



Can snakes hide in plain view? Chromatic and achromatic crypsis of two colour forms of the Western Terrestrial Garter Snake (*Thamnophis elegans*)

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Colours influence numerous aspects of an animal's ecology. One possibility is that colour helps make an animal cryptic against the background on which it is resting. We test this hypothesis for two different, geographically separated colour forms (dark forms and light forms) of the Western Terrestrial Garter Snake, *Thamnophis elegans*. We quantified crypsis of snakes, in terms of colour (chromatic crypsis) and brightness (achromatic crypsis), by using objective measures of spectral reflectance of snakes and the surrounding habitat. These data were visually modelled from the perspective of potential snake predators and human researchers. Overall, snakes of both colour forms selected basking sites that increased chromatic crypsis over that which would have been achievable on random backgrounds. Both colour forms of *T. elegans* appear to exhibit similar achromatic and chromatic crypsis when viewed by potential predators, such as mammals and birds. From the perspective of the human visual model, dark *T. elegans* were generally more chromatically cryptic than light *T. elegans*, contrary to our a priori subjective impression. The main contribution of the present study is that we provide one of the first objective comparisons of snakes and their backgrounds as a measure of crypsis. Although we found some evidence for crypsis as a factor in choice of basking sites for snakes, other factors (e.g. thermoregulatory opportunities) undoubtedly play important roles as well. We also have not addressed whether snakes involved in other activities are cryptic or whether there are differences between the sexes or between reproductive and nonreproductive females. The adaptive significance of colour variation has been studied in diverse taxonomic groups. Although the mechanisms are not straightforward, the opportunities to carry out further work in this area are enhanced by the availability of objective approaches. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 108, 756–772.

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INTRODUCTION

Colour influences numerous aspects of the ecology of organisms, including foraging ability (Hanlon, Forsythe & Joneschild, 1999), thermoregulation (Bittner, King & Kerfin, 2002), communication with conspecifics (Endler, 1987), and defence against predators (Losey *et al.*, 1997). To avoid being preyed upon, animals can use bright, contrasting colours to advertise their unpalatability or cryptic, concealing colours to minimize their detection (Edmunds, 1974). The use of cryptic colours to avoid detection is widespread in

diverse taxonomic groups in both terrestrial and aquatic environments (Kettlewell, 1956; Merilaita, 1998; Hanlon *et al.*, 1999; Wente & Phillips, 2003; Stuart-Fox, Whiting & Moussalli, 2006; Kekalainen *et al.*, 2010; Clarke & Schluter, 2011; Caro *et al.*, 2012).

Crypsis is considered as an adaptation against visually-oriented predators whereby, in the extreme, animals become indistinguishable from the surrounding background. Numerous mechanisms have been proposed to reduce an animal's detectability, including disruptive coloration (Stevens *et al.*, 2006), transparency (Johnsen, 2001), masquerade (Ruxton, Sherratt & Speed, 2004; Skelhorn, Rowland & Ruxton, 2010), mirroring (Johnsen & Sosik, 2003), and countershading (Braude *et al.*, 2001). Because of the many organ-

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isms that resemble their environment either by selecting matching backgrounds (Wente & Phillips, 2003, 2005) or by changing colours to match their surrounding environment (Packard & Sanders, 1971; Kats & van Draft, 1986; Hanlon & Messenger, 1988; Kelman, Tiputus & Osorio, 2006; Vroonen *et al.*, 2012), background matching is often regarded as the principal method of attaining crypsis.

Background matching refers to the visual similarity between an animal and its environment and it requires that both the colour and pattern of the animal prevent detection. Currently, there is no broadly applied approach for quantifying and analyzing the role of pattern elements in crypsis; however, the analytical framework recently proposed by Endler (2012) provides valuable contributions to this area of research. Therefore, in the present study, we focus on background matching from a colour-matching perspective (i.e. from the two perceptual channels that animals use in parallel, namely colour, or chromatic cues, and brightness, or achromatic cues) (Jacobs, 1985; Vorobyev & Osorio, 1998).

Crypsis via background matching is closely linked to the resemblance of an animal to its surrounding habitat and it can be expected that the better an animal matches its background, the less its chance of being detected by a predator. Background matching can become difficult, however, for animals that have fixed coloration and use varied habitats. Snakes, for example, typically use a variety of habitats in which to forage, find mates, bask, and take refuge (Slip & Shine, 1988; Charland & Gregory, 1994; Blouin-Demers & Weatherhead, 2001).

If background matching is closely linked to the resemblance of an animal to its surrounding habitat and multiple habitat types are frequently used, is crypsis still possible? Merilaita, Tuomi & Jormalainen (1999) used mathematical modelling approaches in a simplified heterogeneous environment to demonstrate that crypsis can be optimized either by adopting a compromised coloration to two habitats or, conversely, by adopting a specialized coloration to one background type. The trade-off between these two strategies depends on a number of factors, such as the behaviour of prey and predators (Houston, Stevens & Cuthill, 2007; Bond & Kamil, 2006) and the relative frequency of different habitat types (Merilaita, Tuomi & Jormalainen, 1999; Houston *et al.*, 2007; Bond & Kamil, 2006). Recent computer-based experiments investigating the evolution of crypsis concluded, however, that compromised coloration results in overall poor survivorship, indicating that strategies for optimal concealment are multifaceted (Sherratt, Pollitt & Wilkinson, 2007).

Early studies of animal coloration involved quantifying colours that were visible to human observers

(Poulton, 1890; Cott, 1940) by ranking colours into arbitrary classifications (Sweet, 1985; Agawa & Kawata, 1995; Nicoletto, 1995; Forsman, 1999) and by matching colours to commercial standards (Endler, 1984; Braude *et al.*, 2001; Weiss, 2002). Animal crypsis also has been quantified not by evaluating colour per se but by using the time taken for human observers to detect individuals (Cuadrado, Martin & Lopez, 2001; Cooper, Caldwell & Vitt, 2008). Relying on human assessments of colour and crypsis is problematic for numerous reasons. First, humans are not visually sensitive to shorter wavelengths [ultraviolet (UV): 300–400 nm] and the use of human assessments may completely underestimate the significance of this part of the spectrum (Bennett, Cuthill & Norris, 1994; Majerus, Brunton & Stalker, 2000). Second, the subjective techniques employed assume that colour can be scored in an accurate and repeatable fashion, whereas measurement error, in this case arising from human bias, has been shown to influence the classification of other subjective measures (Eden *et al.*, 2007). Third, human vision may lack the sensitivity or acuteness necessary to detect biologically important colour differences (Aviles, 2008; Ryer *et al.*, 2008). Conversely, human assessments may attach significance to colour differences when these differences may not be functionally significant (Martin, Luque-Larena & Lopez, 2009). Despite these fundamental limitations, human-biased approaches are still utilized in animal signaling research (Fitzstephens & Getty, 2000; Hoffman & Blouin, 2000; Cooper *et al.*, 2008; Ryer *et al.*, 2008; Manriquez *et al.*, 2009; Todd, Lee & Chou, 2010; Mooi, Wiens & Casper, 2011). It is therefore critical to evaluate and interpret achromatic and chromatic data from the perspective of relevant potential predators (Wilson, Heinsohn & Endler, 2007; Aviles, 2008; Defrize, Thery & Casas, 2010; Chiao *et al.*, 2011).

In the present study, which focuses on snakes, the main predators are presumed to be birds and mammals (Hoyer & Stewart, 2000; Fitch, 2003; Placyk & Burghardt, 2005; Shine *et al.*, 2007). The mechanism by which chromatic and achromatic signals are interpreted by these predators depends on the eye's sensitivity to certain wavelengths of light. For example, birds are tetrachromatic, meaning that they have four types of visual cells, or photoreceptors, in the eye that are used to discriminate light wavelengths (Hart, 2001). Avian vision can then be further divided into two visual types based on the very short-wavelength sensitivity of photoreceptors: birds having UV-sensitive (UVS) photoreceptors and those having violet-sensitive (VS) photoreceptors (Oden & Hastad, 2003). Birds with a VS visual pigment can also perceive light in the UV range, although they are less sensitive to this wavelength of light than UVS birds. Mammals, on the other hand, lack sensitivity to either UV or violet

light and their sensitivity varies from monochromatic (Abrams, 1987; Jacobs & Deegan, 1992) to dichromatic (Calderone & Jacobs, 2003) to trichromatic (Wyszecki & Stiles, 1982) visual systems.

The only previous study similar to ours investigated colour-background matching in geographically separated distinct colour morphs of the rattlesnake, *Crotalus lepidus* (Farallo & Forstner, 2012). In that study, the two colour morphs closely matched the colour of homogeneous rocks that formed their main habitat. Studies of 'predation' on foam models showed that models matching their backgrounds suffered fewer attacks than non-matching models, suggesting an important role for predators in maintaining geographical variation in colour. We consider crypsis in snakes against less homogeneous backgrounds than those studied by Farallo & Forstner (2012).

In the present study, we investigate chromatic and achromatic crypsis within one species of garter snake in British Columbia (BC), Canada. We evaluate crypsis in different populations of the Western Terrestrial Garter Snake, *Thamnophis elegans*, which exhibits geographical variation in coloration. The light colour form occurs in interior BC and populations are completely separated geographically from the dark colour form that occurs in coastal BC. We interpret, or model, the chromatic and achromatic data of garter snakes and their backgrounds from the perspective of a mammalian predator (ferret) and two potential avian predators (i.e. V-type and UV-type). We also model the data from the perspective of a human observer to evaluate the possibility of differential snake crypsis to the human visual system. We aimed to address three questions:

1. Do snakes select basking sites that increase chromatic and achromatic crypsis?

We predicted that crypsis would be maximized in backgrounds where snakes were found basking, relative to nearby random sites, suggesting selection of microhabitats where probability of detection is diminished. We do not suggest that crypsis is the sole function of colour in these animals, nor that crypsis is the sole factor influencing choice of basking site by snakes (e.g. thermoregulatory opportunities also should be important). That said, other things being equal, crypsis should nonetheless be advantageous for snakes resting in the open, even for a short time. Crypsis might also be advantageous for nonbasking snakes, although we focus on basking snakes because, unlike moving snakes, they clearly have chosen the particular spot in which they are found and are not simply passing by.

2. Can predators differentially detect snakes based on achromatic and chromatic crypsis?

We predicted that crypsis would vary between predators with different visual models. More specifically, we predicted that snakes would be more cryptic to bird predators because of their enhanced visual sensitivity and acuity.

3. Are snakes differentially cryptic to human observers?

Based on our experience in locating snakes in the field, we predicted that the light colour form of *T. elegans* would be more cryptic to the human visual system than the dark *T. elegans* colour form.

MATERIAL AND METHODS

STUDY AREA, SNAKE CAPTURE, AND MEASUREMENTS

We undertook the present study in the spring and summer of 2008 at three study sites in British Columbia (BC), Canada where the snakes occur. We studied the light form in the wildlife management area at Creston, BC (latitude/longitude: 49°4'N/116°31'W) that consists of wetland, grass areas, shrubby uplands, and riparian forest. The light form of *T. elegans* is light brown in overall dorsal coloration with a tan stripe running down the length of its back. There are numerous black patches that interrupt this stripe conferring a blotched appearance. We studied the dark form at Cowichan Bay, BC (48°47'N/123°44'W) and Rithet's Bog in Victoria, BC (48°25'N/123°21'W). Rithet's Bog is also a wetland habitat that consists of large grassy areas, shrubs, and riparian forest. Cowichan Bay is an estuary into which a nearby river drains and is similar in vegetative structure to both Creston and Rithet's Bog. The dark form of *T. elegans* is black in overall dorsal coloration with a light (tan, yellow, cream) dorsal stripe. Black dorsal blotches are also evident, although the form does not appear blotched because they closely match the dorsal colour.

In all habitats, potential predators include birds, such as crows, ravens, and great blue herons, as well as mammals, such as mink and raccoons. Mink are known to be occasional, probably opportunistic, predators on snakes (reviewed in Verts & Carraway, 1998). In at least some mustelids, olfaction and vision are of equal importance in foraging (Zielinski, 2000), and so we assume that the same applies to mink. Of the many species of potential predators at these sites, both authors (LAI and PTG) have personally observed foraging and foraging attempts by ravens, red-tailed hawks, and mink.

We searched for snakes on foot and captured them by hand. Several variables were measured on each snake captured, including body length (snout-vent length; SVL) and sex. In addition, each adult female's reproductive condition was assessed by gently palpating its abdomen to determine whether it was gravid.

We individually marked each snake for future identification by clipping a unique combination of subcaudal scutes on the underside of the tail to ensure each snake was included only once in the present study.

SAMPLING FOR CRYPSIS

Snakes were used to evaluate crypsis if they met the following predetermined criteria: (1) motionless and coiled in a fixed position when detected, indicative of typical basking behaviour and (2) fully visible from overhead. We used these two criteria as indicators that the snakes had actively selected the sites where they were found for basking, rather than being caught there incidentally as they were just passing by in search of food, retreat sites, etc. Snakes that were visible from overhead were at risk from potential avian predators from above and could be seen by mammal predators on the ground. If snakes met these criteria, they were taken to the laboratory where the colour (or spectral reflectance) and brightness (or luminance) of their dorsal surface were measured. Thus, the present study focuses on the potential role of crypsis in selection of basking sites by snakes, and not its role in general habitat selection.

HABITAT SAMPLES

Because crypsis is a relative measure that depends upon the background against which animals are seen, we collected samples of the habitat surrounding each snake. Selecting sites on the basis of their suitability for basking would have required us to make a subjective assessment of that suitability. Furthermore, we have observed snakes basking in a variety of locations and in different microhabitats. We therefore chose a more objective approach by randomly sampling close to where the snake was actually found. In all cases, the snake could have basked at the random site. For each capture, we collected 36 habitat samples from a 50 × 50 cm grid positioned symmetrically around where the motionless snake was found and divided into 10-cm intervals both horizontally and vertically. The sampling area chosen was selected to capture the area immediately around a basking snake. All basking snakes fit easily into this size of patch. We gathered habitat samples that included herbaceous vegetation, twigs, sand, rocks, etc., at every 10-cm intersection point within the grid, placing each of these 36 samples into separate paper envelopes. Where there were multiple samples of similar habitat types, such as a large area of grass, we collected only one sample and copied the data the appropriate number of times.

Following this, we collected habitat samples from a similar grid that was located in a random plot near the capture site. These plots were positioned at a 2-m distance from the point of capture in one of the four

cardinal directions, which was randomly chosen. All 72 habitat samples for a given snake were taken back to the laboratory, where we measured the spectral reflectance of each item.

SPECTRAL REFLECTANCE OF SNAKES AND THEIR SURROUNDING HABITAT

Prior to any reflectance measurements being collected, we pre-determined the number of scans required to capture a comprehensive profile of dorsal colour variation for each colour form of *T. elegans*. This initial step was required because reflectance measurements are collected according to the relative proportion of different dorsal colours. To do this, we photographed the dorsal surface of a random sample of six snakes (three each of light *T. elegans* and dark *T. elegans*) in the laboratory, using a Nikon D200 digital SLR camera (Nikon Inc.).

Next, we used the digital software package, IMAGE-PRO PLUS, version 6.0 (Media Cybernetics Inc., 2006), to analyze each digital image and calculate the area of each colour region. We quantified (by outlining) the dorsal surface colour, stripe, and blotching and divided these values by the total dorsal area to determine the percentage area of each colour type. This procedure was repeated for the three individuals of each colour form. Following this, we calculated mean values for each colour form (e.g. mean percentage area of dorsal colour, stripe, blotch for the light form, etc.), which were then used to determine the number of spectral scans required for each region. Given the amount of time required to collect one reflectance scan, we had predetermined that 20 scans would be taken of each individual. Thus, if the dorsal colour comprised 85% of the dorsal surface area, then 17 of the 20 scans would be taken of the dorsal colour along the length of the snake. The same logic would apply to the stripes and blotches for both colour forms.

We then took a second round of photographs on a smaller subset of individuals (one each of light and dark *T. elegans*) using a Nikon D200 digital SLR camera (Nikon, Inc.) fitted with a UV-pass filter. This arrangement allowed us to determine whether snakes were reflective in the UV-range of the electromagnetic spectrum. That is, any bright regions on the images would represent areas that are reflective in the UV because only UV light can pass through the filter. None of the snakes were reflective in the UV range, and so we did not require the use of an illumination source that produced light in the UV and could instead use equipment that generated light only from the visible to near-infrared region of the electromagnetic spectrum.

Following the above-described process, we measured the spectral reflectance of all snakes and habitat samples using a reflectance probe (Ocean Optics R200-7-UV/VIS) connected to a dual-channel

spectrophotometer (Ocean Optics SD2000) and a tungsten-halogen light source (Ocean Optics LS-1). All measurements were recorded using a notebook computer (Dell Inspiron 9400) operating SpectraSuite software (Ocean Optics). Prior to each reflectance scanning session, the spectrophotometer was calibrated against a mercury argon light source (Ocean Optics HG-1) using a 100- μm fibre (Ocean Optics QP100-2-UV/VIS).

All spectra were obtained in a dimly lit room to reduce the amount of ambient light that might influence measurements. The reflectance probe was maintained at a 90° angle to the dorsal surface and was kept at a constant 2 mm from all snakes and habitat samples. Immediately prior to each reflectance measurement, we scanned a matte white standard (Ocean Optics WS-1) and removed the dark current from the signal to take into account any potential noise introduced by these measurements. We collected reflectance scans for one snake at a time by gently restraining it under the reflectance probe; if, at any point, the animal appeared to be in distress (e.g. excessive movements, striking, etc.), measurements were stopped and the animal was allowed to rest for at least 1 h. Soon after the measurements were completed, we released snakes at their point of capture under favourable weather conditions.

IRRADIANCE

We measured downwelling irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1}$) using a direct-attach cosine-correcting probe (Ocean Optics CC-3-DA) and a spectrophotometer (Ocean Optics SD2000). Prior to the field season, the irradiance sensor was calibrated with an optical radiation calibrator (Li-Cor LI-1800-02) by Dr Craig Hawryshyn (Queen's University, Kingston, ON, Canada). Irradiance measurements were collected shortly after each capture in the field to assure the same light conditions as at the time of capture. Three irradiance scans were taken for each capture and the resulting mean spectrum was used to transform reflectance values (i.e. 20 per snake and 72 habitat samples per capture) to radiance values ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1} \text{sr}^{-1}$) by multiplying values by mean irradiance. Although we do not have precise weather data for each snake, all snakes were obviously found in conditions conducive for basking.

VISUAL MODELLING

In total, we constructed four visual models from which to interpret garter snake coloration. The ferret (*Mustelo putorius furo*) model was constructed using microspectrophotometry (MSP) data (i.e. λ_{max} values) for the short-wavelength-sensitive (SWS) and long-

wavelength-sensitive (LWS) photoreceptors obtained from Calderone & Jacobs (2003). The human model was constructed using MSP data for SWS, medium-wavelength-sensitive (MWS) and LWS photoreceptors obtained from Wyszecki & Stiles (1982). We then converted these data to Gaussian visual pigment absorbance curves following standardized approaches (Govardovskii *et al.*, 2000). Ferret and human photoreceptors do not possess oil droplets; therefore, no modification of the resulting absorbance spectra was required.

Two bird visual models were constructed using data provided by Nathan Hart (The University of Western Australia). Although MSP data have not been collected for all bird species (Hart, 2001; Hart & Vorobyev, 2005), opsin gene sequencing work performed by Oden & Hastad (2003) suggests that potential snake predators such as large-bodied passerines and gulls have visual systems that are more sensitive to ultraviolet light (or UVS), whereas other predatory birds such as hawks, falcons, and corvids are more sensitive to violet light (or VS). Visual modelling for these two visual types is often represented by two 'model' species for which detailed MSP data have been collected, namely the blue tit, *Parus caeruleus*, a UVS bird, and the Indian peafowl, *Pavo cristatus*, a VS bird. Bird photoreceptors possess oil droplets; therefore, all photoreceptor data for the two bird models were corrected for the modifying effects of these oil droplets, as well as for the effects of other ocular media (e.g. cornea; N. Hart, pers. comm.).

We then estimated the response of the four visual models by multiplying the spectral sensitivity of each cone class (two cone classes for the dichromatic ferret, three cones for the trichromatic human, and four cones for the tetrachromatic birds) by each radiance spectrum (20 of each snake and 72 associated habitat samples). To do this, we derived the photoreceptor quantum catches (Q_i) of each cone class following the formula described in Endler & Mielke (2005):

$$Q_i = \int_{\lambda_{\text{min}}}^{\lambda_{\text{max}}} R(\lambda) I(\lambda) SS(\lambda) d(\lambda)$$

where λ represents wavelength, $R(\lambda)$ is the reflectance spectrum of the item being viewed, $I(\lambda)$ is the irradiance spectrum or ambient light illuminating the item, and $SS(\lambda)$ is the spectral sensitivity of a given photoreceptor type, all integrated over a wavelength of interest, $d(\lambda)$.

The working assumption, as outlined by Fleishman & Persons (2001), is that neural stimulation from each of the cones is equal in response to a white stimulus. To meet this assumption, the resulting values were summed for each cone class and each sum was multiplied by the reciprocal of the area under the spectral sensitivity curves of each associated photoreceptor to

account for the differences in area under the sensitivity curves (Fleishman & Persons, 2001).

COLOUR PERCEPTION

To compare an entire set of colour values, we can treat the photoreceptor output of a given patch (a single scan in this case) as a multivariate value, or vector. Therefore, multivariate statistics can be used to compare a 'cloud' of colour scans or vectors. The perception of colour patches by the three different predator visual models is defined by the relative stimulation values $\{S\}$, where $\{S\} = \{S_{SWS} \text{ and } S_{LWS}\}$ for the ferret model, $\{S\} = \{S_{UVS}, S_{SWS}, S_{MWS}, S_{LWS}\}$ for the UV-type bird model and $\{S\} = \{S_{VS}, S_{SWS}, S_{MWS}, S_{LWS}\}$ for the V-type bird model (Endler & Mielke, 2005). Following Endler & Mielke (2005), an object with N patches (e.g. a snake with 20 colour scans is $N = 20$) comprises an $N \times 2$ matrix, \mathbf{S} , for the ferret model or an $N \times 4$ matrix for the two bird models, where $\{S\}$ represents the rows of the matrix. This \mathbf{S} matrix is then converted to a compositional matrix, \mathbf{S}_e , by dividing each of the cone outputs in \mathbf{S} by its row total, i.e.:

$$u = S_{UVS}/S_{UVS} + S_{SWS} + S_{MWS} + S_{LWS};$$

$$v = S_{VS}/S_{VS} + S_{SWS} + S_{MWS} + S_{LWS};$$

$$s = S_{SWS}/(S_{UVS} \text{ or } S_{VS}) + S_{SWS} + S_{MWS} + S_{LWS};$$

$$m = S_{MWS}/(S_{UVS} \text{ or } S_{VS}) + S_{SWS} + S_{MWS} + S_{LWS};$$

$$l = S_{LWS}/(S_{UVS} \text{ or } S_{VS}) + S_{SWS} + S_{MWS} + S_{LWS}.$$

For the two bird models, the next step is to convert each \mathbf{S}_e , or set of u/v , s , m , and l -values as described above, to tetrahedral coordinates $\{S_t\} = \{x, y, z\}$ using the following formulas described in Endler & Mielke (2005):

$$x = \frac{1 - 2s - m - u}{2} \sqrt{\frac{3}{2}} \quad y = \frac{-1 + 3m + u}{2\sqrt{2}} \quad z = u - \frac{1}{4}$$

where u (or v) = photoreceptor output of the ultraviolet-(or violet-) wavelength-sensitive cone, s = photoreceptor output of the short-wavelength-sensitive cone, m = photoreceptor output of the medium-wavelength-sensitive cone, and l = photoreceptor output of the long-wavelength-sensitive cone. The result is that every stimulus is represented as a point that lies within tetrahedral colour space.

Because ferrets are dichromatic and humans are trichromatic, conversion of points to tetrahedral colour space is inappropriate. We converted ferret cone outputs to single data points using the formula: $x = S_{SWS}/S_{SWS} + S_{LWS}$. The result is that every stimulus value, rather than falling within tetrahedral colour

space, is represented as a point that falls on a two-dimensional plane (J. Endler, pers. comm.). We converted human cone outputs to two data points using the formula $x = S_{MWS} + S_{LWS}/2$; $y = (\sqrt{3}/2) \times S_{LWS}$ resulting in points that fall within a three-dimensional space (J. Endler, pers. comm.).

This approach results in a description of snake coloration as $\{S_t = x, y, z\}$ for the two bird models, $\{S_t = x\}$ for the ferret model, and $\{S_t = x, y\}$ for the human visual model. Similarly, a second group of colour points each with comparably sized colour parameters (i.e. x, y, z for birds, x for ferrets, and x, y for humans) describes the surrounding habitat. The two sets of colour coordinates can then be compared using compositional-type analyses. Distances between the clouds of colour points in the tetrahedral space as well as along the two- and three-dimensional plane can therefore be interpreted as perceived differences among the colours.

BRIGHTNESS PERCEPTION

The mechanisms that control achromatic signals in animals are not fully understood, but evidence suggests that double cones, containing the LWS pigment, are probably involved in brightness discrimination in birds (Osorio, Miklosi & Gonda, 1999; Hart, 2001). Double cones contain two structures, the principal and accessory members, each of which contains the LWS pigment but which differ in their oil droplet characteristics (Hart, 2002). We calculated the mean absorbance curve for the two oil droplet types and multiplied this by the absorbance spectrum of the LWS pigment.

In animals that lack double cones, such as mammals, it is presumed that LWS cones function in achromatic discrimination (Osorio & Vorobyev, 2005). We therefore used the λ_{\max} value for the LWS pigment ($\lambda_{\max} = 558 \text{ nm}$) obtained from Calderone & Jacobs (2003) and Wyszecki & Stiles (1982). We then modelled the data following approaches outlined in Govardovskii *et al.* (2000).

COMPARING ENTIRE COLOUR PATTERNS

The distribution of colour coordinates is such that it violates numerous multivariate statistical assumptions, such as normality and homogeneity of variances. Because of this, we used a distribution-free statistical approach, LSED-MRPP, that measures differences between colour patches in any aspect of their distributions, such as differences in mean, variance, and skewness (Endler & Mielke, 2005). LSED-MRPP yields an effect size measure called 'disparity' or ' K ', and increased divergence between groups that differ in their distributions results in higher ' K ' values. This

approach has been broadly applied in work on colour conspicuousness in various taxonomic groups, including birds (Endler *et al.*, 2005), fish (Kemp, Reznick & Grether, 2008), lizards (Macedonia *et al.*, 2009), and pythons (Wilson *et al.*, 2007).

The analytical approach used here compares differences in animal and background colours from the perspective of various viewing organisms by calculating colour differences in multivariate space. Unlike other visual modelling methods, such as the model of Vorobyev & Osorio (1998) (referred to as the V-O model), this compositional approach assumes that all cone classes contribute equally to colour perception. In addition, another simplifying assumption is that photoreceptor noise, or the variability induced by the mechanisms of light transduction, is not taken into account (Vorobyev & Osorio, 1998). Also, the compositional analysis applied here could be described as a more conservative approach because it may not have the precision to differentiate between spectrally similar colours, particularly at low light levels. This limitation is minimized, however, in garter snakes, in which diurnal activity (hence high light levels) is more common.

Despite these limitations, the main advantage of the disparity method is that it compares an entire set of colour points, or quantum catches, rather than being restricted to the discrimination of pairs of spectral points. Because the background colour surrounding garter snakes in the present study is typically heterogeneous, one would have to pick two values arbitrarily to compare if the V-O model were employed. We therefore argue that the compositional approach is more appropriate because it includes all colour elements in proportion to how they are represented both on the snake and in the surrounding habitat.

We calculated disparity values for each snake against the respective background on which it was found basking, as well as for the same snake against the background of a nearby random habitat sample. We then repeated this approach for all light and dark *T. elegans* from the perspective of the four visual models. In this and all subsequent statistical analyses, chromatic and achromatic values were calculated separately and 'K' values were treated as the dependent variable. We evaluated whether snakes selected basking sites that increased achromatic and chromatic crypsis by comparing disparity values using paired *t*-tests, in which the independent variable was background type (i.e. snake against selected basking background versus same snake against corresponding random background). We conducted separate tests for light and dark *T. elegans* for each visual model (UV-type bird, V-type bird, ferret, and human).

We then evaluated differential crypsis between colour forms for both brightness and colour. We there-

fore used two-way analysis of variance models with individuals nested within colour form to compare mean crypsis (dependent variable) between individuals, colour forms, and visual models (independent variables). Colour form and visual model were treated as fixed-effects factors and individuals nested within colour form were treated as levels of a random-effects factor.

Finally, using independent sample *t*-tests, we tested whether a human observer could differentially distinguish between snake forms based on achromatic and chromatic crypsis.

All statistical tests were performed using SAS, version 9.2 (SAS Institute). Post-hoc model comparisons were performed using the Tukey–Kramer method and we assessed significance at $\alpha = 0.05$. All animal maintenance and experimental procedures complied with guidelines for live reptiles and were approved by the University of Victoria Animal Care Committee.

RESULTS

In total, we captured 25 snakes that fit our criteria for analysis of crypsis: 12 dark and 13 light *T. elegans*. Samples included adult males, and nongravid and gravid females ranging from 419 mm to 645 mm in SVL. Analyses could not be divided by sex or reproductive condition because of the small sub-samples.

QUESTION 1: DO SNAKES SELECT BASKING SITES THAT INCREASE CRYPSIS?

In general, achromatic crypsis was similar between basking sites that were selected and nearby random backgrounds for light and dark *T. elegans* (Fig. 1). These similarities were consistent across all three predator visual models (Table 1).

In contrast to achromatic crypsis, chromatic crypsis was generally greater (i.e. lower disparity values, 'K') in selected backgrounds where snakes were basking than in corresponding random backgrounds. This trend held for both colour forms and visual models, although the strength of these differences varied between visual models (Table 1). That is, both dark and light *T. elegans* were significantly more chromatically cryptic in selected backgrounds from the perspective of the two bird models (Fig. 2).

QUESTION 2: DO SNAKES EXHIBIT DIFFERENTIAL CRYPSIS TO MAMMAL AND AVIAN PREDATORS?

The interaction between visual model and colour form was nonsignificant for both achromatic ($P = 0.2145$) and chromatic ($P = 0.6397$) crypsis and was therefore deleted from the analysis. As expected, there was significant variability between individuals in achro-

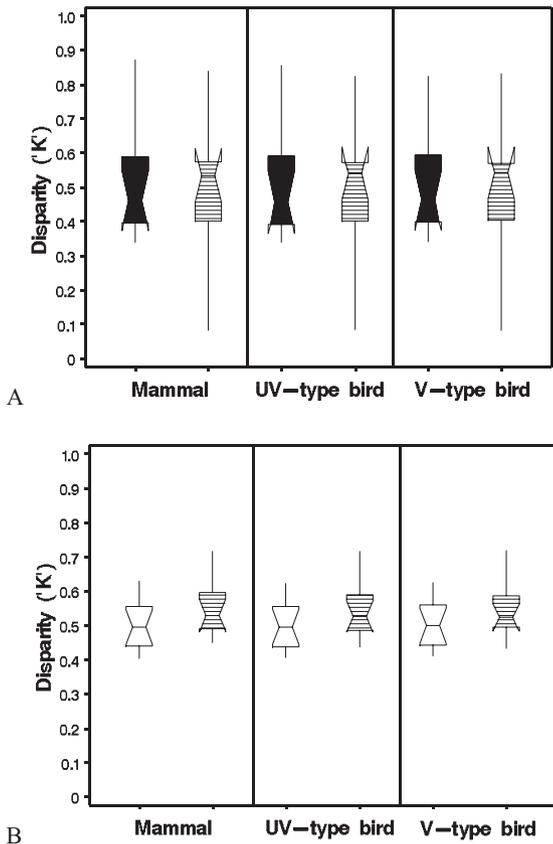


Figure 1. Achromatic crypsis (disparity, 'K') in backgrounds that snakes selected for basking (solid colour) versus nearby random backgrounds (hatched lines) for (A) dark *Thamnophis elegans*, and (B) light *T. elegans*. Shown are *K*-values from the perspective of three predator models: mammal (*Mustelo putorius furo*), ultraviolet (UV)-type bird (*Parus major*), and violet (V)-type bird (*Pavo cristatus*). Overall, there was no difference in achromatic crypsis between snakes at capture sites versus the same snakes at nearby random sites from the perspective of the three predator models. Each box represents 50% of the data, the median is indicated by notches, and lines extend to minimum and maximum values.

matic ($P < 0.0001$) and chromatic ($P = 0.0018$) crypsis as seen by mammals, UV-type birds, and V-type birds.

Dark and light *T. elegans* were equally cryptic ($F_{1,48} = 0.69$, $P = 0.4118$) from an achromatic perspective to the bird and mammal predators ($F_{2,48} = 0.67$, $P = 0.5180$; Fig. 3A). Both colour forms also exhibited similarity in chromatic crypsis ($F_{1,48} = 1.71$, $P = 0.1967$) to the three predators ($F_{2,48} = 0.05$, $P = 0.9471$; Fig. 3B).

QUESTION 3: ARE SNAKES DIFFERENTIALLY CRYPTIC TO HUMAN OBSERVERS?

Achromatic crypsis did not differ between the two colour forms of *T. elegans* from the perspective of the

human observer ($t_{14,5} = -0.220$, $P = 0.828$ based on unequal variances). In terms of colour, light *T. elegans* were significantly less cryptic than dark *T. elegans* to the human model ($t_{23} = -2.190$, $P = 0.039$).

DISCUSSION

The application of objective methods to collect, analyze, and interpret crypsis using the visual systems of potential predators is perhaps the most important contribution of the present study. Our approach contrasts with most other research on snakes, in which subjective methods have been used to quantify and evaluate the importance of colour pattern variation (Jackson, Ingram & Campbell, 1976; Sweet, 1985; Brodie, 1989; King, 1992; Shine, Shine & Shine, 2003; Niskanen & Mappes, 2005; Webb & Whiting, 2005; Brown, Kery & Hines, 2007; Mooi *et al.*, 2011). Our study begins to address at least some of the concerns with using subjective methods, by using spectrophotometry, to objectively quantify the colour of snakes and their backgrounds and assess snake crypsis from the perspective of mammal and avian predators using visual modelling approaches.

The results suggest that dark and light colour forms of *T. elegans* basked on backgrounds that increased chromatic crypsis compared to nearby random sites, although the strength of these differences varied with predator type. Dark and light *T. elegans* appeared equally cryptic in terms of colour and brightness to both bird and mammal models and dark *T. elegans* was more chromatically cryptic than light *T. elegans* from the perspective of human observers.

Crypsis is a function of the contrast of an animal to its surrounding background (Endler, 1978). On backgrounds where snakes were found basking versus nearby randomly chosen backgrounds, snakes were more chromatically cryptic to all three predator models. This trend held for both colour forms, suggesting that snakes select sites for basking at least partly on the basis of their potential for crypsis, at least in terms of colour. Early research demonstrated the close relationship between animal and background colours in a variety of amphibians and reptiles (Norris & Lowe, 1964). Subsequent to this extensive correlational work, empirical research has demonstrated active selection for matching backgrounds in other taxa such as spiders (Heiling *et al.*, 2005), moths and butterflies (Moss, Jackson & Pollard, 2006; Shreeve, 2008), cephalopods (Chiao & Hanlon, 2001), and a variety of anurans (Tordoff, 1980; Morey, 1990; Heinen, 1993; Wentz & Phillips, 2003, 2005). Background matching also has been shown in snakes; juvenile green tree pythons, *Morelia viridis*, which can be either red or yellow in colour, selected habitats at the ground level near the rainforest edge where

Table 1. Summary of paired *t*-tests comparing achromatic and chromatic crypsis (disparity values, 'K') in selected basking sites versus random habitats for dark and light *Thamnophis elegans*

Crypsis type	Colour form	Mammal (<i>Mustelo putorius furo</i>)	UV-type bird (<i>Parus major</i>)	V-type bird (<i>Pavo cristatus</i>)
Achromatic	Dark <i>Thamnophis elegans</i>	$t_{11} = -0.07, P = 0.5267$	$t_{11} = -0.18, P = 0.5715$	$t_{11} = -0.21, P = 0.5799$
Achromatic	Light <i>Thamnophis elegans</i>	$t_{12} = -1.80, P = 0.9512$	$t_{12} = -1.68, P = 0.9411$	$t_{12} = -1.63, P = 0.9360$
Chromatic	Dark <i>Thamnophis elegans</i>	$t_{11} = -2.144, P = 0.055$	$t_{11} = -3.098, P = 0.010$	$t_{11} = -3.425, P = 0.006$
Chromatic	Light <i>Thamnophis elegans</i>	$t_{12} = -1.113, P = 0.287$	$t_{12} = -2.427, P = 0.032$	$t_{12} = -2.407, P = 0.033$

Comparisons were made from the perspective of the three predator visual models: mammal, ultraviolet (UV)-type bird and violet (V)-type bird model. There was no difference in achromatic crypsis between the three predator models, whereas dark and light *T. elegans* were significantly more chromatically cryptic to the UV-type and V-type bird model. Significant values shown in bold.

they were most cryptic and, as green adults, moved to interior rainforest canopy habitats, where crypsis was maximized (Wilson *et al.*, 2007). However, this strong correlation between the colour of animals and their backgrounds does not appear to be universal (Brattstrom & Warren, 1955; Gray, 1978; Capula & Luiselli, 1995; Shine *et al.*, 2003; Wente & Phillips, 2005). In addition to crypsis, other conflicting factors might influence background matching, such as sexual differences in microhabitat use (Merilaita & Jormalainen, 1997), the degree of predation risk experienced in different microhabitat types (Houston *et al.*, 2007), and thermoregulatory constraints (Adolph, 1990; Ahensjo & Forsman, 2006). Nonetheless, there is growing evidence to support the hypothesis that active selection of matching backgrounds operates in at least some animal groups, and the broad applicability of these results across different snake taxa remains to be tested.

What then is the adaptive significance, if any, of microhabitat selection that improves crypsis? Although crypsis is an intuitively accessible concept (Bond, 2007), demonstrating its function and quantifying its effects on fitness has proven difficult. Researchers often hypothesize that crypsis is an effective anti-predator strategy (Cott, 1940; Belk & Smith, 1996; Hanlon *et al.*, 1999; Wauters *et al.*, 2004; Hoekstra, Krenz & Nachman, 2005) but, to demonstrate the adaptive significance of cryptic coloration, studies must illustrate how crypsis contributes to fitness. Research, mostly in insects, has demonstrated how crypsis can contribute to increased survivorship (Cott, 1940; Kettlewell, 1956; Edmunds, 1974; Gillis, 1982; Sandoval, 1994; Losey *et al.*, 1997; Forsman & Appelqvist, 1999; Lyytinen, Lindstrom & Mappes, 2004; Ahensjo & Forsman, 2006). In vertebrates, however, similar types of research showing a selective advantage for colour matching are lacking. Empirical demonstrations in live animals and plastic replicas suggest that conspicuous forms of some fish (Endler,

1980), birds (Gotmark & Hohlfalt, 1995), mammals (Vignieri, Larson & Hoekstra, 2010), amphibians (Tordoff, 1980; Morey, 1990), and snakes (Andren & Nilson, 1981; Bittner, 2003; Niskanen & Mappes, 2005; Farallo & Forstner, 2012) can be nonrandomly preyed upon. In some cases, the relationship between colour and predation can depend on differences between ages/sizes (King, 1993) or between sexes (Forsman & Shine, 1995). Differential selection pressure can therefore play a role in the maintenance of colour variation both within (Tordoff, 1980; Morey, 1990; Vignieri *et al.*, 2010; Bond & Kamil, 2006) and between populations (Hoekstra & Nachman, 2003; Nachman, Hoekstra & D'Agostino, 2003). Ultimately, colour-biased predation can have important implications for the evolution of animal coloration, at least in those species in which a genetic mechanism controlling colour occurs (Ritland, Newton & Marshall, 2001; Hoekstra & Nachman, 2003; King, 2003; Hoekstra, Drumm & Nachman, 2004; Mundy *et al.*, 2004; Rosenblum, Hoekstra & Nachman, 2004).

Our working hypothesis is that *T. elegans* select basking sites at least partly on the basis of crypsis in response to risk of predation. An assumption of this hypothesis is that all other potentially influential factors in basking-site selection are equal and this is not necessarily the case. We might expect costs to occur if optimal crypsis occurs at a time or in a place where alternative activities cannot be pursued and certain habitats cannot be used (i.e. opportunity costs) or if the interaction with the environment is costly (Ruxton *et al.*, 2004). As a result, we should expect trade-offs to occur between crypsis and other behaviours, such as foraging behaviour. In snakes, a classic example of trade-offs between crypsis and thermal ecology occurs in the colour polymorphic common adder, *Vipera berus*, which has two distinct colour morphs. Compared to the typical zigzag morph, melanistic individuals experience thermal advantages (Forsman, 1993), which contribute to increased body

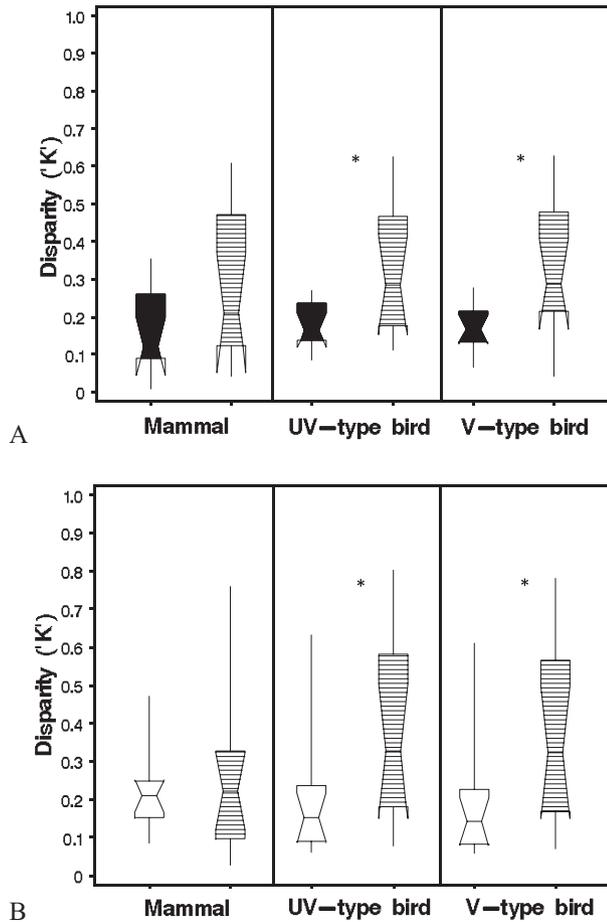


Figure 2. Chromatic crypsis (disparity values, 'K') in backgrounds that snakes selected for basking (solid colour) versus random backgrounds (hatched lines) for (A) dark *Thamnophis elegans*, and (B) light *T. elegans*. Shown are K-values from the perspective of three predator models: mammal (*Mustelo putorius furo*), ultraviolet (UV)-type bird (*Parus major*), and violet (V)-type bird (*Pavo cristatus*). Dark and light *T. elegans* were significantly more cryptic in terms of colour to the UV-type and V-type bird model. Significant differences between pairs are indicated by an asterisk (*). Each box represents 50% of the data, the median is indicated by notches, and lines extend to minimum and maximum values.

size (Luiselli, 1993), reproductive success (Andren & Nilson, 1981), and reproductive frequency (Capula & Luiselli, 1994). Differential patterns of intermorph survival between males and females have been shown, however, suggesting that the fitness costs associated with colour differ by sex (Forsman, 1995). Thus, an important extension to our work would be an analysis of how potential for crypsis interacts with other factors (e.g. thermoregulatory potential) to determine how basking sites are selected.

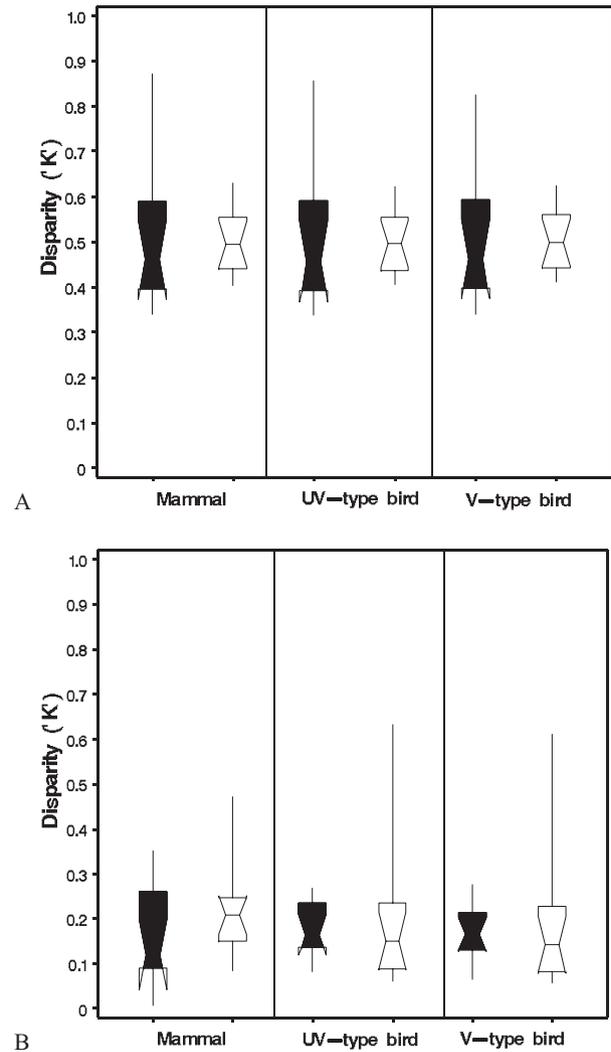


Figure 3. Comparison of (A) achromatic and (B) chromatic crypsis (disparity values, 'K') between dark *Thamnophis elegans*, and light *T. elegans* as seen by the mammal, ultraviolet (UV)-type bird, and violet (V)-type bird model. Dark and light *T. elegans* were equally achromatically and chromatically cryptic to the three predator models. Dark *T. elegans* = black boxes; light *T. elegans* = white boxes. Each box represents 50% of the data, the median is indicated by notches, and lines extend to the minimum and maximum values.

In the present study, crypsis was measured when snakes were found lying motionless in the field and presumably basking; in other words, at one point in time and in one microhabitat type. We also need to assess the potential role of crypsis in other activities undertaken by snakes and the degree to which coloration represents a compromise that confers differential crypsis in multiple habitat types (Merilaita *et al.*, 1999). Snakes should therefore be followed

closely over time and relocated on a regular basis to characterize potential colour-specific patterns of habitat use (Reinert, 1994). Research could expand on previous habitat work (Charland & Gregory, 1994) to quantify parameters such as snake and background colour, as well as the frequency and visual complexity of habitat types (Houston *et al.*, 2007). Ultimately, more detailed study could elucidate temporal and spatial patterns of crypsis and determine whether coloration of garter snakes represents a compromised or specialized strategy for crypsis or is more important for other functions.

What is interesting is that we did not detect any significant differences in crypsis, achromatic or chromatic, from the perspective of either the mammal or the two-bird predator models. Given the increased visual acuity and breadth of birds (Hart, 2001), we anticipated snake crypsis could evolve to that very strong selective pressure. It may be, however, that the strength of the selective pressure between birds and mammals in our site may be of similar intensity not to drive the evolution of crypsis in a particular direction (Gray & McKinnon, 2007). There may be also key differences in predator search behaviour that also may confound our results. For example, mammals may rely more or at least equally on olfactory and visual cues, whereas birds may be more reliant on visual cues, including the detection of prey movement (Jones, Pierce & Ward, 2007; Martin, 2007).

From the perspective of the human visual model, the results obtained in the present study were contrary to expectation. Although light *T. elegans* appear to be more difficult to detect in the field, the results suggest that light *T. elegans* were generally more conspicuous to humans in terms of colour. Detection difficulty in this case could be more related to differences in visual processing rather than visual reception functions (i.e. conspicuousness of colour and brightness). In vertebrates, visual processing mechanisms contain receptive fields that are differentially sensitive to lines and gratings, which affect the perception of differences in colour and pattern composition (Bruce, Green & Georgeson, 2003). For example, humans (Farmer & Taylor, 1980; Bohlin *et al.*, 2012) and birds (Dimitrova & Merilaita, 2010) have difficulty in detecting objects as the visual complexity of backgrounds, independent of background matching, increases. Thus, detection could perhaps be influenced by the complexity of dorsal colour patterns of snakes themselves [light *T. elegans* typically have a more complex dorsal pattern (stripes and blotches) than dark *T. elegans* (stripes only)] in the context of these habitats. It is becoming increasingly apparent that minimizing detection is not just a matter of background matching (Merilaita, 2003; Dimitrova & Merilaita, 2010) and future research needs to take

into account both visual and cognitive processes (Bond, 2007; Stevens, 2007) when studying the evolution of animal colours.

In addition to colour, visual signals also consist of complex combinations of form (Cuthill *et al.*, 2006; Lanridge, 2006) and movement (Hailman, 1977; Stevens, 2007), which can influence detection. Patterned animals may create a blurred image when moving and blend into the background as a result, referred to as the flicker-fusion effect (Pough, 1976; Ruxton *et al.*, 2004). If an animal moves faster than a predator's temporal acuity (i.e. ability to resolve differences between pattern elements), not only do patterns become difficult to distinguish but speed and direction of movement is also difficult to determine. To date, there is no strong experimental support for the flicker-fusion theory, although it has been suggested that flicker-fusion might be more effective in low-light environments where the visual temporal acuity of animals is often reduced (Jarvis *et al.*, 2002). Future work in this area should combine experimentation with the knowledge of visual image processing of predators (Bond, 2007; Stevens, 2007) using novel approaches, such as artificial neural networks (Merilaita, 2007).

Animals simultaneously use two perceptual channels (i.e. achromatic and chromatic cues) to discriminate the brightness and colour in visual signals. It has been suggested that some animals may preferentially rely on one type of cue to detect objects, which presumably assists with the discrimination of food items and the detection of conspecifics. For example, domestic chicks rely largely on changes in surface brightness to detect prey objects (Osorio *et al.*, 1999). In other work on lizards, the detection probability of anoline dewlaps increased when achromatic contrast was high (Persons *et al.*, 1999). Other animals, such as some groups of primates, use colour cues primarily for foraging tasks (Sumner & Mollon, 2000), whereas moths and passerines have been shown to use both chromatic and achromatic cues in object detection (Kelber, 2005; Stobbe *et al.*, 2009). It may be that both achromatic and chromatic cues are important in prey detection, although the relative importance of each at this point remains unknown. Currently, there is no general model that considers the relationship between both brightness and colour and the results presented here consider achromatic and chromatic crypsis separately. Consequently, the relative importance of differences in achromatic and chromatic crypsis observed between the different colour forms is uncertain. If there is an interaction between achromatic and chromatic cues, our data cannot reveal it because we consider these variables separately; this is a potentially important interaction that should be explored.

In the present study, crypsis was measured from a similar proportion of males, as well as nongravid and gravid females, for dark and light *T. elegans*. Although we sampled even numbers of both sexes and reproductive states between the colour forms, gravid females were disproportionately represented in the total sample. This is not necessarily problematic because colour dimorphism does not occur between males and females, nor does colour change with reproductive state in *T. elegans*. However, potential issues may arise if these groups either use microhabitats differently or are active at different times of the day. For example, individuals that are slower and therefore less likely to evade predation, such as gravid females (Shine, 1980), or are less likely to survive a predation attempt, such as small juvenile snakes (Mushinsky & Miller, 1993), may select habitats that are unfavourable for crypsis but favourable for other factors such as the number and proximity of retreat sites. Furthermore, Endler (1993) demonstrated that light quality varies with weather conditions, forest structure, and time of day, which can influence the appearance of animals in these environments. Thus, if small changes in habitat use are associated with either sex or reproductive state, then future research of this type should either focus on one group, or increase overall sample sizes to capture these potential differences. The rigour of future analyses could be increased by including sex and reproductive state as potential factors.

In retrospect, our approach to measuring backgrounds could have been improved by taking into account the spatial arrangement of different elements of the background. That is, a background with leaf litter, for example, all clumped in one place is very different from one in which the same amount of leaf litter is spread evenly over the entire space measured. Background complexity, in conjunction with the regularity of the prey's pattern, can significantly affect crypsis (Bond & Kamil, 2006; Dimitrova & Merilaita, 2012). Endler (2012) provides an important framework for future studies of crypsis (and other colour-related phenomena), in which the adjacency of different pattern elements, and not just their proportions, is measured. Thus, the present study is simply a first step in the study of crypsis in these snakes; more detailed data collection and analysis taking pattern complexity and arrangement into account might well modify some of our conclusions.

A final vexing issue concerns how snakes that lack colour vision could use colour as part of their background matching strategy. This is an important question for which we have no answer, although we note the precedent of the European cuttlefish, *Sepia officinalis*, which employs highly effective colour matching against its background, relative to the visual systems

of potential predators, despite being colour blind itself (Chiao *et al.*, 2011).

Background matching is typically evoked as a mechanism for animal crypsis. It is becoming increasingly apparent, however, that strategies other than background matching may be involved in minimizing animal conspicuousness (Schaefer & Stobbe, 2006; Stevens, 2007). For example, disruptive coloration operates by obscuring the true form of an animal through the use of strongly contrasting patterns to distract the attention of the viewer from the outline and contour of the animal (Cott, 1940) and has been shown to minimize detection from predators (Merilaita, 1998). Whether or not these mechanisms operate in an alternative or interrelated manner remains to be determined, although disruptive coloration has been shown to increase crypsis in natural (Merilaita, 1998; Chiao & Hanlon, 2001) and experimental systems (Cuthill *et al.*, 2005; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006). Although *T. elegans* exhibits variation in colour patterns, identifying if and how pattern contributes to individual crypsis remains to be tested. Recent work carried out by Dimitrova & Merilaita (2012) suggests that the spatial regularity of prey patterns can compromise crypsis. Mechanisms by which crypsis is achieved are still unclear and future work should focus on the development of objective approaches to quantify spatial elements and novel ways to consider the contribution of both colour and pattern into studies of crypsis.

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