sprint velocities must also increase proportionally to conserve the flicker-fusion illusion. Although quantitative tests of the relationship between size and speed in milksnakes has not been studied, a test of the common garter snake showed that adult snakes sprinted three times faster than juveniles half their length, and that sprint speed increased at the same rate with increasing external temperatures, regardless of body length (Heckrotte, 1967). Considering the similarities in morphological measurements and velocities for garter snakes and the milksnakes, we predict that adult *L.t. campbelli* will also exhibit faster sprint speeds such that the capacity for flicker-fusion is not lost during ontogeny.

A second consideration is the effect of temperature on sprint speed. Thermoregulatory behavior in milksnakes may vary depending on species, climate, sex, and feeding status; and resultant body temperatures will influence the capacity for fast sprint speeds. Our study showed that flicker-fusion is viable when snakes are acclimatized to an environment of 22–25 degrees C; however, the precise impact of lower temperatures on sprint speeds in milksnakes is not known. The aforementioned study in garter snakes revealed that from 15–32 degrees C, sprint velocity increased roughly 1 cm/s per degree C (Heckrotte, 1967). Assuming that milksnakes exhibit a similar temperature-dependent response, low temperatures will place constraints on their ability to achieve flicker-fusion. Because *L.t. campbelli* experience average low temperatures of 15−18 degrees C, this temperature change will probably impact sprint speeds. However, because predator CFF is also much lower at night, this may not significantly hinder their ability to achieve flicker-fusion. Low daytime temperatures have a much greater effect on the feasibility of flicker-fusion in snakes, and additional thermoregulatory factors may impact movement patterns in more complex ways.

The potential for flicker-fusion defense has implications for both the evolution of Batesian mimicry and the occurrence of Batesian mimics outside the geographic range of their model (Pfennig and Mullen, 2010). The evolution of Batesian mimicry is thought to be a challenging process, in that it is generally presumed to involve the crossing of a fitness valley from a cryptic state to a mimetic one, which may be susceptible to strong stabilizing selection (Gamberale-Stille et al., 2011). Predator generalization (or relaxation of selective pressures on the mimetic form) is thought to contribute significantly to this evolution (Kikuchi and Pfennig, 2010; Ruxton et al., 2004). In the case of our findings, if flicker-fusion does provide an advantage to mimics, then selection may be relaxed on potential mimics that have evolved banded patterns.

The second interesting aspect of Batesian mimicry is the existence of allopatric mimics (Pfennig and Mullen, 2010). This phenomenon is often predicted to be selected against because there are no longer any benefits of mimicry, and individuals remain highly conspicuous (Kikuchi and Pfennig, 2012; Leimar et al., 2012). However, an aposematic coloration pattern may still be able to persist in allopatry if selection does not act against it (Pfennig and Mullen, 2010). In the case of the coral snake mimics, if a species possesses a banded pattern that is both mimetic and capable of flicker-fusion, selection against the phenotype may be relaxed, thus permitting the persistence of the mimetic form.

Although our results suggest that flicker-fusion is a plausible defensive strategy in banded coral snake mimics, its precise impact on the ability of predators to accurately deceive and capture prey is not yet known. We suggest that specific studies of the effectiveness of flicker-fusion in lowering the success of avian predator attack, while difficult to conduct, would demonstrate the selective benefit of banding and sprint behavior in snakes. Studies such as this may show that the selective benefits of flicker-fusion depend largely on the visual acuity and behavior of predators. However, based on our results, we propose that the nature of bands in mimics provides an interesting functional duality: while stationary these bands act as a precise warning signal, causing predators to mistake them for aposematic models; but in motion, bands function as a confusing illusion. If the ability to induce flicker-fusion during escape sprints is indeed selectively beneficial, it may provide further explanation for the evolution and persistence of the vibrant color patterns of coral snakes and their mimics.

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