



Original Article

Body size and evolution of motion dazzle coloration in lizards

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“Motion dazzle” patterns are a form of defensive coloration suggested to prevent successful capture during motion by causing predators to misjudge the direction or speed of prey movement. Several studies have found results supporting this idea but little is known about the factors that favor the evolution of these antipredator colorations. A recent experimental study has suggested that the longitudinal striped patterns on the body of lizards can redirect attacks to the tail via the motion dazzle effect. Using a virtual predation experiment with humans and a phylogenetic comparative analysis, we show that evolution of longitudinal striped coloration is associated with prey size. Experiments showed that longitudinal stripes located at the anterior reduced lethal attacks (i.e., attacks directed to the *anterior* and *centre*) but this benefit was greater for shorter prey. Our comparative analysis revealed a negative association between stripe occurrence and body length but no association between stripes and body width. Overall, our results suggest that the dazzle effect produced by stripes is more advantageous in shorter lizards than in longer ones and that the error induced by stripes might be distributed along the axis parallel to the prey trajectory. We discuss reasons why dazzle coloration could be associated with evolution of smaller body size in animals.

Key words: antipredator adaption, lizards, motion dazzle, prey size, redirection, stripes.

INTRODUCTION

Animals exhibit a tremendous diversity of color patterns, and research over a century has identified numerous ways in which animals use these patterns to reduce predation (Thayer 1909; Cott 1940; Ruxton et al. 2004). The most common strategies include camouflage through background matching (Stevens and Merilaita 2009), masquerade (Skelhorn et al. 2010), disruptive coloration (Cuthill et al. 2005), and countershading (Rowland et al. 2008), all of which decrease the probability of detection or recognition, and are most effective when the animal remains stationary (Stevens et al. 2011; Hall et al. 2013). However, animals need to move for many reasons including foraging and searching for mates, and the probability of detection by predators is higher when the prey is in motion (Martel and Dill 1995; Hailman 1977; Cooper et al. 2008; Ioannou and Krause 2009). Yet, we are only now beginning to understand how certain color patterns can protect prey during motion (Stevens et al. 2008; Stevens et al. 2011; Pike 2015; Umeton et al. 2017).

Thayer (1909) hypothesized that certain high contrast repetitive color patterns (stripes, bands, and zigzags) now termed

“motion dazzle” patterns, can inhibit capture by disrupting predators’ perception of trajectory or speed of a moving prey (Thayer 1909). This form of protective color patterns are thus expected to be found in actively moving animals where the benefit of the lowered probability of successful capture outweighs the cost of enhanced detectability (Stevens et al. 2011). Several recent studies utilizing humans attacking virtual patterned prey on a computer screen have found support for the idea that motion dazzle coloration can reduce predation when the prey is moving (Stevens et al. 2008; von Helversen et al. 2013; Hogan et al. 2016). Experimental studies have examined aspects such as varying speed (Hogan et al. 2017), internal contrast (Scott-Samuel et al. 2011; Hogan et al. 2016), and orientation of the patterns (Hughes et al. 2015) on the effectiveness of dazzle markings. Yet, we lack an understanding of why certain species rely on motion dazzle coloration, while others rely on camouflage as primary defensive strategy. We also know little about the morphological or life-history traits of prey animals that could influence the evolution of dazzle markings and their effectiveness.

One such trait which can affect the evolution of dazzle patterns could be prey body size. Since large animals are inherently more conspicuous, signals which require conspicuousness are expected to be favored in larger animals (Hagman and Forsman 2003; Hossie

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et al. 2015) and conversely, evolution of cryptic coloration might be favored in smaller animals (Karpestam et al. 2014). On the other hand, a larger prey is also more easily caught during motion compared to smaller ones (Van Damme and Van Dooren 1999; Clemente and Wilson 2015). Therefore, dazzle patterns may not be effective for larger prey. Thus, the benefit of conspicuous protective patterns such as dazzle markings which operate in motion may depend on the body size of the animal, although this has not been tested.

Recently, Murali and Kodandaramaiah (2016) expanded the motion dazzle hypothesis by proposing the *redirection hypothesis*, where dazzle coloration on the anterior part of a moving prey animal can redirect attempted strikes to less vulnerable posterior parts (Murali and Kodandaramaiah 2016). Since high contrast longitudinal striped color patterns are commonly found on the body (i.e., trunk) of lizards, they proposed that stripes on lizards might function by redirecting attacks to the expendable tail. A recent comparative analysis also supports the idea that stripes in lizards may work in motion against predation (Halperin et al. 2016).

Interestingly, longitudinal stripes in many lizard species are present only in juveniles (e.g., *Acanthodactylus beershebensis* and *Plestiodon laticeps*; Taylor 1935; Hawlena et al. 2006) and this ontogenic loss of stripes appears to be restricted to species with longer body length (Taylor 1935). Moreover, in many lizard species that are polymorphic with respect to presence or absence of stripes, striped individuals tend to be smaller (*Podarcis hispanicus*, Ortega et al. 2015; *Scelarcis perspicillata*, Carretero et al. 2006). In the skink *Plestiodon latiscutatus*, individuals of populations with reduced predation pressure become larger as well as lose stripes (Brandley et al. 2014). The above studies thus suggest that the functioning of longitudinal stripes in lizards might be dependent on body size.

We use 2 approaches to address the role of body size in the functioning of longitudinal stripes in attack redirection via the motion dazzle effect. First, using a phylogenetic comparative analysis, we examined 1) the association between presence of striped coloration and 3 parameters of prey size - body length (Snout Vent Length: SVL), body width (BW), and tail length (TL). Second, to address the question of size-dependence empirically, we adopted a virtual predation experiment to test whether 2) the redirective effect of stripes (i.e., misdirection of attempted anterior attacks to the posterior due to the presence of anterior striped patterning in a moving prey) becomes less pronounced with increasing body size. We designed prey differing in color pattern, overall size (area) and length, to distinguish between the effects of body width and length on the functioning of stripes.

METHODS

Influence of prey size on presence of striped body coloration

Information on phylogenetic relationships among lizards used in this study was taken from the species-level time-calibrated phylogeny of 4162 Squamate reptiles representing all lizard families including Amphisbaenia (Zheng and Wiens 2016). Although it is usually ideal to analyze monophyletic groups in comparative analyses such as those used in this study, it is common practice to exclude morphologically and ecologically derived taxa when their inclusion may obscure understanding of selective forces (Meiri 2008). For instance, bats and marine mammals have not been considered

in comparative studies on mammals (e.g., Brown and Maurer 1989; Fritz et al. 2009), tetrapods have been excluded in studies on fishes (Olden et al. 2007) and marine species have been omitted from studies on birds (Orme et al. 2006). Although snakes are likely nested within lizards (Zheng and Wiens 2016, but see Zhou et al. 2006 who show that snakes are sister to lizards), comparative studies on lizards (e.g., Meiri 2010; Halperin et al. 2016; Gainsbury and Meiri 2017) have not included snakes because of their distinctness from lizards. We have similarly excluded snakes in our analysis, as they are not relevant to our hypotheses, which are explicitly based on the redirection of attacks by anterior stripes towards plainly colored tails. Following a previous study (Halperin et al. 2016), we also eliminated the below families from the analysis based on specific reasons. Most species in the family Gekkonidae are nocturnal, which are not directly relevant to the hypotheses under consideration. We also excluded chameleons (Chamaeleonidae), which are known to change color rapidly based on the signaling context (Ligon and McGraw 2013).

Color pattern judgment is dependent on many factors, including the receiver's visual system and environmental factors (Endler 1991, 1992). Despite this, pattern classification by human observers is commonly employed in comparative studies involving body patterns of animals (Kodandaramaiah 2009; Allen et al. 2013; Kelley et al. 2013; Arbuckle and Speed 2015). Although it would be ideal to develop a computer vision based tool to categorize color patterns (e.g., see Stoddard et al. 2014), this requires photographic images taken in controlled conditions, which is not feasible for the current study given the large scale. We acknowledge that pattern classification by humans can have subjective bias but we employed multiple strategies to ensure that our pattern categorization was robust. First, pattern classification was performed by 3 volunteers all of whom were naïve to the hypotheses and were recruited opportunistically. Volunteers were first year undergraduate students from the same institute. Each volunteer was given written instructions for classifying the color patterns. The classification task was performed in a custom written graphical user interface (Supplementary Figure S5) in MATLAB R2015a (Mathworks).

We included a species in the analysis only if 1) at least 3 images were available for the species, and 2) information was available on the phylogenetic placement of the species in Zheng and Wiens (2016). Images were collected from online sources including The Reptile Database (<http://reptile-database.reptarium.cz/>), Arkive (<http://www.arkive.org/>), The Australian Reptile Online Database (<http://www.arod.com.au/arod/>), and Google (www.google.com) search images. There were a total of 7907 images, averaging 4.840 per species. Volunteers viewed all available images per species simultaneously on a single window and recorded their response. Species in which adults are polymorphic with respect to presence of stripes, or in which stripes occur only at particular life stages, were coded as striped. We further sampled a subset of species ($n = 100$) from our main dataset randomly and asked 10 more volunteers to do the pattern classification, this dataset was used to check the consistency among volunteers. Volunteers were recruited as in the previous case.

Stripes were classified as present (either laterally or dorsally positioned) or absent (Supplementary Figure S4a). A species was considered striped if the stripes were clearly visible and occurred from the tip of the snout to the tail base. Species with red or blue lateral stripes ($n = 2$; *Carlia pectoralis* and *C. tetradactyla*) were not included in the analysis, as these stripes are found only in males and are known to function as sexual signals (Pérez i de Lanuza

and Font 2016). We excluded 78 more species for which at least 2 volunteers reported that they were unable to classify the body pattern. The final coloration dataset had a total of 1634 species. Since there was strong concordance among the 3 volunteers for the complete dataset (Fleiss' Kappa index of reliability = 0.958) (McHugh 2012) as well as among the ten volunteers for the subset of 100 species (Fleiss' Kappa index of reliability = 0.942), stripe presence-absence data for each species was randomly taken from the responses of one of the 3 volunteers. For the given 1634 species, each volunteer classified 430, 418 and 436 species of lizards to be striped respectively, out of which 31 were classified to have stripes completely covering both body and tail (List of genera given in Supplementary Text S1).

Maximum Snout to Vent Length (SVL, a measure of body length) data for each species were compiled from various published sources (Meiri 2008; Feldman et al. 2016). Since body width (BW) data was unavailable for most lizard species, we estimated this using information on body mass and SVL. This was done by assuming the lizard body to be a cylinder, and therefore the diameter to be the width of the body. Lizard body mass (mean) information for different species of lizards was obtained from a previous study (Meiri 2010). Body width information was calculated using the equation below, where ρ represents the volumetric mass density, which was assumed to be 1 g/mL.

$$\text{Body width (BW)} = 2\sqrt{(\text{mass} / (\pi * \text{SVL} * \rho))}$$

To validate the approach above, we performed a linear regression analysis between BW information available from literature and estimated values (Supplementary materials Section A (i)). A strong positive relationship between observed and estimated body widths (linear regression: t -value = 5.632, $P < 0.0001$, $R^2 = 0.5827$; Supplementary Figure S1) indicates the validity of the method employed. The calculated BW values were used for further analyses. Tail Length (TL) data for 170 species was obtained from (Fleming et al. 2013).

All analyses were performed in RStudio v 3.2.3 "Another canoe" (R Foundation for Statistical Computing, www.R-project.org). The relationship between body size and presence of longitudinal stripes was analyzed by Phylogenetic Generalized Least Squares regression (PGLS) using the packages *geiger* (Harmon et al. 2008) and *nlme* (Pinheiro et al. 2014). Log transformed SVL, log transformed BW and the log ratio of TL to SVL values were used as the response variable against presence or absence of striped coloration as a predictor variable in separate models with 1475, 537, and 170 species for the analyses on body size, body width and tail length datasets. The data were fitted with the Ornstein-Uhlenbeck, Brownian motion and Pagel's Lambda models of evolution, and the best fit model was then chosen based on Akaike information Criterion values (AIC).

The estimated log BW was strongly correlated to log SVL (Supplementary material Figure S2). To examine the independent association of body width on coloration, we corrected BW for SVL using the allometric exponent equation $\log [BW/SVL^b]$ following (Blomberg et al. 2003). The exponent b is slope of the regression line obtained from a PGLS analysis between log BW against log SVL (Supplementary section A(ii)). We then tested for an association between SVL-corrected-BW and body coloration using the PGLS procedure.

Virtual predation experiment: effect of prey size on the redirective effect

The experiment involved a SCRATCH (2014) program adapted from (Murali and Kodandaramaiah 2016). In brief, the experiment involved human participants ($n = 77$) attacking moving prey on a 52×38 cm touchscreen (ca. $43.603^\circ \times 32.558^\circ$) with a refresh rate of 60 Hz. Participants signed an informed consent form prepared in accordance with the Declaration of Helsinki and the experiment was approved by Indian Institute of Science Education and Research Thiruvananthapuram Ethics committee. The achromatic prey had black and white (RGB: 255,255,255) longitudinal striped or blotched patterns (Supplementary Figure S4b) on the anterior half (the striped pattern approximating stripes on the head and trunk of lizards, and the blotched patterns serving as a control), and a black posterior. The direction of motion was parallel to stripe orientation (Supplementary Figure S4b). We recorded the number of attacks to the anterior half (*anterior*), *centre* (touching both *anterior* and *posterior* half), and *posterior* half (*posterior*). To differentiate which half of the prey was attacked, the *anterior* and *posterior* halves were coded differently as black (RGB: 0,0,0) and "greyish-black" (RGB: 20,20,20) respectively in half of the samples (*Set 1*), while the colors were switched in the other half (*Set 2*). We used prey of 3 dimensions 1) 1×2 cm (0.881×1.763 degrees) 2) 2×2 cm (1.763×1.763 degrees), and 3) 1×4 cm (0.881×3.525 degrees), to test the influence of prey size on the location of attacks to the prey. Each volunteer was presented all prey sequentially, in a random order. The prey entered the screen from one of the 4 edges (chosen randomly), and moved across the screen in an erratic manner with an approximate speed of ca. 17.4390 cm/s (15.281 visual angles/s). Participants were instructed to "attack" (i.e., touch) the *anterior* half of the moving prey, and were allowed one minute per prey type. The prey disappeared if it was attacked or if it reached another edge, and re-entered from another randomly chosen edge (Refer to Supplementary Material Section C for more details).

The effect of prey length on the number of lethal attacks (i.e., number of attacks to *anterior* and *centre*) was tested by comparing 1×2 or 2×2 with 1×4 . We assume that the number of lethal attacks is negatively correlated to the redirective effect, as has been shown in (Murali and Kodandaramaiah 2016) who used similar prey as in the current experiment. If the redirective effect is dependent on length of the prey, then the number of lethal attacks should be higher for 1×4 compared to 2×2 or 1×2 . The comparison between 1×4 and 2×2 allows us to infer the relative importance of body length over total area of the prey.

The data were analyzed using Generalized Linear Mixed-Models (GLMM) using the function *glmer* in the *lme4* package (Bates et al. 2014). The dataset was analyzed with counts of lethal and total number of attacks (i.e., number of attacks to *anterior* + *centre* + *posterior*) as the Poisson dependent variable. Unlike Murali and kodandaramaiah (2016) we did not use the proportion of lethal to nonlethal attacks in our analysis because the total number of attacks differed across prey patterns (Figure 3c). In all models, prey pattern, prey size and presentation order were included as fixed effect terms, while subject ID and *Set* were included as random intercept terms. The best model was selected based on backward stepwise elimination of nonsignificant terms. The global model contained all individual main effects and 2-way interaction terms. We did not include a 3-way interaction between prey size, pattern, and presentation order as the model failed to converge when this

term was included. Tables containing AIC values for model selection for each dependent variable are given in Supplementary materials Tables S7–S9.

The pairwise significance of the interaction term was estimated using the *testInteractions* function from the *phia* package (De Rosario-Martinez 2013). Tukey's post hoc multiple contrasts (HSD: honest significant difference tests) were done using the *multcomp* package to test the significance of individual factors with multiple levels (Bretz et al. 2010). We present estimated slopes with 95% confidence interval from the best fit model as a measure of effect size (Nakagawa and Cuthill 2007). The 1×4 prey was chosen as the reference level in all analyses.

RESULTS

Influence of body size on evolution of striped body coloration

In the PGLS analysis testing the relationship between SVL and presence of stripes, Pagel's lambda model of evolutionary change ($\lambda = 0.9793$) resulted in a better fit than the model assuming Brownian motion ($\Delta\text{AIC} = 227.9246$) or the Ornstein–Uhlenbeck model ($\Delta\text{AIC} = 174.8166$). Longitudinal stripes were associated with shorter body length, as indicated by a significant negative relationship between maximum SVL and presence of striped coloration ($t = -4.1586$; $\text{df} = 1473$; $P < 0.0001$; Supplementary Table S4a; Figure 1; Figure 2a).

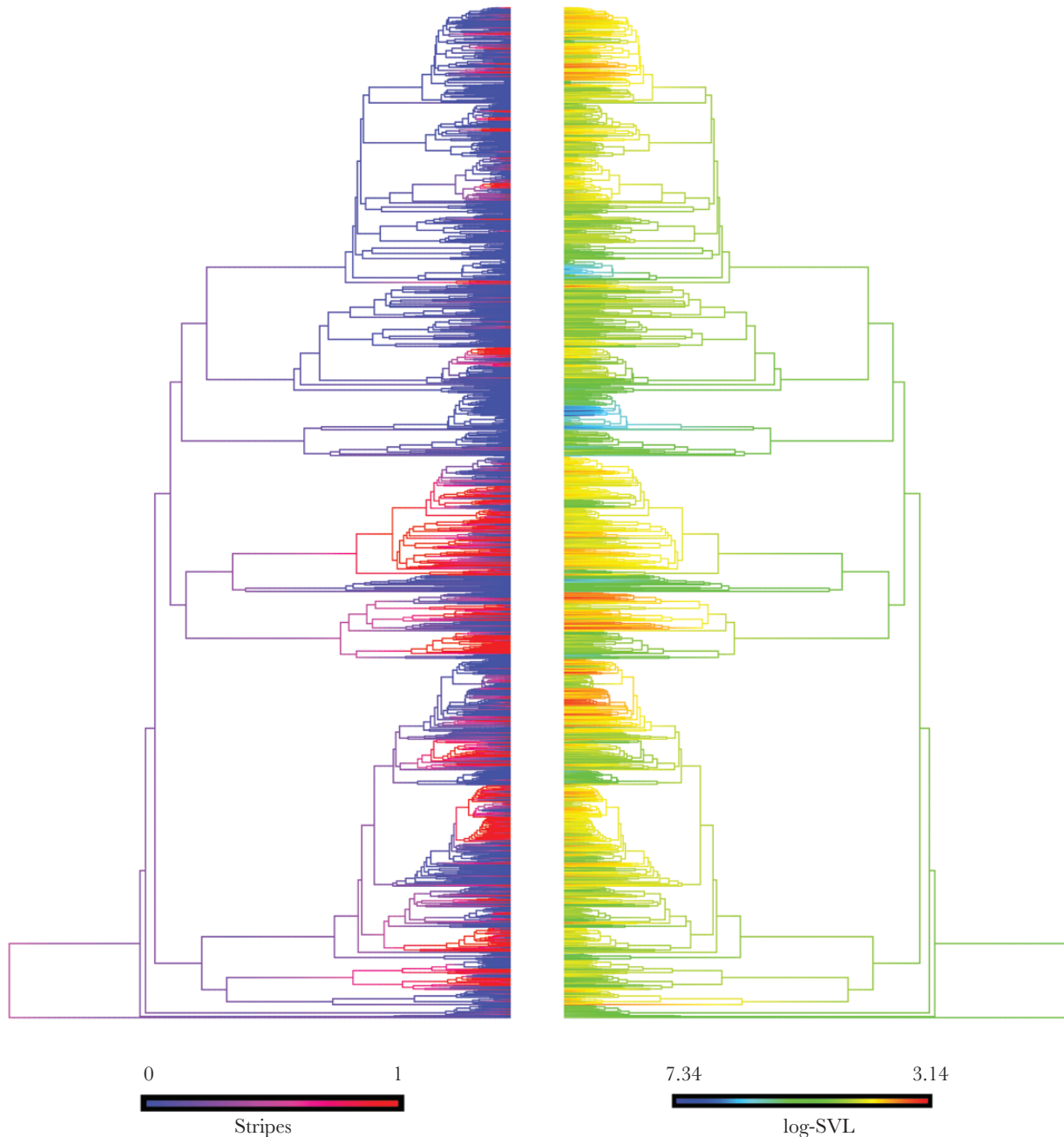


Figure 1

Left: Ancestral states of striped coloration estimated from stochastic character mapping against Right: Ancestral states of body length (log transformed SVL) in lizards.

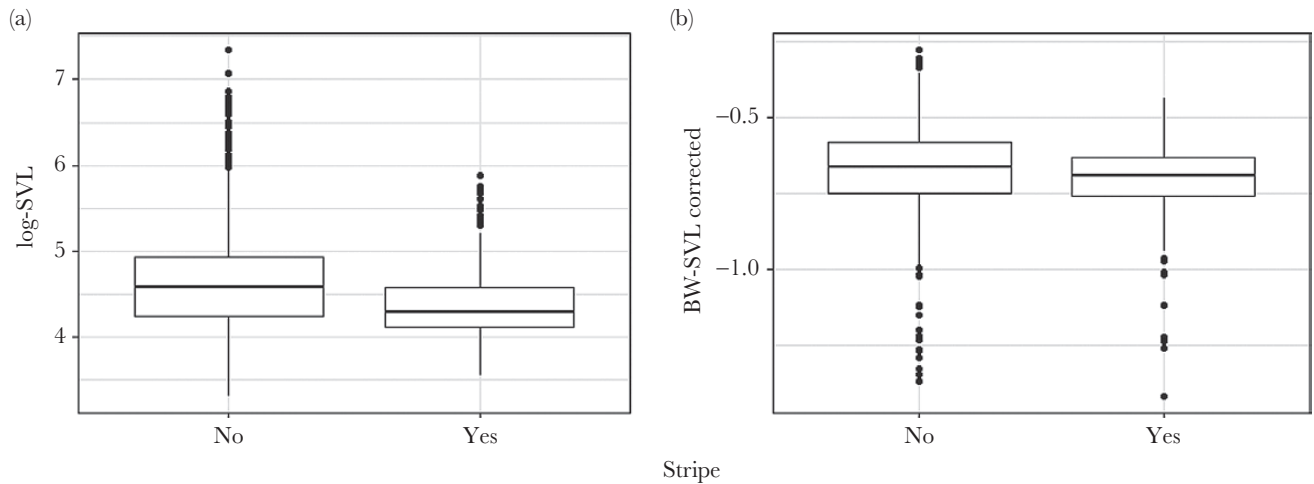


Figure 2

Boxplots depicting the median, interquartile range of log transformed (a) Snout to Vent Length (SVL) ($P < 0.0001$) and (b) SVL corrected Body Width (BW) ($P = 0.1016$) for species with and without striped coloration. Statistics are presented in results section.

Stripes are more likely to be present in slender lizards than in broad ones ($t = -4.1586$; $df = 535$; $P < 0.0001$; Supplementary Table S4b) when fitted with Pagel's lambda model ($\lambda = 0.9281$). The effect was nonsignificant after correcting for SVL ($t = -1.6398$; $df = 537$; $P = 0.1016$; Figure 2b; Supplementary Table S4c). The ratio of log-TL to SVL was significantly greater for striped species ($t = 3.6952$; $df = 170$; $P < 0.0001$; Supplementary Table S4d), when fitted using a PGLS with Ornstein–Uhlenbeck model.

Virtual predation experiment: effect of body size on capture success

The number of lethal attacks (i.e., attacks directed to *anterior* and *centre*) was influenced by both prey pattern (LRT: $df = 1$, $\chi^2 = 63.769$, $P < 0.0001$; Figure 3a) and size (LRT: $df = 2$, $\chi^2 = 179.02$, $P < 0.0001$; Figure 3a). Prey with stripes received fewer lethal attacks compared to prey with blotched patterns (GLMM: $z = -10.45$; $P < 0.0001$), for all prey sizes. Irrespective of prey pattern, lethal attacks increased as the prey size increased: 1×2 versus 2×2 (Tukey HSD: $z = 8.452$; $P < 0.001$) and 1×2 versus 1×4 (Tukey HSD: $z = 5.145$; $P < 0.001$).

As predicted, the interaction between prey size and pattern was significant (LRT: $df = 2$, $\chi^2 = 54.232$, $P < 0.0001$). The benefit of striped pattern in relation to blotched patterns in terms of lethal attacks was significantly lesser in the longer prey (1×4) when compared to that in 1×2 (post-hoc chisq test: $df = 1$, $\chi^2 = 44.7273$, $P < 0.0001$; Figure 3a) and 2×2 (post-hoc chisq test: $df = 1$, $\chi^2 = 31.7080$, $P < 0.0001$; Figure 3a). This result is also depicted as estimated slopes in Figure 3b. However, there was no significant interaction effect across 1×2 and 2×2 with prey pattern (post-hoc chisq test: $df = 1$, $\chi^2 = 2.9293$, $P = 0.0869$; Figure 3a), indicating that the benefit of stripes did not depend on width (See also estimated slopes: Figure 3b). Prey presentation order had no effect on the number of lethal attacks, and did not interact significantly with prey pattern or size (Supplementary materials Table S7).

The total number of attacks (i.e., attacks directed to *anterior*, *centre*, and *posterior* combined) was significantly affected by both prey pattern (LRT: $df = 1$, $\chi^2 = 30.45$, $P < 0.0001$; Figure 3c) and size (LRT: $df = 1$, $\chi^2 = 204.7199$, $P < 0.0001$; Figure 3c). Irrespective of prey size, striped prey received fewer total attacks compared to prey with blotched patterns (GLMM: $z = -3.94$; $P < 0.0001$).

The total number of attacks was lesser for smaller prey irrespective of pattern; 1×2 versus 2×2 (Tukey HSD: $z = 4.825$; $P < 0.001$) and 1×2 versus 1×4 (Tukey HSD: $z = 3.186$; $P < 0.0001$).

We found a significant interaction between prey pattern and size (LRT: $df = 2$, $\chi^2 = 43.5257$, $P < 0.0001$) on total number of attacks. The benefit of striped pattern in relation to blotched patterns in terms of total attacks was significantly lesser in the longer prey (1×4) when compared to that of 1×2 (post-hoc chisq test: $df = 1$, $\chi^2 = 35.4383$, $P < 0.0001$; Figure 3c) and 2×2 (post-hoc chisq test: $df = 1$, $\chi^2 = 295.1440$, $P < 0.0001$; Figure 3c). However, the total attacks were not significantly influenced by an interaction between 1×2 and 2×2 with prey pattern (post-hoc chisq test: $df = 1$, $\chi^2 = 1.126$, $P = 0.2886$; Figure 3c, d). We found no effect of presentation order on total attacks. However, presentation order interacted significantly with prey size and pattern (Supplementary materials Table S8).

The results on number of nonlethal attacks (i.e., number of attacks to *posterior*) are presented in Supplementary materials Section C (Figure S3 and Table S9).

DISCUSSION

By employing both comparative and experimental approaches, we found clear evidence for the role of prey size in the protective functioning of motion dazzle patterning. The virtual predation experiment indicates that stripes accord a benefit in terms of lowering the lethal attacks (i.e., *anterior* and *centre*) when compared to blotched patterns, similar to that found in Murali and Kodandaramaiah (2016). This benefit decreased as the length increased, but was not affected by change in prey width. The results imply that the error (i.e., redirection of attempted anterior attacks to the posterior due to the presence of anterior striped patterning) induced by stripes is distributed along the axis parallel to prey trajectory.

As a result of the redirective effect of stripes, attacks may be redirected to the posterior part or miss the prey entirely, the probability of the latter being greater in shorter prey. Therefore, shorter striped prey has the additional advantage of attacks being deflected away from both the body and tail. Indeed, when considering the total number of attacks (i.e., *anterior*, *centre*, and *posterior* combined), stripes benefitted only the shorter prey types (i.e., 1×2 and 2×2 ; Figure 3c), whereas there was no difference between striped and

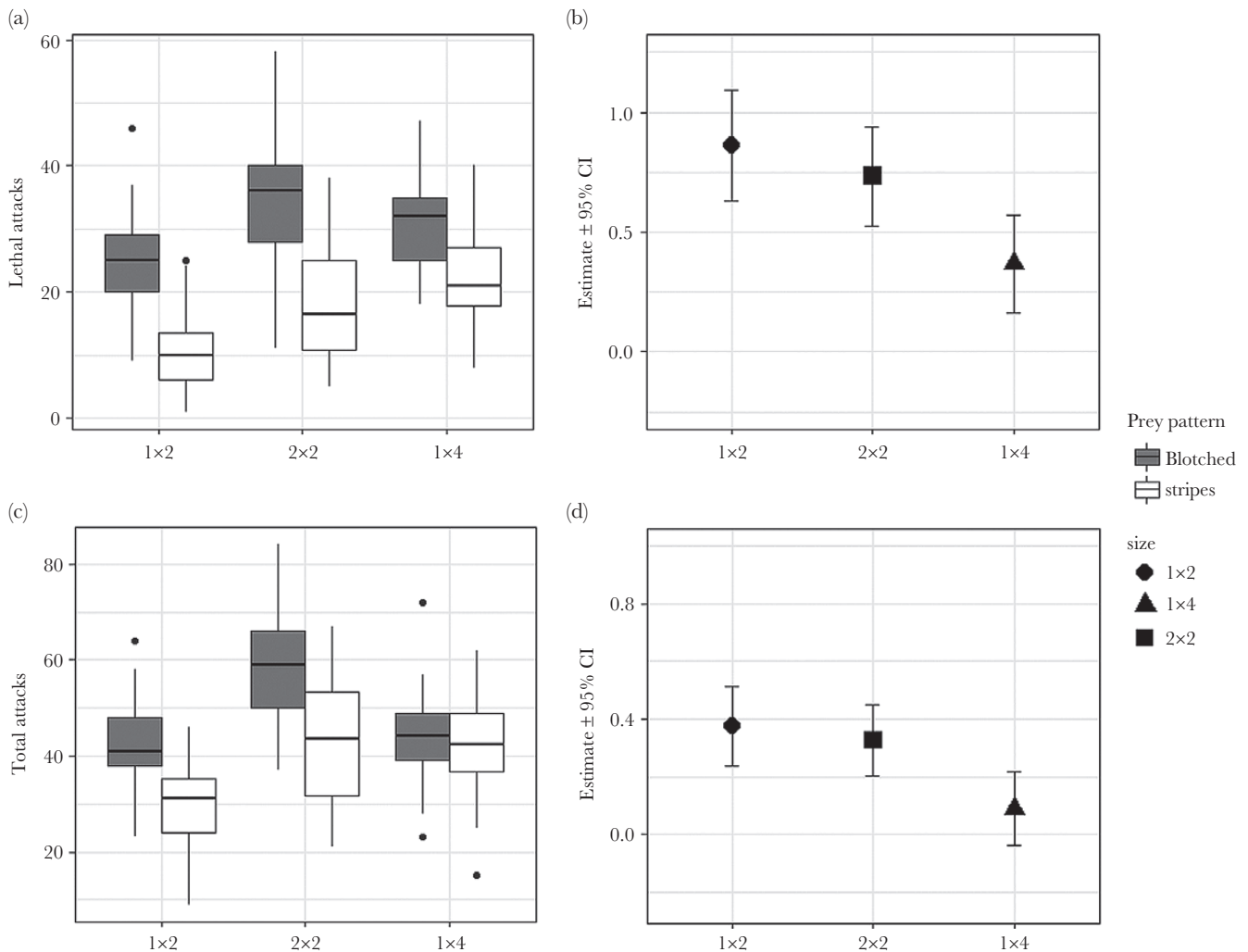


Figure 3

Boxplots depicting the median and interquartile range of (a) lethal attacks (anterior and centre) (c) total attacks (anterior, centre and posterior combined). Effect size represented as estimate \pm 95% C.I extracted from the best fit model for (b) lethal attacks (anterior and centre) and (d) total attacks (anterior, centre and posterior combined). Note that the effect size reduces as prey size increases.

randomly patterned 1×4 prey. This may be important in terms of attacks directed by predators pursuing terrestrially (mammals or snakes) than aerial ones (like birds), where a missed attack would give enough time for the lizards to flee to the shelter and prevent subsequent encounter.

The comparative analysis revealed a significant negative relationship between presence of stripes and body length (SVL; Figure 2a), and therefore corroborates the results of the predation experiment. We did not find an association between body width and striped coloration after correcting for SVL (Figure 2b). This suggests that body length is more important than body width for the effective functioning of stripes, and this is also corroborated by the predation experiment where the 2×2 and 1×2 prey were equally protected.

Interestingly, our analysis also revealed a positive association between presence of stripes and TL-to-SVL ratio. As the error induced by stripes is distributed parallel to the prey trajectory, it would be advantageous to have a smaller body with a relatively longer tail, which will result in a higher chance of the predator attacking the tail. Alternatively, stripes on the body may hamper trackability during motion (Hogan et al. 2016; see

section *Why do lizards have stripes only on head and trunk* in Murali and Kodandaramaiah 2016) and therefore a long tail may serve as a better trackable feature for the predators. This is supported by the fact that the number of attacks to posterior is greater in prey of size 1×4 compared to 2×2 and 1×2 (Supplementary Figure S3). Thus, the association between stripes and TL-to-SVL ratio further strengthens the idea that striped body coloration in lizards might function by redirecting attacks to the tail, as proposed earlier (Murali and Kodandaramaiah 2016).

Similar to ours, a phylogenetic comparative study (Allen et al. 2013) found longitudinally striped snakes to be shorter than snakes with other patterns. One critical factor essential for animals to benefit from attack redirection is detachable posterior parts, and in lizards, it seems that evolution of striped body is correlated to the presence of caudal autotomy (Murali et al. 2017). Since stripes run along the entire length in snakes (Allen et al. 2013) and caudal autotomy is absent in these animals (Arnold 1984), the dazzle effect of these stripes may help entirely avoid capture (Stevens et al. 2008), rather than redirecting attacks to the tail as in lizards. Therefore, the results from Allen and colleagues (Allen et al. 2013)

support the notion that the effectiveness of longitudinal stripes in reducing the overall capture might also depend on body size.

Some experimental studies have reported no effect of longitudinal striped coloration (stripes running along the entire prey) on capture success (e.g., von Helversen et al. 2013) and this perhaps could be related to the size of prey used in the trials. Indeed, a comparison of visual angles of prey used suggests that studies which have reported a significant effect of longitudinal stripes have tended to use smaller prey (see comparison of visual angles; Supplementary Table S11). However, it remains unclear whether the evolution of other forms of dazzle patterns (stripes diagonal or orthogonal to prey movement) depends on body size. We suggest that future experimental studies on dazzle coloration should critically consider prey size as an important factor in designing experiments.

Why are stripes more beneficial to smaller prey?

We propose the following explanations, not necessarily mutually exclusive, for why stripes may not be beneficial to bigger animals.

1. Larger prey animals are more easily detected when stationary (Mänd et al. 2007; Karpeštam et al. 2014), and hence striped patterning may not be favored in larger individuals if the cost of increased detectability outweighs probability of prey escape in motion (Stevens et al. 2011). Thus, stripes may have the same benefit for shorter and longer prey but have a higher cost in longer prey.
2. Alternately, the cost of stripes, increased conspicuousness for instance, may be the same for longer and shorter prey, but for the shorter prey the costs may be outweighed by benefit accorded by redirection, while the costs may outweigh the benefit in longer prey. Indeed, the virtual predation experiment suggests that benefit of stripes is greater for shorter prey (Figure 3).
3. High contrast striped patterns are known to alter the perceived speed (von Helversen et al. 2013; Hall et al. 2016; Murali and Kodandaramaiah 2016), and as larger objects are known to lower the perceived speed (Brown 1931), it is possible that increasing body size can induce an antagonistic effect on the manipulation of perceived speed by stripes.
4. Erratic prey movement has been suggested to be the key factor for the confusion effect created by dazzle coloration (Hogan, Cuthill, et al. 2016). Hence, selection might favor evolution of dazzle coloration in smaller prey, which have greater maneuverability (Webb 1976; Witter et al. 1994) (i.e., ability to suddenly change escape the trajectory).
5. Smaller size is associated with higher sprint speed, at least in reptiles (Huey and Hertz 1982; Bauwens et al. 1995). Evidence suggests that motion dazzle patterns might create higher targeting error in more rapidly moving prey (Stevens et al. 2008; von Helversen et al. 2013) and therefore selection might favor evolution of striped coloration in smaller species.

Overall, our results add support to the long-standing idea that antipredator coloration can be strongly influenced by body size (Hagman and Forsman 2003; Mänd et al. 2007; Hossie et al. 2015). In general, we propose that motion dazzle and other forms of protective color patterns functioning in motion have a strong tendency to evolve in smaller animals. While evidence so far suggests that longitudinal stripes are associated with smaller body size in lizards (current study) and snakes (Allen et al. 2013), it remains to be seen if this association also exists for other forms of protective coloration operating in motion, for instance flicker fusion (Umeton et al. 2017) or interference coloration (Pike 2015).

SUPPLEMENTARY MATERIAL

Supplementary materials are available at *Behavioral Ecology* online.

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Conflict of interest: None declared.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Murali and Kodandaramaiah (2017).

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REFERENCES

- Allen WL, Baddeley R, Scott-Samuel NE, and Cuthill IC. 2013. The evolution and function of pattern diversity in snakes. *Behav Ecol.* 24:1237–1250.
- Arbuckle K, Speed MP. 2015. Antipredator defenses predict diversification rates. *Proc Natl Acad Sci USA.* 112:13597–13602.
- Arnold EN. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. *J Nat Hist.* 18:127–169.
- Bates D, Maechler M, Bolker B, Walker S (2015). Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw.* 67: 1–48.
- Bauwens D, Garland T Jr, Castilla AM, Van Damme R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution.* 49:848–863.
- Blomberg SP, Garland T Jr, Ives AR, Crespi B. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution.* 57:717–745.
- Brandley MC, Kuriyama T, Hasegawa M. 2014. Snake and bird predation drive the repeated convergent evolution of correlated life history traits and phenotype in the Izu Island Scincid Lizard (*Plestiodon Latiscutatus*). *PLoS One.* 9:e92233.
- Bretz F, Hothorn T, Westfall P. 2010. *Multiple comparisons using R*. Boca Raton, FL: CRC Press.
- Brown JH, Maurer BA. 1989. Macroecology: the division of food and space among species on continents. *Science.* 243:1145.
- Brown JF. 1931. The visual perception of velocity. *Psychologische Forschung.* 14:199–232.
- Carretero MA, Vasconcelos R, Fonseca M, Kaliontzopoulou A, Brito JC, Harris DJ, Perera A. 2006. Escape tactics of two syntopic forms of the lacerta perspicillata complex with different colour patterns. *Can J Zool.* 84:1594–1603.
- Clemente CJ, Wilson RS. 2015. Speed and maneuverability jointly determine escape success: exploring the functional bases of escape performance using simulated games. *Behav Ecol.* 27:45–54.
- Cooper WE, Caldwell JP, Vitt IJ. 2008. Effective crypsis and its maintenance by immobility in Craugastor frogs. *Copeia.* 2008:527–532.
- Cott HB. 1940. *Adaptive coloration in animals*. London (UK): Methuen & Co. Ltd.
- Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga CA, Troscianko TS. 2005. Disruptive coloration and background pattern matching. *Nature.* 434:72–74.
- De Rosario-Martínez H. 2013. Phia: post-hoc interaction analysis. *R Package Version 0.1–3*. <http://CRAN.R-project.org/package=phia>.
- Endler JA. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research.* 31:587–608.
- Endler JA. 1992. Signals, signal conditions, and the direction of evolution. *Am Nat.* 139:S125–S153.

- Feldman A, Sabath N, Pyron RA, Mayrose I, Meiri S. 2016. Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Glob Ecol Biogeogr*. 25:187–197.
- Fleming PA, Valentine LE, Bateman PW. 2013. Telling tails: selective pressures acting on investment in lizard tails. *Physiol Biochem Zool*. 86:645–658.
- Fritz SA, Bininda-Emonds ORP, Purvis A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol Lett*. 12:538–549.
- Gainsbury A, Meiri S. 2017. The latitudinal diversity gradient and interspecific competition: no global relationship between lizard dietary niche breadth and species richness. *Glob Ecol Biogeogr*. 26: 563–572. doi:10.1111/geb.12560
- Geisler WS. 1999. Motion streaks provide a spatial code for motion direction. *Nature*. 400:65–69.
- Hagman M, Forsman A. 2003. Correlated evolution of conspicuous coloration and body size in poison frogs (Dendrobatidae). *Evolution*. 57:2904–2910.
- Hailman JP. 1977. *Optical signals: animal communication and light*. London: Indiana U Press.
- Hall JR, Cuthill IC, Baddeley R, Attwood AS, Munafò MR, Scott-Samuel NE. 2016. Dynamic dazzle distorts speed perception. *PLoS One*. 11:e0155162.
- Hall JR, Cuthill IC, Baddeley R, Shohet AJ, Scott-Samuel NE. 2013. Camouflage, detection and identification of moving targets. *Proc R Soc Lond B Biol Sci*. 280:20130064.
- Halperin T, Carmel L, Hawlena D. 2016. Movement correlates of lizards' dorsal pigmentation patterns. *Funct Ecol*. 31: 370–376. doi:10.1111/1365-2435.12700
- Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics*. 24:129–131.
- Hawlena D, Boochnik R, Abramsky Z, Bouskila A. 2006. Blue tail and striped body: why do lizards change their infant costume when growing up? *Behav Ecol*. 17:889–896.
- von Helversen B, Schooler LJ, Czienskowski U. 2013. Are stripes beneficial? Dazzle camouflage influences perceived speed and hit rates. *PLoS One*. 8:e61173.
- Hogan BG, Cuthill IC, Scott-Samuel NE. 2016. Dazzle camouflage, target tracking, and the confusion effect. *Behav Ecol*. arw081.
- Hogan BG, Cuthill IC, Scott-Samuel NE. 2017. Dazzle camouflage and the confusion effect: the influence of varying speed on target tracking. *Anim Behav*. 123:349–353.
- Hogan BG, Scott-Samuel NE, Cuthill IC. 2016. Contrast, contours and the confusion effect in dazzle camouflage. *Open Science*. 3:160180.
- Hossie TJ, Skelhorn J, Breinholt JW, Kawahara AY, Sherratt TN. 2015. Body size affects the evolution of eyespots in caterpillars. *Proc Natl Acad Sci USA*. 112:6664–6669.
- Huey RB, Hertz PE. 1982. Effects of body size and slope on sprint speed of a lizard (Stellio (Agama) Stellio). *J Experiment Biol*. 97:401–9.
- Hughes AE, Magor-Elliott RS, Stevens M. 2015. The role of stripe orientation in target capture success. *Front Zool*. 12:1.
- Ioannou CC, Krause J. 2009. Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biol Lett*. 5:191–193.
- Karpestam E, Merilaita S, Forsman A. 2014. Body size influences differently the detectabilities of colour morphs of cryptic prey. *Biol J Linn Soc*. 113:112–122.
- Kelley JL, Fitzpatrick JL, Merilaita S. 2013. Spots and stripes: ecology and colour pattern evolution in butterflyfishes. *Proc R Soc Lond [Biol]*. 280:20122730.
- Kodandaramaiah U. 2009. Eyespot evolution: phylogenetic insights from Junonia and related Butterfly Genera (Nymphalidae: Junoniini). *Evol Dev*. 11:489–497.
- Ligon RA, McGraw KJ. 2013. Chameleons communicate with complex colour changes during contests: different body regions convey different information. *Biol Lett*. 9:20130892.
- Mänd T, Tammaru T, Mappes J. 2007. Size dependent predation risk in cryptic and conspicuous insects. *Evolut Ecol*. 21:485–498.
- Martel G, Dill LM. 1995. Influence of movement by Coho Salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). *Ethology*. 99:139–149.
- McHugh ML. 2012. Interrater reliability: the kappa statistic. *Biochemia Medica*. 22:276–282.
- Meiri S. 2010. Length–weight allometries in lizards. *J Zool*. 281:218–226.
- Meiri S. 2008. Evolution and ecology of lizard body sizes. *Glob Ecol Biogeogr*. 17:724–734.
- Murali G, Kodandaramaiah U. 2016. Deceived by stripes: conspicuous patterning on vital anterior body parts can redirect predatory strikes to expendable posterior organs. *Open Science*. 3:160057.
- Murali G, Kodandaramaiah U. 2017. Data from: body size and evolution of motion dazzle coloration in lizards. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.16g90>
- Murali G, Merilaita S, Kodandaramaiah U. 2017. Grab my tail: evolution of dazzle stripes and divertive tail colorations in lizards. Manuscript in Preparation.
- Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev*. 82:591–605.
- Olden JD, Hogan ZS, Zanden M. 2007. Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Glob Ecol Biogeogr*. 16:694–701.
- Orme CD, Davies RG, Olson VA, Thomas GH, Ding TS, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Owens IP, et al. 2006. Global patterns of geographic range size in birds. *PLoS Biol*. 4:e208.
- Ortega J, Pellitteri-Rosa D, López P, Martín J. 2015. Dorsal pattern polymorphism in female Iberian wall lizards: differences in morphology, dorsal coloration, immune response, and reproductive investment. *Biol J Linn Soc*. 116:352–363.
- Pérez i de Lanuza G, Font E. 2016. The evolution of colour pattern complexity: selection for conspicuousness favours contrasting within-body colour combinations in lizards. *J Evolut Biol*. 29:942–51.
- Pike TW. 2015. Interference coloration as an anti-predator defence. *Biol Lett*. 11:20150159.
- Pinheiro J, Bates D, DebRoy S, Sarkar D. 2014. R Core Team Nlme: linear and nonlinear mixed effects models. R Package Version 3.1–117. <http://CRAN.R-Project.Org/Package=Nlme>.
- Rowland HM, Cuthill IC, Harvey IF, Speed MP, Ruxton GD. 2008. Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. *Proc R Soc Lond B Biol Sci*. 275:2539–2545.
- Ruxton GD, Sherratt TN, Speed MP. 2004. *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. New York: Oxford University Press.
- Scott-Samuel NE, Baddeley R, Palmer CE, Cuthill IC. 2011. Dazzle camouflage affects speed perception. *PLoS One*. 6:e20233.
- Skelhorn J, Rowland HM, Ruxton GD. 2010. The evolution and ecology of masquerade. *Biol J Linn Soc*. 99:1–8.
- Stevens M, Merilaita S. 2009. Animal camouflage: current issues and new perspectives. *Philos Trans R Soc Lond B Biol Sci*. 364:423–427.
- Stevens M, Searle WTL, Seymour JE, Marshall KLA, Ruxton D. 2011. Motion dazzle and camouflage as distinct anti-predator defenses. *BMC Biol*. 9:1.
- Stevens M, Yule DH, Ruxton GD. 2008. Dazzle coloration and prey movement. *Proc R Soc Lond B Biol Sci*. 275:2639–2643.
- Stoddard MC, Kilner RM, Town C. 2014. Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. *Nat Comm*. 5: 4117.
- Taylor EH. 1935. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Uma*: with an account of the distribution and relationships of its species. Vol. 23. 1. University of Kansas Bull 23:1–643.
- Thayer GH. 1909. *Concealing-coloration in the animal kingdom: being a summary of Abbott H. Thayer's discoveries*. New York (NY): Macmillan Company.
- Umeton D, Read JCA, Rowe C. 2017. Unravelling the illusion of flicker fusion. *Biol Lett*. 13:20160831.
- Van Damme R, Van Dooren TJM. 1999. Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. *Anim Behav*. 57:347–352.
- Webb PW. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. *J Exp Biol*. 65:157–177.
- Witter MS, Cuthill IC, Bonser RHC. 1994. Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. *Anim Behav*. 48:201–222.
- Zheng Y, Wiens JJ. 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol Phylogenet Evol*. 94:537–547.
- Zhou K, Li H, Han D, Bauer AM, Feng J. 2006. The complete mitochondrial genome of Gekko Gecko (Reptilia: Gekkonidae) and support for the monophyly of sauria including Amphisbaenia. *Mol Phylogenet Evol*. 40:887–892.