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Rattlesnake colouration affects detection by predators

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Short Title: Colouration affects detection by predators

Abstract

Crypsis, or the ability of an animal to avoid detection by other animals, is strongly impacted by an animal's colouration and pattern. Crypsis may be especially important for ambush foragers, which spend much of their time above ground and therefore benefit from being inconspicuous to predators and prey. The purpose of this study was to investigate the effect of rattlesnake skin colouration on the likelihood of it being detected and attacked by a predator, on the latency (time) to attack, and on the attack frequency on each physical body section of the models. Clay models representing four commonly observed rattlesnake colour morphs (light, dark, and two intermediate colour patterns) were deployed in two different habitat types (wooded area and open field), and the marks made on the models by predators were quantified over time. We found that light snake models, which have little contrast with substrate, were less likely to be attacked and were attacked later than darker model types, which have higher contrast with substrate. Predators attacked the various body segments of the models at similar frequencies. Our data suggest dark-coloured rattlesnakes, which have the most contrast with the golden-coloured grasses and therefore have the lowest crypsis, are most at risk from predation.

Keywords: Colouration, *Crotalus oreganus helleri,* crypsis, pitviper, predation risk, clay models

Introduction

Colour and its perception by organisms has been of long-standing interest to biologists studying predator and prey species alike (Endler, 1978; Thayer, 1918; Carter, 1948; Brodie & Janzen, 1995; Hinman, Throop & Adams,1997; Kikuchi & Pfennig, 2010; Farallo & Forstner, 2012). An organism's bold pattern or bright colouration can cause pause and warrant investigation or avoidance by other organisms, while colouration and patterns that blend with the landscape can aid the animal in crypsis, or avoidance of detection by predators (Endler, 1978; Stevens & Merilaita, 2009; Schaefer & Stobbe, 2006; Martínez-Freiría *et al.*, 2017; Merilaita, Scott-Samuel & Cuthill, 2017; Cuthill, 2019). Cryptic colouration may be especially important for animals that rely on ambush to capture prey. Not only does their colouration allow ambush foragers to successfully avoid detection by prey (Godfrey, Lythgoe & Rumball, 1987; Greco & Kevan, 1994), but given that they often spend extended periods of time above ground and immobile while foraging, cryptic colouration may assist these animals in evading detection by predators (Isaac & Gregory, 2013).

Rattlesnakes have emerged as model organisms for the study of ambush foraging behaviours in part due to modern technologies that allow scientists to observe behaviours remotely

(Clark, 2006). Although the roles of colour in diverse topics ranging from sexual dichromatism to Batesian mimicry have been studied in several species of snakes including the common garter snake (*Thamnophis sirtalis),* coral snakes (*Micrurus* and *Micruroides*), hog-nosed snakes *(Heterodon nasicus)*, and European *Vipera* species, there are few studies investigating the role of colour in ambush-foraging rattlesnakes (Edgren, 1957; Smith, 1975; Brodie & Janzen, 1995; Capula & Luiselli, 1995; Hinman *et al.*, 1997; Bittner, 2003; Santos *et al.*, 2014; Martínez-Freiría *et al*., 2017). Farallo and Forstner (2012) found that rattlesnake models with patterns more dissimilar to the surrounding substrate were attacked at higher frequencies than models that blended in with substrate. Numerous techniques have been developed to investigate the effect of animal colouration on detection by predators (Smith, 1975; Brodie & Janzen, 1995; Hinman *et al.*, 1997; Bittner, 2003; Kikuchi & Pfennig, 2010; Farallo & Forstner, 2012; Cuthill *et al.*, 2017; Winebarger, 2017). It is difficult to quantify predation attempts on live snakes due to experimental design constraints; furthermore, the variation in behaviour of live snakes when confronted with predators could confound any effects specifically of colour on predation. As a result, researchers have developed techniques included building model snakes out of clay, rubber, foam-like substances, pvc pipe, and shaped wood (Smith, 1975; Brodie & Janzen, 1995; Hinman *et al.*, 1997; Bittner, 2003; Kikuchi & Pfennig, 2010; Farallo & Forstner, 2012; Bateman, Fleming, & Wolfe, 2016; Winebarger, 2017; Cuthill *et al.*, 2017; Rößler, Pröhl, & Lötters, 2018). By using these materials, marks created by predators' teeth, beaks, talons, and claws are left behind as imprints, allowing quantification of predator attacks. However, many of these studies were short term (3-5 days) where models were frequently replaced and new ones left behind to continue collecting data (Edgren, 1957; Smith, 1975; Brodie III & Janzen, 1995; Hinman *et al.*, 1997; Bittner, 2003; Winebarger, 2017). Having an extended trial period increases the resolution of the results by allowing for a more thorough examination of model attack latency as well as providing increased exposure to seasonally active predators, such as birds of prey. By curing clay models in an oven, the durability of the models increases, which allows researchers to leave models in the field for longer durations, where cumulative numbers of predatory attacks can be calculated.

Our study aimed to test the hypothesis that rattlesnake colouration affects detection by predators. We made rattlesnake models painted in four colours and patterns encompassing the range of phenotypes observed in rattlesnakes at our field site, and we deployed these models along transects in both wooded and open habitats to quantify predator attacks. In this study, we define detection by a predator as a predation attempt, which left marks on the clay. We placed game cameras at a subset of the models to collect qualitative data about which animals left the marks on the models. If rattlesnake colouration affects detection by predators, then the snake models exhibiting the highest contrast with the substrate (darker models) should be attacked by predators more frequently than the snake models exhibiting the lowest contrast with the substrate (lighter models). In addition, we predicted that dark models would be attacked by predators earlier (e.g., lower latency to attack), and we expected predators to attack the heads of the models most frequently to debilitate the snake's defensive bite.

Materials and Methods

Study Species and Site

The Southern Pacific rattlesnake (*Crotalus oreganus helleri*) is a common ambush forager found in habitats throughout southern California, USA and northern Baja California, Mexico. Ranging from tan to greenish-yellow to almost completely black, the colouration of this species varies dramatically, even within a single study site (Figure 1a). Therefore, the degree of crypsis of this species may also vary, and snakes with certain colouration may be more detectable by predators. We conducted this project at the Sedgwick Reserve, a 2,386 ha property in the University of California Natural Reserve System in the Santa Ynez Valley, Santa Barbara County, California, USA (34.6928°N, 120.0406°W). The reserve ranges in elevation from 290 to 793 meters and is characterised primarily by chaparral and valley oak savannah, interspersed with live oak woodland and riparian habitat (University of California Reserve System, 2018).

Snake Models

We constructed 32 snake models using red polymer clay (Sculpey III®, Polyform Products Company, Elk Grove Village, Illinois, USA) molded around paracord rope to mimic the shape and size of adult, male *C. o. helleri* (Smith, 1975; Brodie & Janzen, 1995; Bittner, 2003; Kikuchi & Pfennig, 2010). Total "body length" of snake models were about 88cm, and were molded into a sinusoidal shape such that snake models were about 58cm end to end (Figure 1b). Snake models were cured in an oven at 133°C for 11 minutes, cooled overnight, then primed with black priming paint (Rust-oleum, Vernon Hills, Illinois, USA) so no red clay was visible after the priming. We divided the 32 oven-cured snake models into four types (n = 8 snake models/type, see below) to encompass the range of colours observed at the field site. After drying overnight, primed snake models were wrapped in tulle fabric (EXPO-International, Houston, Texas, USA) and painted with their respective body base-pattern colour; this created a faint scale-like pattern. Three colours (black, brown, and white) from the Rust-oleum camouflage line were used to make up the colour schemes for the different snake model types. The snake model types (Figure 1b) included: (1) “dark:” dark body base colour with dark bands (bands slightly lighter than body base, so bands exhibited little contrast to body base colour; this was achieved using black paint for the body and black paint mixed with a small amount of white paint to make the slightly lighter bands), (2) “intermediate-tan:” intermediate base colour with tan-coloured bands (bands lighter than body base, so bands exhibit some contrast with body base; this was achieved using brown paint for the body and brown paint mixed with a small portion of white paint to make the tan bands), (3) “intermediate-white:” intermediate base colour with white bands (bands much lighter than body base, so bands exhibit extreme contrast with body base; this was achieved using brown paint for the body and white paint for the bands) and (4) “light:” light base colour with light bands (bands slightly lighter than base, so bands exhibited little contrast to body base colour; this was achieved by mixing white and brown paint for the body and white paint with less brown paint for the bands). Rust-oleum flat matte clear sealant was applied after snake models were painted to mask any paint scents. For the duration of the assembly, snake models were handled with gloves to reduce the impacts of human odors on predator interactions. To prevent predators from making off with the snake models in the field, snake models were adhered to 61 x 5 cm pieces of wood using Liquid Nails extreme heavy-duty construction grade adhesive (Liquid Nails, Strongsville, Ohio, USA). In the field, the wood was sunk into the ground, a metal eyelet was screwed into each end (one per side) of the wood, and steel nails were used to secure the whole assembly to the substrate, and the wood was covered with substrate so that only snake models were visible.

Colour Analysis

To quantify the degree of crypsis for each model type, we took photographs of snake models to compare the contrast between the snake model and the substrate (golden-coloured dead grasses). Snake models were photographed from a height of 1.8m directly above each model using a Nikon D5500 DSLR full spectrum camera with UV-IR cut and UV pass filters attached to a 35mm lens to capture data points in the light spectrum invisible to the human eye. Raptors, a common predator of *C. o. helleri*, are able to see in some portions of the UV light spectrum (Bennett & Cuthill, 1994). Photographs of the snake models were all taken post-field deployment on the same overcast day between 1200-1400 h. After images were captured in a RAW format, they were processed using the open source software RawTherapee 5.4 (Kendal *et al.*, 2013; RawPedia, 2018). Photographs loaded into RawTherapee were linearised and standardised using Kodiak colour control patches and non-reflective grey scales in the values of 0%, 18%, 95% prior to lightness value (L*) analysis (Kendal *et al.*, 2013; Brooks, 2018). The RAW data files were first assessed to determine if there was overexposure to light (Kendal *et al.*, 2013) by reading the colour histograms stored in the RAW data files and produced through the open source program; none of the photographs were overexposed, as the histograms showed even distribution of RGB (red-green-blue) and L*a*b* values (RawPedia, 2018). L*a*b* values are spectrum values where lightness (L*) ranges from 0 (dark) to 100 (light); a* represents red/green values with +a representing more red and less green; *b represents blue/yellow values with +b representing more yellow and less blue. L*a*b* values were taken from 10 randomly selected areas of each snake model and 10 randomly selected areas on the surrounding substrate (Table 1). Our main goal was to compare L* values between snake models and substrate because this reflects crypsis; we also provide data on a* and b* values for reference.

Quantifying Predator Interactions

Snake models were distributed in straight line transects across two 80m x 20m grids in the Sedgwick Reserve in mid-July 2017. One grid was an open field with short grasses and no overstory coverage, and the other was a wooded valley with mid- and overstory oak coverage. Snake models were randomly selected by colour and placed along transect lines within each grid (Brodie & Janzen, 1995; Winebarger, 2017). The number of snake models from each colour morph was equal within and between grids. Additionally, game cameras (Reconyx HyperFire Infrared Digital Game Camera HC600, Holmen, Wisconsin, USA) were positioned alongside eight randomly selected snake models (4 in wooded grid, 4 in open grid) to capture model-predator interactions for qualitative analysis of predation attempts. Over a four month period (July-October 2017), snake models were visually inspected four to five days a week, and any marks left by predators, which appeared red when the underlying red clay was exposed, were recorded in a journal and also on a large 20.32 cm x 27.94 cm print of each model taken upon deployment. New marks were recorded on these large prints to eliminate the possibility of counting the same marks twice. If multiple marks were made on a snake model between days checking them, we recorded that as a single predation attempt because multiple marks could have been made by a single predator at one time. Because snake models were oven-cured for long-term durability, even though attack marks were visible in the red clay, the majority of the marks appeared as small scratches, making it unlikely that they would impact future detection by other predators. Snake models were left in the field for the entirety of the study and only removed and replaced if broken (N=2) or removed from its board (N=1; this occurred in the final 2 weeks of the study so was not replaced). We treated subsequent attacks on the snake models as independent because those attacked multiple times were attacked continually over the course of the study by unique predators rather than all at once. The tradeoff with durability rendered classification of attacks as mammalian or avian impossible. The body of each snake model was divided into five ~18 cm segments, from rostral to caudal: H (head and neck), 1 (next segment), 2 (next segment), 3 (next segment), and T (tail); the physical locations of marks were also recorded.

Data Analysis

Statistical analysis of predation attempts was performed using JMP 13.0.0 (JMP®). L* values from RawTherapee of snake models and substrates were compared with separate ANOVAs for each snake model type using snake model ID as a random effect. We analysed the probability of snake models being attacked using a Cox proportional hazards model with snake model type (Figure 1b) and grid type (wooded or open field) as variables. For the first attack event on a snake model, the time variable was the number of days since the model was deployed. For subsequent attack events on a snake model, the time variable was the number of days since each snake model was last attacked. At the end of the experiment, the number of days since each snake model was last attacked was included as a censored variable. We then analysed the effects of snake model type and grid on latency to attack (time until first attack) using a Cox proportional hazards model as above, but with only the first attack included. In both Cox proportional hazards models, grid type was not significant and was removed from the model; this did not change the model's results. Lastly, we analysed the relationship between snake models type and the total number of marks on the body segment of the attack location using a GLM.

Results

Analyses of L*a*b* colour values (Table 1) showed that the dark snake models had the highest contrast (difference in L* values) with the substrate, followed by the intermediate-tan and the intermediate-white snake models. Light snake models did not exhibit significant contrast with the surrounding substrate, suggesting that they are cryptic. Light snake model a* values were higher than the substrate, indicating that light snake models were more red and less green than substrate; other snake model a* values were lower than substrate, although this was not significant for intermediate-white band snake models. Light snake model b* values were not different from substrate, and all other snake model b* values were lower than substrate, indicating that snake models were more blue and less yellow than the substrate.

Light snake models were attacked the least frequently, dark the most frequently, with the intermediate tan and intermediate white models in between (Figure 2). Since grid type was not a significant predictor of likelihood of attack and hazards ratio results were the same whether or not grid type was in the model, grid type was removed from the final model; however, data are shown separately for open and wooded grids in Figure 2 to facilitate visual comparison. Overall, light snake models were less likely to be attacked than dark (hazard ratio = 2.3, 95% CI = 1.0 - 5.2, p = 0.049) and intermediate white (hazard ratio = 2.3, 95% CI = 1.0 - 5.3, p = 0.043) snake models. No other hazards ratios were significant (all p > 0.15). Latency to the first attack event differed by snake model type but not grid, with light snake models attacked later than dark (hazard ratio = 10.3, 95% CI = 2.5-42.5, p = 0.001), intermediate white (hazard ratio = 7.6, 95% CI = 1.9 - 30.7, p = 0.004), and intermediate tan (hazard ratio = 5.2, 95% CI = 1.3-20.1, p = 0.02) snake models. No other hazards ratios were significant (all p > 0.18).

The cameras showed many predation attempts on the snake models. Although the camera data could not be used quantitatively to assess predation attempts because cameras were only placed on a subset of snake models, we captured images of multiple bobcats, foxes, coyotes, and feral pigs stalking and/or biting the snake models. In addition, we occasionally observed non-predators including deer, quail and ground squirrels investigating the snake models, although physical contact with the snake models was rare. There was no significant difference in the number of marks across the five body segments of the snake models ($\chi^2 = 3.55$, DF = 4, p = 0.47; Figure 3).

Discussion

The snake models used in this study were life-like representations of the study animal, *C. o. helleri*, eliciting predatory responses from various known predator species throughout the course of the study. Our data support the hypothesis that rattlesnake colouration affects detection by predators, with light-coloured snake models attacked less often and later than intermediate and dark snake models. Dark snake models were attacked the earliest and most frequently in both the wooded and open grid, suggesting that dark-coloured snakes are at higher risk of being preyed upon than light-coloured snakes. Our results agree with those of Farallo & Forstner (2012), who found that models of banded rock rattlesnakes were attacked more often when they exhibited high contrast with the colour of the forest floor. Indeed, in our study, light snake models had little contrast with the substrate (no difference in L* between model and substrate), and the other, darker snake models had high contrast with the substrate (L* much lower for models than substrate). It is also worth noting that snake models differed in their a* and b* colour values and that these colours could contribute to snake detection by predators (Table 1): light a* values were higher than the substrate while other models' a* values were lower than substrate, and light b* values were not different from substrate while other models' b* values were lower than substrate. However, interpretation of a* and b* values is based on trichromatic vision exhibited by humans, and the colours of the snake models would appear different to most mammalian predators, which have dichromatic vision (Jacobs, 2009). L* values, on the other hand, should be relevant to all vertebrate visual systems and therefore reflect the greater crypsis of light models in this study.

The two intermediate model types, with dark background colouration and white or tan bands, showed intermediate contrast with the substrate in terms of L* and also exhibited overall predation risk and latency to attack that were intermediate between those of dark and light models. However, there were no significant differences in risk of attack or latency to attack among dark and intermediate models. We had expected the patterning to reduce predation risk because such pattering can enhance crypsis, at least in wooded habitats where such patterns help in blending in with vegetation shadows (Niskanen & Mappes, 2005; Schafer & Stobbe, 2006; Westphal *et al.*, 2011; Santos *et al.*, 2014). However, it is also possible that bold patterns like bands act as aposematic signals, as disruptive colouration (e.g., breaks up outline of animal to assist in crypsis), or they may confuse predators when fleeing from predation attempts (Godfrey *et al.*, 1987, Madsen, 1987; Brodie, 1989; Bowen, 2003; Wüster *et al.*, 2004; Creer, 2005; Valkonen *et al.*, 2011; Santos *et al.*, 2014; Martínez-Freiría *et al.*, 2017; Brooks, 2018). These patterns may be context dependent;

for example, turtle-headed sea snakes exhibit industrial melanism with reduced banding pattern in heavily polluted waters, where the melanin may serve to bind and assist with the excretion of toxic trace elements (Goiran, Bustamante & Shine, 2017). Stepanek *et al.* (2019) showed that the contrast between dark and light bands in rattlesnakes increases when snakes are subjected to capture stress, and that the degree of contrast is related to circulating levels of corticosterone, raising the possibility that colour change in rattlesnakes occurs in response to stress. Dark-coloured snakes whose contrast increases when they become stressed may enjoy temporarily reduced predation risk due to heightened crypsis or aposematism, but our data suggest that this would be minimal. Overall, the major difference in predation risk was between the light snake models, that blended in with the substrate and were rarely attacked, and the dark snake models, that stood out against the substrate and were attacked most often.

Images from game cameras confirmed that predators found the snake models realistic, as numerous mammalian predators including bobcats, foxes, coyotes, and feral pigs were observed actively stalking and biting the models during both daytime and nighttime. Interestingly, we failed to observe raptors such as hawks and owls attacking the models, even though raptors regularly prey upon rattlesnakes (Klauber, 1956; Steenhof & Kochert, 1985; Vanderpool, Malcolm & Hill, 2005), and some of the marks could have been beak and talon marks. We also observed numerous deer and several ground squirrels investigating the snake models, although none appeared to make contact with them. Ground squirrels are a major prey item for rattlesnakes in California (Owings & Coss, 1977; Sparks, Lind & Taylor, 2015), and adult ground squirrels often interact with rattlesnakes, exhibiting vigilance behaviour and sometimes even clawing or biting rattlesnakes (Owings & Coss, 1977; Hennessy & Owings, 1978; Swaisgood *et al.*, 1999). However, most marks were obviously made by teeth and claws much larger than those belonging to a ground squirrel, making it likely that the vast majority of quantified marks were made by predators.

Predators did not appear to preferentially attack certain body segments of the snake models. We had expected that predators might preferentially attack the snakes' heads, as some predators have been observed to crush the head or decapitate rattlesnakes prior to feeding to avoid envenomation (Smith, 1975; Langkilde, Shine & Mason, 2004). However, there is little literature reporting the actual mechanisms that avian and mammalian predators use to physically capture and kill a rattlesnake, and it is possible that predators would strike at areas farthest away from the fangs to incapacitate the snake without being bitten (Langkilde *et al.*, 2004). Further data collection with larger sample sizes, along with detailed observations of predators' behaviour when preying upon live rattlesnakes, are needed to further examine this phenomenon.

Because dark rattlesnake snake models were attacked so much more frequently than light snakes in our study, it begs the question as to why the dark coloured phenotypes still persist at our field site. In fact, very dark rattlesnakes are common at this site and other sites in Southern California. Darker colouration has been shown to arise due to mutations in garter snakes (Bittner, 2003), hog-nosed snakes (Edgren, 1957), and European vipers (Wüster *et al.*, 2004). If dark snakes experience high predation risk, it is reasonable to hypothesize that they may experience other beneficial trade-offs that offset the cost of dark colouration. It is possible that darker skin colour allows snakes to thermoregulate more effectively (Rahn, 1942; Santos *et al*., 2014). For example, Bittner *et al*. (2002) found that melanistic garter snakes had body temperatures slightly elevated above other garter snakes. Melanistic vipers may be favored in cold climates because they have a thermoregulatory advantage (Luiselli, 1992; Capula & Luiselli, 1995). It is possible that dark rattlesnakes may be able to heat more rapidly when basking in the sun, which could lend them more precise regulation of body temperature. Rattlesnakes also tend to exhibit stronger blotching and banding patterns as juveniles than as adults (Eskew, Willson & Winne, 2009; Westphal *et al.*, 2011); indeed, most of the dark snakes we typically observe in the field are large adults. This is likely the result of many factors; blotching may assist juveniles in avoiding predators (Bowen, 2003), and perhaps this benefit is outweighed by potential thermal or other benefits of dark colouration as adults. This hypothesis deserves further study.

Colour and colour pattern are clearly complex traits in rattlesnakes, as in other organisms. In this study, we found that snake colouration impacts detection by predators, with darker coloured snake models attracting more predator attention earlier and more often. While blotched and banded patterns may help snakes to blend in, especially in habitats with higher amounts of vegetation and shade (Langkilde *et al.*, 2004; Westphal *et al.*, 2011; Santos *et al.,* 2014; Martínez-Freiría *et al.*, 2017; Brooks, 2018), predation risk was not greatly impacted by patterning. In terms of avoiding predation by means of crypsis, being a light-coloured snake appears to be the most effective method, at least at sites like ours with seasonal golden-coloured substrates. Further studies investigating not only the relationship between predation pressure and snake colour in different environments, but also examining how season, predator prevalence and composition in the area, and where and how predator attacks actually occur, are necessary to better understand cryptic colouration and its role in predator avoidance for snakes.

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Competing Interests

The authors declare no competing interests associated with this article.

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Data, Code and Materials

Attack mark counts, latency data, L*a*b* analysis, and photographs of snake models used for L*a*b* analysis doi: (To be submitted to Dryad upon acceptance)

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Table Captions

Table 1. L*a*b* values of four types of rattlesnake models and their substrates. Light models and their substrate did not differ in L*, indicating no overall contrast with substrate. All other snake models (especially dark) had significantly different model and substrate L* values, showing that they exhibit high contrast with the substrate. Light snake model a* values were higher than the substrate (snake model more red, substrate more green), and other snake model a* values were lower than substrate (snake model more green, substrate more red), although this was not significant for intermediate-white band snake models. Light model b* values were not different from substrate, and other snake model b* values were lower than substrate (snake model more blue, substrate more yellow).

Figure Captions

Figure 1: (a) The colouration of Southern Pacific Rattlesnake varies dramatically within our field site (shown here) and even more so across their range. (b) Four clay model types were used

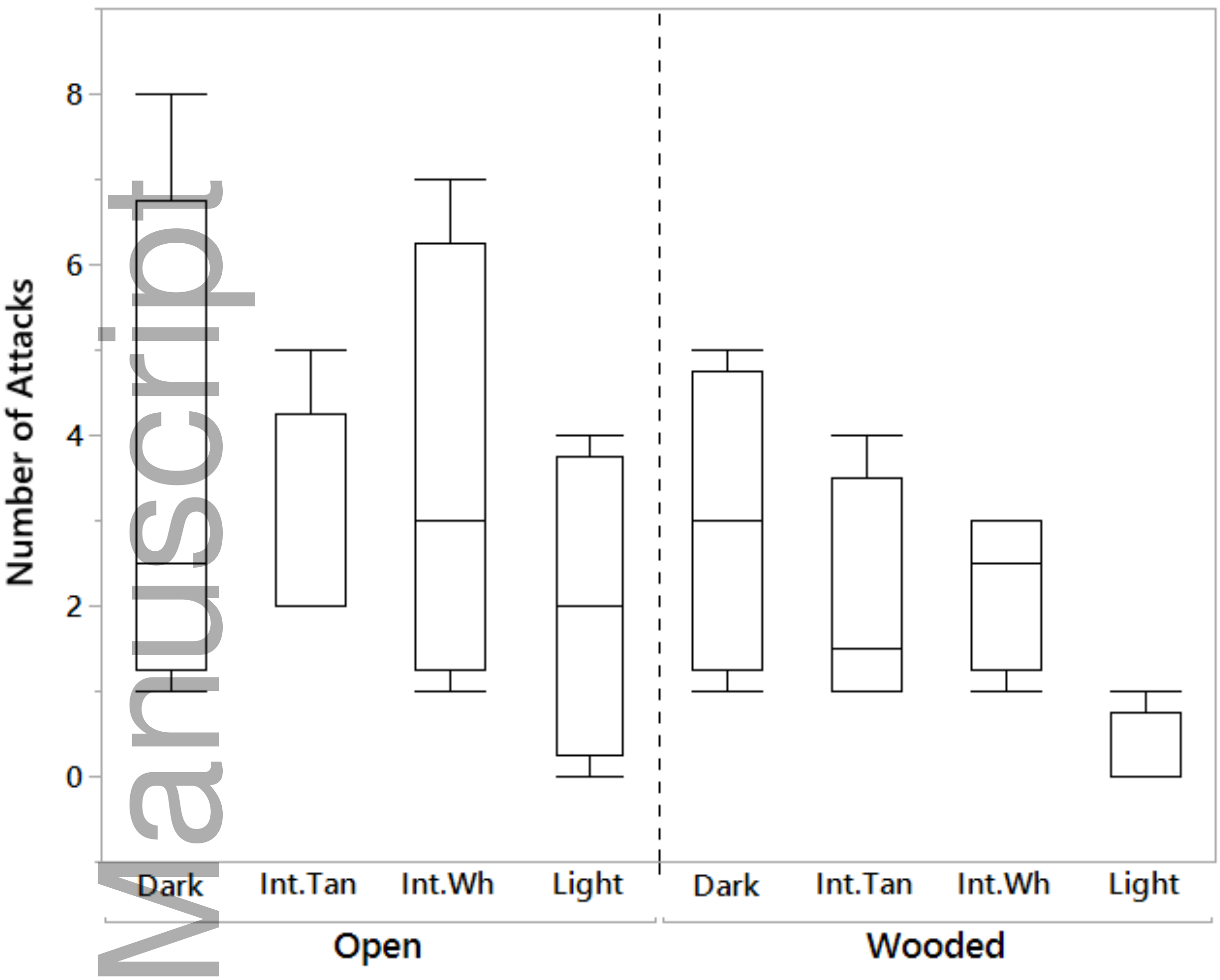
to examine how rattlesnake skin colour affects predation attempts on them. From left to right: (1) "dark:" dark body base colour with dark bands, (2) "intermediate-tan:" intermediate base colour with tan-coloured bands, (3) "intermediate-white:" intermediate base colour with white bands, and (4) "light:" light base colour with light bands. The tail of the light snake model shows an example of a destructive predatory attack. Models were mounted on wood that was sunk and secured under the substrate (see Methods).

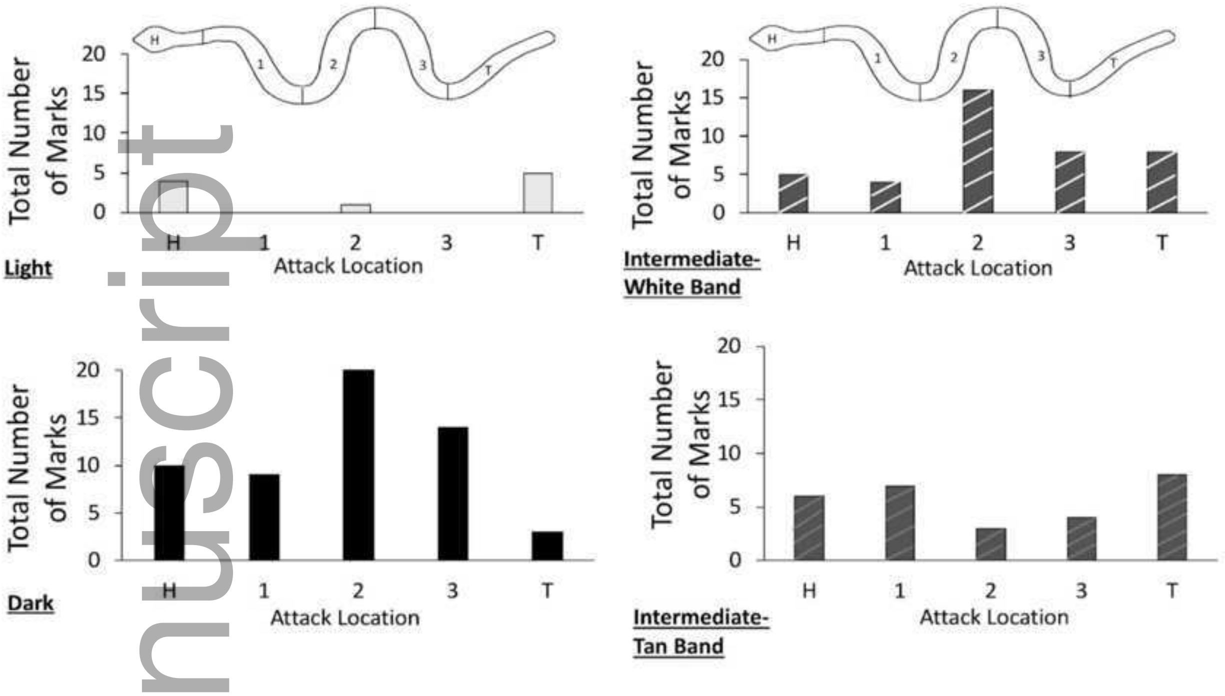
Figure 2. Rattlesnake model colouration impacts the likelihood of attack by predators. Hazards ratio analysis (see text) showed that regardless of grid type, light snake models were significantly less likely to be attacked than dark and intermediate white snake models, and that light models were detected later in the study than the other three snake model types.

Figure 3. Rattlesnake model colour did not impact the location of predatory attacks. Each model was divided into five equal length segments, from rostral to caudal: H (head and neck), 1 (next segment), 2, (next segment), 3 (next segment), and T (tail). There was no significant difference in the total number of marks among attack locations.

Model Type	**L*a*b* Value**	**Mean Model LAB Value ± 1 SEM**	**Mean Substrate LAB Value ± 1 SEM**	**F-ratio**	**p-value**
Light	L*	41.19 ± 1.23	41.27 ± 1.62	0.002	0.96
	a*	38.99± 0.55	36.42±0.56	19.27	< **0.0001**
	b*	26.13± 0.64	26.00± 0.71	0.035	0.85
Intermediate-White Band	L*	32.14 ± 1.70	41.59 ± 2.06	17.97	< **0.0001**
	a*	32.6± 1.22	35.06± 0.94	3.00	0.085
	b*	17.71± 0.98	24.71± 1.09	27.26	< **0.0001**
Intermediate-Tan Band	L*	32.43 ± 1.09	42.69 ± 1.71	28.80	< **0.0001**
	a*	30.94± 0.61	35.73± 1.10	14.70	**0.0002**
	b*	15.56± 0.63	24.65 ± 0.92	99.92	< **0.0001**
Dark	L*	19.77 ± 0.78	44.91± 1.61	219.19	< **0.0001**
	a*	25.23± 0.64	36.54±0.59	166.48	< **0.0001**


(a)
(b)


Number of Attacks
8
6
4
2
0
Dark
Int.Tan
Int.Wh
Light
Dark
Int.Tan
Int.Wh
Light
Open
Wooded


H
1
2
3
T
Total Number of Marks
20
15
10
5
0
H
1
2
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T
Attack Location
Light
Total Number of Marks
20
15
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Attack Location
Intermediate-White Band
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20
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