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Original Article

What makes motion dazzle markings effective against predation?

Ullasa Kodandaramaiah,[a] Shuaib Palathingal,[a,b] Gayathri Bindu Kurup,[a] and Gopal Murali[a]
[a]IISER-TVM Centre for Research and Education in Ecology and Evolution (ICREEE), School of Biology, Indian Institute of Science Education and Research Thiruvananthapuram, Maruthamala PO, Vithura, Thiruvananthapuram 695 551, India and [b]Centre for Ecological Sciences, Indian Institute of Science, Bengaluru 560 012, India

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Motion dazzle markings comprise patterns such as stripes and zig-zags that are postulated to protect moving prey by making predators misjudge the prey's speed or trajectory. Recent experiments have provided conflicting results on their effect on speed perception and attack success. We focus on motion dazzle stripes and investigate the influence of four parameters—stripe orientation, stripe contrast, target size, and target speed—on perceived speed and attack success using a common experimental paradigm involving human "predators" attacking virtual moving targets on a computer touchscreen. We found that high-contrast stripes running parallel or perpendicular to the direction of motion reduce attack success compared to conspicuous uniform targets. Surprisingly, parallel stripes induced underestimation of speed, while perpendicular stripes induced overestimation of speed in relation to uniform black, suggesting that misjudgment of speed per se is sufficient to reduce attack accuracy. Across all the experiments, we found some support for parallel stripes inducing underestimation of target speed but these stripes reduced attack success only when targets were small, moved at an intermediate speed, and had high internal contrast. We suggest that prey features (e.g., size or speed) are an important determinant of capture success and that distortion of speed perception by a color pattern does not necessarily translate to reduced capture success of the prey. Overall, our results support the idea that striped patterns in prey animals can reduce capture in motion but are effective under a limited set of conditions.

Key words: **animal coloration, antipredator strategy, camouflage, motion dazzle, speed perception**

INTRODUCTION

The intense selection pressure on prey animals to avoid predatory attacks has given rise to some of the most stunning adaptations known in nature (Cott 1940; Ruxton et al. 2018). Visual information from the prey constitute one of the dominant cues used by many predators during predation, and prey animals have hence evolved a wide array of antipredatory color patterns. Examples include aposematism, wherein bright colors are used as warning signals to advertise unprofitability (Wallace 1867; Poulton 1890) and Batesian mimicry where harmless prey resemble harmful or unpalatable species (Bates 1862; Cott 1940). Another widespread antipredatory strategy is camouflage, where color patterns on the prey hinder detection or recognition of the prey by predators (Poulton 1890; Thayer 1909; Cott 1940; Merilaita et al. 2017). Camouflage is effective when the prey is still (Thayer 1909; Regan 2000; Ioannou and Krause 2009; Brunyé et al. 2018), and has been extensively studied for over a century. However, there has been a recent surge in studies attempting to understand color patterns that may protect moving prey from predators (Stevens et al. 2008, 2011; Pike 2015; Hogan et al. 2016a; Umeton et al. 2017; Murali 2018). One strategy includes motion dazzle patterns (Thayer 1909; Stevens et al. 2008), also called dazzle camouflage patterns (e.g., Stevens et al. 2008; Scott-Samuel et al. 2011; Hogan et al. 2016a; Ruxton et al. 2018), which are repetitive colorations such as stripes, bands, and zig-zags. Motion dazzle patterns have been proposed to benefit the prey by preventing predators from accurately judging the speed or trajectory of the moving prey (Thayer 1909; Stevens et al. 2008; Scott-Samuel et al. 2011).

Experiments involving natural predators predating on real moving prey are difficult to undertake, and, therefore, almost all studies on motion dazzle patterns so far have relied on computer-based touchscreen experiments where virtual targets are attacked by humans (exceptions are How and Zanker 2014; Hämäläinen et al. 2015; Zlotnik et al. 2018). Many studies have shown that motion dazzle patterns can reduce attack success (e.g., Stevens et al. 2008, 2011; Hughes et al. 2014; Murali and Kodandaramaiah 2016, 2018), possibly because they alter perception of speed

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Address correspondence to G. Murali. E-mail: gopal13@iisertvm.ac.in.

(Scott-Samuel et al. 2011; Hall et al. 2016; Murali and Kodandaramaiah 2016) or trajectory of the moving objects (Hughes et al. 2017). However, in some other studies, motion dazzle patterns did not differ from uniform colors, or even were easier to capture (e.g., von Helversen et al. 2013; Hughes et al. 2015). Therefore, it is not known under what conditions motion dazzle markings are beneficial, and what properties of the object, and of the markings themselves, determine the effectiveness of these patterns. For instance, it is unclear whether the orientation of stripes in relation to the direction of prey motion affects prey capture success. Previous studies suggest that perpendicular stripes are more beneficial than parallel ones (von Helversen et al. 2013; Hughes et al. 2015). Stevens et al. (2008), however, found no influence of stripe orientation on capture success. Hogan et al. (2016a) found that targets with stripes parallel to the direction of motion were generally more difficult to track compared to targets with stripes perpendicular to motion, although they did not measure attack rates.

Although it is often assumed that strong contrast between the pattern elements is a necessary feature of motion dazzle markings, comparisons of prey with high- and low-contrast patterns have rarely been done. Hogan et al. (2016b) found that the contrast between elements constituting dazzle markings did not affect how easily humans were able to track moving objects. However, Stevens et al. (2011) found that stimuli with low-contrast stripes were more difficult to capture compared to those with high-contrast stripes. Further work is needed before excluding the role of contrast in the functioning of motion dazzle markings.

Two other factors that may interact with dazzle coloration are prey size and speed. A phylogenetic comparative analysis (Allen et al. 2013) found that smaller snakes tend to have parallel stripes whereas larger ones tend to have other patterns. Another comparative study (Murali and Kodandaramaiah 2018) reported that smaller lizards are more likely to have bodies with stripes parallel to the length of the body, presumably redirecting attacks to the dispensable tail through the motion dazzle effect. This study also included a virtual predation experiment which suggested that the benefit of parallel stripes decreased with increasing length. Therefore, prey size appears to influence the effectiveness of dazzle markings, but whether this is because of speed perception distortion is not known. Similarly, the effect of prey speed is not established. Speed perception distortion by zig-zags and checkered patterns (but not stripes) has been shown to be greater at higher speeds (Scott-Samuel et al. 2011), suggesting that at least some motion dazzle patterns function better at higher speed. On the other hand, speed per se can influence attack success (Van damme and Van dooren 1999; Clemente and Wilson 2015), and the effect of motion dazzle markings may interact with that of speed. This was tested in Stevens et al. (2008) where different patterned objects (unicolored, striped, zig-zagged) were all more difficult to capture at higher speeds, but, surprisingly, the relative effectiveness of these patterns did not vary with speed. However, more work is needed to understand the influence of speed on the motion dazzle effect.

In summary, work so far has highlighted the potential influence of some features of the prey and of motion dazzle markings on the protective benefit of these color patterns to the prey. However, there are several conflicting results—particularly with respect to the influence of dazzle markings parallel to the direction of motion. This is possibly because of differences in experimental protocols across studies. Moreover, several untested attributes may also influence the effectiveness of such markings. To understand the evolution of the diversity of motion dazzle markings in nature, it is important to understand what makes them effective. We designed a series of touchscreen experiments with a total of 809 human volunteers, the aim of which were to understand what parameters affect the effectiveness of stripes, with emphasis on stripes running parallel to the direction of motion. In separate experiments, we manipulated two putatively crucial aspects of motion dazzle stripes—contrast and orientation, as well as the size and speed of the patterned objects, to test the role of these four parameters in influencing capture success by humans. We also performed psychophysical experiments to test the prediction that the distortion of perceived speed (i.e., the difference between the actual and perceived speeds) is correlated with capture outcome.

MATERIALS AND METHODS

The experiments involved interactive tasks where human volunteers were displayed moving objects on a computer touchscreen monitor (DELL S2240T), and the volunteers either attempted to attack (i.e., touch) the object (Capture experiments) or estimated the relative speeds of pairs of stimuli (Speed perception experiments). All participants signed a consent form and the protocols adhered to the Declaration of Helsinki. The monitor had a resolution of 1920 × 1080 pixels (52 × 38 cm), 60 Hz refresh rate, and was gamma corrected. Participants viewed the screen from ca. 60 cm away. The tasks were created in SCRATCH v2.0 (https://scratch.mit.edu/; 2017). The background image for all trials was a square of dimensions (37.5 × 37.5 cm) on the screen, comprising equal numbers of black and white pixels arranged randomly (Figure 1). The targets were square or rectangular and had different grayscale patterns depending on the experiment. Unicolored black (RGB 0, 0, 0) and/or unicolored white (255, 255, 255) rectangles were used as controls. The bicolored striped targets comprised white stripes alternating with black or gray stripes, with all stripes on a target having the same width (Figure 1). Thus, both white and dark (black or gray) stripes occupied half the total area of a striped target. The average gray value of all striped targets matched that of the background, while the uniform white and black targets were more conspicuous against the background (uniform black had lower luminance, and uniform white had a higher luminance than the striped targets).

Capture experiments

The capture experiments involved a total of 210 volunteers. Four experiments tested the effects of stripe orientation, stripe contrast, object size, and object speed, respectively. The experiment on object contrast had 50 participants, while the rest had 40 each. In the experiments, the object moved through the screen one after the other for 2 or 3 min (standardized to 30 s for each object type) at a speed of 17.235 cm/s (except in the experiments testing the effect of absolute speed; see *Effect of object speed*). The object appeared from the central area of the screen and headed towards one of the four edges of the screen, with one of the four angles—0°, 90°, 180°, and 270°—randomly assigned along with a ±30° deviation. All objects moved for approximately the same duration and a distance of 13–20 cm across the screen for each appearance (standardized according to object size). The volunteers were instructed to "capture" all the objects by touching them. The order of appearance of objects was randomized. The object was considered to have been successfully attacked (i.e., caught or captured) if the participant touched it, and the number of successful attacks was recorded.

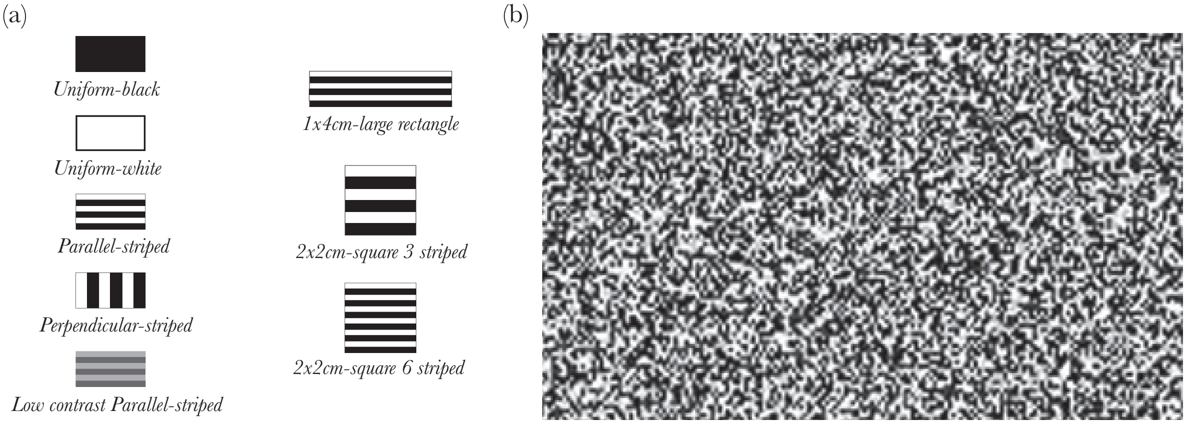

Figure 1
Illustration of targets and background used; (a) object types with respective names and (b) an exemplar pixelated background.

Effect of stripe orientation

The effect of stripe orientation was tested by comparing four 1 × 2 cm objects (visual angle: 0.881 × 1.763°; Figure 1): 1) three black stripes parallel to the direction of motion (with ca. 0.333 cycles/deg; hereafter *Parallel-striped*); 2) three black stripes perpendicular to the direction of motion (with 1.701 cycles/deg; hereafter *Perpendicular-striped*); 3) unicolored black (hereafter *Uniform-black*); and 4) unicolored white (hereafter *Uniform-white*). The two striped objects had equal numbers of white and black stripes, alternating with each other.

Effect of stripe contrast

The effect of contrast was tested by comparing *Low contrast Parallel-striped* (1 × 2 cm object having three stripes each of RGB 102, 102, 102 and RGB 153, 153, 153; Figure 1) with *Parallel-striped*, *Uniform-black*, and *Uniform-white*. *Parallel-striped* had a total contrast of 100% between the stripes, while *Low contrast Parallel-striped* had 20% contrast, but the two objects were otherwise identical in the configuration of the white and dark stripes.

Effect of object size

The effect of object size was tested using comparisons of four objects that had parallel black and white stripes but differed in dimensions or stripe width. 1) A 1 × 2 cm object (visual angle: 0.881 × 1.763°; hereafter *1 × 2 cm-small rectangle*) that was identical to *Parallel-striped*; 2) A 1 × 4 cm object (visual angle: 1.763 × 3.525°; hereafter *1 × 4 cm-large rectangle;* with 0.333 cycles/deg); 3) A 2 × 2 cm object with the same number of, but broader, stripes as *1 × 2 cm-small rectangle* (visual angle: 1.763 × 1.763°; hereafter *2 × 2 cm-square 3 striped;* with 0.333 cycles/deg); and 4) A 2 × 2 cm object with twice the number of stripes as that in *2 × 2 cm-square 3 striped*, but with the width of stripes as in *1 × 2 cm-small rectangle* (visual angle: 1.763 × 1.763°; hereafter *2 × 2 cm-square 6 striped*; with 0.166 cycles/deg) (Figure 1). The comparisons between *1 × 2 cm-small rectangle* and *1 × 4 cm-large rectangle* tested the effect of length, while the comparisons between *1 × 2 cm-small rectangle* and the two 2 × 2 cm objects (*2 × 2 cm-square 3 striped* and *2 × 2 cm-square 6 striped*) tested the effect of area and the relative importance of stripe number and width.

Effect of object speed

Comparisons between *Parallel-striped* and *Uniform-black* were done at three speeds: *Low* (13.160 cm/s or 12.516°), *Intermediate* (17.235 cm/s or 16.346°), and *High* (20.706 cm/s or 19.580°).

Effect of luminance

An additional experiment was done to test whether the luminance of targets affected capture success. This involved a comparison between *Uniform-black*, *Uniform-white*, *Parallel-striped* and a fourth target with uniform gray (*Uniform-gray*; RGB 128, 128, 128) that matched the average luminance of the background (Supplementary Section C).

Speed perception experiments

A SCRATCH task similar to that used by Murali and Kodandaramaiah (2016) in their speed perception experiment (their Experiment 4) was used to test whether perceived speed differed between a pair of objects. The task was based on an adaptive staircase paradigm (Leek 2001; von Helversen et al. 2013). Multiple sets of experiments were performed using selected pairs of object types to test the effect of different attributes (i.e., stripe orientation, contrast, object size, and object speed) on speed perception by participants.

An experiment involved a comparison between two objects by 60 participants. Both objects appeared multiple times, alternating with each other. A step involved two appearances (one by each object), and after every step, a screen prompt asked the participants which object they judged to move faster, with participants recording their response by touching the object. One object had a constant speed (17.235 cm/s) throughout the experiment (hereafter "standard") for half ($n = 30$) of the participants. The starting speed of the other object (hereafter "target") was 15.293, 17.235, or 19.018 cm/s, with each speed represented by 10 participants. The speed of the *target* was changed through the steps depending on the participant's response in the previous step: if the participants judged the *target* to move faster than the *standard*, the speed of the *target* was decreased in the next step (by 0.388 cm/s), and increased (by 0.388 cm/s) if the participant judged the *standard* to move slower. If the participant judged both objects to be equally fast, the response in the step before was used to modulate the *target* speed in the next step.

In this paradigm, the speed of the *target* increased and decreased throughout the trials depending on the participant's responses, eventually oscillating within a range of speeds where the *target* was perceived to move as fast as the *standard*. The average of the speeds at which the participant responded that both objects moved at equal speed between two adjacent reversal points (i.e., points where the subject perceived the *target* speed to change from faster than the *standard* to slower, or from slower to faster) was taken as the matched speed of the target (i.e., the speed at which the target is perceived to be as fast as the target). Objects were presented until a maximum of 10 data points were obtained for the matched speed calculation. The *standard* and *target* objects were switched for the remaining 30 participants, 10 per each initial *target* speed. For the experiments testing the influence of object speed (see *Effect of object speed*), the *standard* speed and initial *target* speeds differed based on the experiment (given in Table 1). Readers are referred to Murali and Kodandaramaiah (2016; section 2.1.2) for a more detailed description of the procedure. Since the duration of motion is known to affect the perceived speed (Anstis and Kim 2018), the objects moved for the same duration in all experiments (including the capture experiments). For example, this was done by adjusting the starting position of the objects in experiments comparing the effect of target size, such that the shorter object was ahead of the longer one.

Effect of stripe orientation

Three separate experiments compared 1) *Uniform-white* with *Uniform-black*, 2) *Uniform-black* with *Parallel-striped*, and 3) *Uniform-black* with *Perpendicular-striped*. The comparison between *Uniform-white* and *Uniform-black* was done to check whether the grayscale value of the uniformly colored objects affected speed perception. Since there was no difference between the two, *Uniform-black* was used as the unicolored control in this and subsequent experiments.

Effect of stripe contrast

The effect of contrast was tested by comparing *Low contrast Parallel-striped* with *Parallel-striped* and *Uniform-black*. The results were also compared with those from the previous experiment where *Uniform-black* was matched against *Parallel-striped*.

Effect of object size

To test the effect of length, *1 × 2 cm-small rectangle* was first compared with *1 × 4 cm-large rectangle*. Then, *1 × 2 cm-small rectangle* was compared with *2 × 2 cm-square 6 striped* and *2 × 2 cm-square 3 striped* to test the effect of object area.

Effect of object speed

This included two sets of experiments (low and high speed) that both involved comparisons between *Parallel-striped* and *Uniform-black*, but differed in the speed of the *standard* and the *target* initial speeds (Table 1). The results were also compared with results from the previous experiment (medium speed) where *Uniform-black* was matched against *Parallel-striped* (*Effect of stripe orientation*).

Statistical analyses

All analyses were done in R (R Core Team 2015) via Rstudio v.3.3.3 (RStudio 2015). Data from the speed perception experiments were analyzed using linear mixed-effects models (LMM) in the *lme4* package v.1.1-15 (Bates et al. 2014). Participant ID was included as a random effect (random intercept), while the initial *target* speed, object type, and the interaction between the two were considered as fixed effects against the matched speed values (speed at which the participant responded that both stimuli moved at equal speed). The main effects of the models were obtained using the *anova* function (Gałecki and Burzykowski 2013).

Table 1

Speeds of the *standard* and respective initial speeds of the *target* used in the speed perception experiments testing the effect of absolute speed values (in cm/s)

	Low	Medium	High
Speed of the *Standard*	13.160	17.235	20.706
Initial speed of the *Target*	10.869	15.293	19.018
	13.160	17.235	20.706
	15.293	19.018	22.370

The *standard* speed varied in the experiment testing the effect of object speed, and we estimated standardized regression coefficients (β) (Nakagawa and Cuthill 2007) across the different speed conditions to compare effect sizes. The model selection procedures and variables included in the model for the analysis of data from this experiment were the same as that for previous experiments. The model comparisons are presented in the Supplementary Sections A and B.

Data from the capture experiments were analyzed using generalized linear mixed-effects models (GLMM) with the *glmer* function in the *lme4* package (Bates et al. 2014). To account for repeated measures from the same volunteer, participant ID was taken as the random intercept and object type as the fixed effect. A Poisson GLMM model was used because the outcome was in the form of count data. Tukey post hoc pairwise comparisons among object types were done using the *multcomp* v.1.4-8 package (Hothorn et al. 2016). The figures represent the mean and 95% confidence intervals calculated from the fitted regression models using the *effects* package (Fox 2003).

RESULTS

Capture experiments

Effect of stripe orientation

Stripe orientation did not affect capture success (*Parallel-striped* vs. *Perpendicular-striped*: $n = 40$, $z = 0.78$, $P = 0.863$). Likewise, there was no difference in capture success between uniform light and dark objects (*Uniform-white* vs. *Uniform-black*: $n = 40$, $z = 2.07$, $P = 0.162$; Figure 2a). However, striped objects had significantly lower capture success than uniform ones (*Perpendicular-striped* vs. *Uniform-black*: $n = 40$, $z = -4.78$, $P < 0.001$; *Perpendicular-striped* vs. *Uniform-white*: $n = 40$, $z = -2.72$, $P = 0.033$; *Parallel-striped* vs. *Uniform-black*: $n = 40$, $z = -5.55$, $P < 0.001$; *Parallel-striped* vs. *Uniform-white*: $n = 40$, $z = -3.49$, $P = 0.002$).

Effect of stripe contrast

Objects with high-contrast stripes received fewer attacks compared to uniform black ones (*Parallel-striped* vs. *Uniform-black*: $n = 50$, $z = -3.28$, $P = 0.005$; Figure 3a), but did not differ from objects with low-contrast stripes (*Parallel-striped* vs. *Low contrast Parallel-striped*: $n = 50$, $z = 1.82$, $P = 0.264$) or from uniform white (*Uniform-white* vs. *Parallel-striped*: $n = 50$, $z = -1.82$, $P = 0.264$). Objects with low-contrast stripes also did not differ from either of the two uniform light or dark targets (*Low contrast Parallel-striped* vs. *Uniform-black*: $n = 50$, $z = 1.51$, $P = 0.430$; *Low contrast Parallel-striped* vs. *Uniform-white*: $n = 50$, $z = 0.001$, $P = 0.999$). There was no difference between the two uniformly colored objects (*Uniform-white* vs. *Uniform-black*: $n = 50$, $z = -1.51$, $P = 0.430$).

Effect of object size

Size influenced capture success—the small (2 cm^2; *1 × 2 cm-small rectangle*) object had significantly fewer attacks than all three large (4 cm^2) objects (*1 × 2 cm-small rectangle* vs. *1 × 4 cm-large rectangle*:

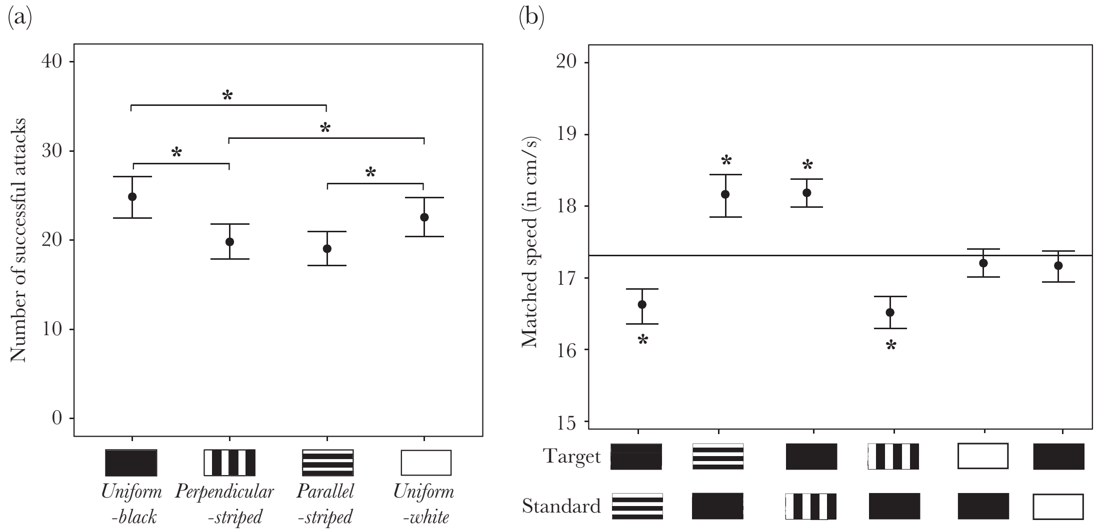

Figure 2
Mean and 95% CI estimated for the regression model testing the effect of stripe orientation; (a) for the number of successful attacks, (b) speed matched values (i.e., the speed at which the two objects were perceived by the participants to move at the same speed). The horizontal line represents the speed of the *standard* in the speed perception experiment. *Significant difference with P <0.05. Nonsignificant comparisons are not highlighted.

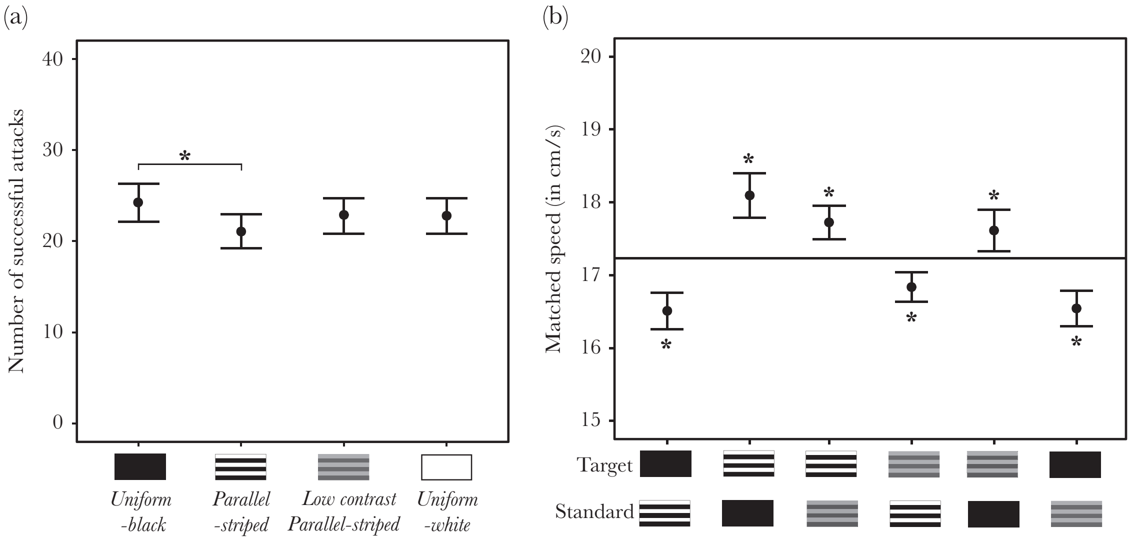

Figure 3
Mean and 95% CI estimated from the regression model testing the effect of stripe contrast; (a) for the number of successful attacks, (b) speed matched values (i.e., the speed at which the two objects were perceived by the participants to move at the same speed). The horizontal line represents the speed of the *standard* in the speed perception experiment. The speed perception comparison between *Parallel-striped* and *Uniform-black* is from the experiment *Effect of stripe orientation*, while the remaining comparisons are from the experiment *Effect of stripe contrast*. *Significant difference with P <0.05. Nonsignificant comparisons are not highlighted.

$n = 40$, $z = 5.94$, $P < 0.001$; *1 × 2 cm-small rectangle* vs. *2 × 2 cm-square 3 striped*: $n = 40$, $z = 4.59$, $P < 0.001$; *1 × 2 cm-small rectangle* vs. *2 × 2 cm-square 6 striped*: $n = 40$, $z = 4.80$, $P < 0.001$; Figure 4a). There was no difference in attacks between the large objects (*2 × 2 cm-square 6 stripes* vs. *1 × 4 cm-large rectangle*: $n = 40$, $z = -1.16$, $P = 0.655$; *2 × 2 cm-square 3 striped* vs. *1 × 4 cm-large rectangle*: $n = 40$, $z = -1.36$, $P = 0.522$; *2 × 2 cm-square 6 striped* vs. *2 × 2 cm-square 3 striped* stripes: $n = 40$, $z = 0.21$, $P = 0.997$).

Effect of object speed

Object speed influenced capture success—the striped objects (*Parallel-striped*) had lower capture success than uniform ones (*Uniform-black*) at medium speed ($n = 40$, $z = -3.83$, $P = 0.001$; Figure 5b), but not at low ($n = 40$, $z = -0.26$, $P = 0.998$; Figure 5a) or high speeds ($n = 40$, $z = -0.30$, $P = 0.999$; Figure 5c).

Effect of luminance

Objects with intermediate luminance (*Uniform-gray* and *Parallel-striped*) had lower capture success than objects with both low (*Uniform-black*) and high (*Uniform-white*) luminance (Supplementary Section C and Figure S1). There was no difference between the two objects with intermediate luminance (*Uniform-gray* vs. *Parallel-striped*) or between the high- and low-luminance objects (Supplementary Section C and Figure S1).

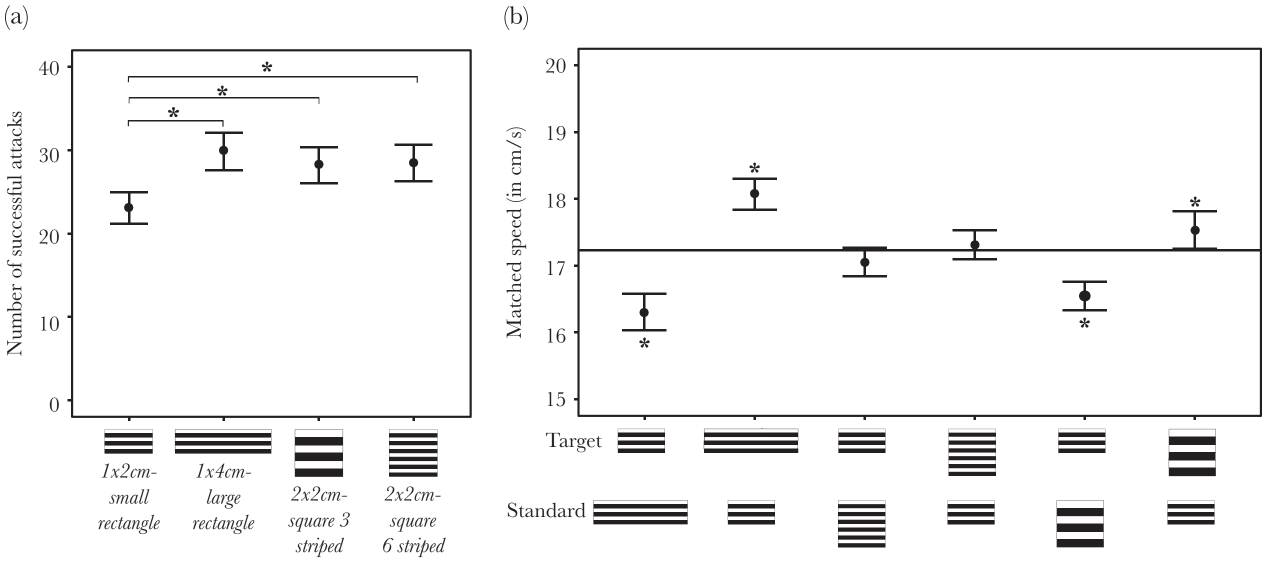

Figure 4
Mean and 95% CI estimated from the regression model testing the effect of object size; (a) for the number of successful attacks, (b) speed matched values (i.e., the speed at which the two objects were perceived by the participants to move at the same speed). The horizontal line represents the speed of the *standard* in the speed perception experiment. *Significant difference with $P < 0.05$. Nonsignificant comparisons are not highlighted.

Speed perception experiments

The pairwise comparisons testing the influence of object type on the matched speed from the LMM model are presented below. The main effects of each factor, that is, initial *target* speed, object type, and their interaction, are presented in Supplementary Section B.

Effect of stripe orientation

Compared to uniform black, parallel stripes induced underestimation of speed (Figure 2b; comparison of *Uniform-black* and *Parallel-striped*) whereas perpendicular stripes induced overestimation (Figure 2b; comparison of *Uniform-black* and *Perpendicular-striped*). Specifically, in the comparison between *Uniform-black* and *Parallel-striped*, with *Parallel-striped* as the *standard*, the matched speed of *Uniform-black* (the *target*) was significantly lower than that of the *standard* (LMM: $n = 30$, $t = -4.72$, $P < 0.001$; Figure 2b). When *Uniform-black* was the *standard*, the matched speed of the *Parallel-striped* was significantly higher (LMM: $n = 30$, $t = 5.00$, $P < 0.001$; Figure 2b). In the comparison between *Uniform-black* and *Perpendicular-striped*, with *Perpendicular-striped* as the *standard*, the matched speed of the *Uniform-black* was significantly higher (LMM: $n = 30$, $t = 6.41$, $P < 0.001$; Figure 2b). With *Uniform-black* as *standard*, the matched speed of *Perpendicular-striped* was significantly lower (LMM: $n = 30$, $t = -4.66$, $P < 0.001$; Figure 2b). There was no difference in speed perception between the two uniform targets (Figure 2b; comparison between *Uniform-black* and *Uniform-white*), both with *Uniform-black* (df = 1, $\chi^2 = 0.43$, $P = 0.511$) and *Uniform-white* as the *standard* (df = 1, $\chi^2 = 1.03$, $P = 0.309$; Figure 2b).

Effect of stripe contrast

Low-contrast stripes induced overestimation of speed compared to high-contrast ones (*Low contrast Parallel-striped* vs. *Parallel-striped*). Specifically, with *Low contrast Parallel-striped* as the *standard*, the matched speed of *Parallel-striped* was significantly higher (LMM: $n = 30$, $t = 2.83$, $P = 0.005$; Figure 3b). With *Parallel-striped* as the *standard*, the matched speed of *Low contrast Parallel-striped* was significantly lower (LMM: $n = 30$, $t = -2.55$, $P = 0.011$; Figure 3b). However, low-contrast stripes induced underestimation of speed compared to uniform black (*Low contrast Parallel-striped* vs. *Uniform-black*; Figure 3b). With *Uniform-black* as *standard*, the matched speed of *Low contrast Parallel-striped* was significantly higher (LMM: $n = 30$, $t = 2.503$, $P = 0.013$; Figure 3b). With *Parallel-Low Contrast* as the *standard*, the matched speed of the *Uniform-black* was significantly lower (LMM: $n = 30$, $t = -4.13$, $P < 0.001$; Figure 3b).

Effect of size

Speed perception was influenced by the overall size of the targets—the small rectangle induced overestimation of speed compared to both the large rectangle (*1 × 2 cm-small rectangle* vs. *1 × 4 cm-large rectangle*) and the square that had the same area as the large rectangle (*1 × 2 cm-small rectangle* vs. *2 × 2 cm-square 3 striped*; Figure 4b). Specifically, in the comparison between *1 × 2 cm-small rectangle* and *1 × 4 cm-large rectangle*, with *1 × 4 cm-large rectangle* as the *standard*, the matched speed of the *1 × 2 cm-small rectangle* was significantly lower (LMM: $n = 29$, $t = -4.79$, $P < 0.001$; Figure 4b). When *1 × 2 cm-small rectangle* was the *standard*, the matched speed of *1 × 4 cm-large rectangle* was significantly higher (LMM: $n = 30$, $t = 4.54$, $P < 0.001$; Figure 4b). In the comparison between *1 × 2 cm-small rectangle* and *2 × 2 cm-square 3 striped*, with *2 × 2 cm-square 3 striped* as the *standard*, the matched speed of *1 × 2 cm-small rectangle* was significantly lower (LMM: $n = 30$, $t = -5.21$, $P < 0.001$; Figure 4b). When *1 × 2 cm-small rectangle* was the *standard*, the matched speed of the *2 × 2 cm-square 3 striped* was significantly higher (LMM: $n = 30$, $t = 2.00$, $P = 0.047$; Figure 4b).

The number of stripes in the object affected the perceived speed—the small rectangle induced overestimation of speed compared to the square with three stripes (*1 × 2 cm-small rectangle* vs. *2 × 2 cm-square 3 striped*; results presented above), but not compared to the square with six stripes (*1 × 2 cm-small rectangle* vs. *2 × 2 cm-square 6 striped*). With *2 × 2 cm-square 6 striped* as the *standard*, the matched speed did not differ between *1 × 2 cm-small rectangle* and *2 × 2 cm-square with 6 striped* (df = 1, $\chi^2 = 1.14$, $P = 0.286$; Figure 4b). Likewise, when *1 × 2 cm-small rectangle* as the *standard*, speed perception did not differ between the two objects (df = 1, $\chi^2 = 0.21$, $P = 0.646$; Figure 4b).

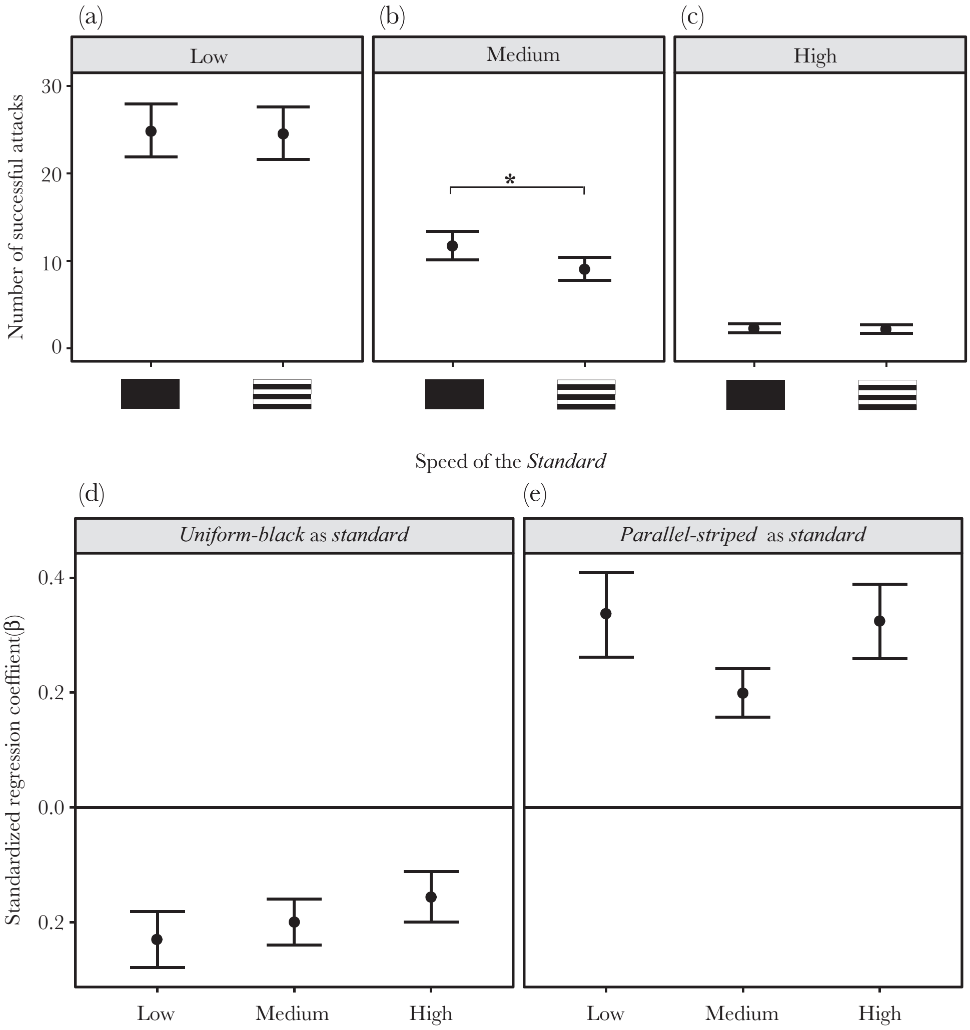

Figure 5
Mean and 95% CI estimated from the regression model testing the effect of object speed; for the number of successful attacks when objects moved at (a) Low, (b) Medium, and (c) High speed. Standardized regression coefficients (β) of matched speed at different object speeds when (d) *Uniform-black* was set as the *standard*, and (e) *Parallel-striped* was set as the standard. For the speed perception results, the low and high speed comparisons are from the experiment *Effect of object speed*, while the medium speed comparison is from *Uniform-black* versus *Parallel-striped* in the experiment *Effect of stripe orientation*. *Significant difference with P <0.05. Nonsignificant comparisons are not highlighted.

Effect of object speed

Parallel stripes induced underestimation of speed at both high and low object speeds (*Uniform-black* vs. *Parallel-striped* at low and high speeds). Specifically, with *Uniform-black* as *standard*, the matched speed of *Parallel-striped* was significantly higher (LMM: low speed, $n = 30$, $t = 4.74$, $P < 0.001$; high speed, $n = 30$, $t = 3.54$, $P < 0.001$). With *Parallel-striped* as *standard*, the matched speed of *Uniform-black* was significantly lower than that of the *standard* (LMM: low speed, $n = 30$, $t = -4.57$, $P < 0.001$; high speed, $n = 30$, $t = -5.00$, $P < 0.001$).

We also compared standardized regression coefficients (β) of object type across all three *standard* speeds tested (results of low and high speed above; medium speed from *Uniform-black* vs. *Parallel-striped* in the experiment *Effect of stripe orientation*). The standardized regression coefficients of object type increased with the speed of the *standard* when *Uniform-black* was the *standard*, implying a stronger effect on speed perception with increasing speed (Figure 5d). However, when *Parallel-striped* was the *standard*, the effect on speed perception was lowest at medium speed, with no difference between low and high speed conditions (Figure 5e).

DISCUSSION

We find that striped patterning can reduce capture accuracy, supporting results from previous studies (Stevens et al. 2008, 2011; Hughes et al. 2014; Murali and Kodandaramaiah 2016, 2018) and the idea that prey can gain significant protection from predation during motion by having stripes on their bodies. In previous studies, stripes reduced capture success when compared to uniform white or black, although stripes either increased attacks compared to uniform gray (Stevens et al. 2008), or did not differ from uniform gray (Hughes et al. 2014). This was corroborated in our study where there was no difference between uniform gray and striped targets (Supplementary Section C and Figure S1). The uniform gray target and all striped targets in our study matched the average luminance of the background, while the uniform white and black targets were more conspicuous against the background. Considering these results and those from previous studies (Stevens et al. 2008, 2011; Hughes et al. 2014; Hämäläinen et al. 2015), it appears that stripes confer a benefit over conspicuous uniform color, but are not any more effective than uniform color matching the average background color. Our results also suggest that the benefit of stripes depends on the object (Figures 4a and 5a–c) and pattern characteristics (Figures 2a and 3a). Further, the results show that color pattern influences perceived speed, suggesting a potential link between speed perception and capture success. We first discuss the influence of the four factors tested—stripe orientation, stripe contrast, object size, and object speed—and then discuss the general relationship between capture success and the extent of speed perception distortion.

Effect of stripe orientation

There was no difference in capture success between parallel (*Parallel-striped*) and perpendicular (*Perpendicular-striped*) striped targets (Figure 2a). We note that the spatial frequency of stripes differed between *Parallel-striped* and *Perpendicular-striped* (0.333 vs. 1.701 cycles/deg), which was because we controlled for the number of stripes. However, the comparison of *2 × 2 cm-square 3 striped* and *2 × 2 cm-square 6 striped* indicates that spatial frequency does not have an effect, at least for parallel stripes. We, therefore, assume that the spatial frequency difference did not affect the results in the comparison between *Parallel-striped* and *Perpendicular-striped*. The absence of an effect of stripe orientation corroborates results from Stevens et al. (2008) who found no effect of stripe orientation on capture success. On the other hand, von Helversen et al. (2013) and Hughes et al. (2015) found that parallel stripes increased attack success compared to perpendicular ones. Results from different studies may not be directly comparable because of differences in target size, speed, and experimental protocols. However, taking together results from all studies that have tested the effect of stripe orientation on capture success, parallel stripes appear to have no advantage over perpendicular ones. We surmise that prey animals can benefit from the presence of stripes irrespective of orientation. Comparative analyses on snakes (Allen et al. 2013) suggest that parallel stripes are associated with rapid escape behavior and perpendicular ones with erratic movement. Thus, the ecological conditions that favor the evolution of these two patterns may be different. For instance, certain stripes might also be better at preventing detection by predators based on the principles of disruptive camouflage (Ruxton et al. 2018) or may function in thermoregulation (although see Horváth et al. 2018). Detailed comparative studies are required to understand what ecological factors promote the evolution of parallel and perpendicularly oriented stripes.

One of the important results of our study is that the relationship between capture success and speed perception differed for parallel and perpendicular striped targets; parallel stripes induced underestimation of speed, whereas perpendicular stripes induced overestimation (Figure 2b). This may be related to how humans process motion signals of striped objects (see Hughes et al. 2015 for a discussion on how motion of targets with parallel and perpendicularly oriented markings are processed). Alternatively, distortion of speed may not be the sole mechanism through which stripes reduce capture success. For instance, perpendicular stripes may benefit from the flicker fusion effect (Pough 1976; Umeton et al. 2017) wherein patterns on an object moving at sufficiently high speeds become blurred, and the blurred patterns enhance background matching. In our study, the flicker rate of perpendicular striped targets was 27.8 Hz which was lower than the refresh rate of the display and the critical flicker fusion threshold of humans (Davis et al. 2015). Thus, we rule out the possibility of perpendicular stripes having a flicker fusion effect. In nature, stripes may benefit a prey through motion dazzle or flicker fusion or both, depending on the background and the critical flicker fusion threshold of the predator. If perpendicular stripes can induce both flicker fusion and motion dazzle effects, such markings should be more beneficial than parallel ones, and therefore more common in prey animals.

Effect of contrast

High contrast between constituent elements has implicitly been considered as prerequisite for motion dazzle markings to be effective, although there is little empirical support for this (Stevens et al. 2011; Hogan et al. 2016b). In the capture experiments, targets with high-contrast stripes (*Parallel-striped*) were caught less often than the uniform black target (*Uniform-black*), whereas the low-contrast striped target (*Low contrast Parallel-striped*) did not differ in capture success from uniform black ones (Figure 3a). Although this suggests that high contrast can enhance the motion dazzle effect, there was no difference in capture success between targets with high- and low-contrast stripes (no difference among *Parallel*, *Low contrast Parallel-striped*, and *Uniform-white*; Figure 3a). Thus, we conclude that contrast can enhance the motion dazzle effect of parallel stripes, but the effect is not strong.

Hogan et al. (2016b) found no effect of stripe contrast on the ability of humans to track moving targets. However, they did not measure capture success, and their high contrast treatment included stripes with 100% contrast, that is, black and white, while the low contrast treatment included dark and pale gray stripes with 50% contrast. In our study, the contrast difference between the high- and low-contrast targets was much stronger—100% for *Parallel-striped* and 20% for *Low contrast Parallel-striped*. We conclude that parallelly oriented motion dazzle stripes may not be selected to have maximal contrast, but stripes with very low contrast may confer no benefit. Thus, prey animals may benefit from having motion dazzle patterns of intermediate contrast when moving and may avoid the cost of conspicuousness associated with strong contrast when still. Further work is needed to understand the role of contrast in the functioning of different types of motion dazzle patterns, especially the interaction between contrast and pattern orientation.

Effect of object size

The smaller objects (1 × 2 cm; area 2 cm^2) received fewer attacks than the larger ones (1 × 4 cm and 2 × 2 cm; area 4 cm^2; Figure 4a). Therefore, the predominant effect appears to be that of the target area. Our results support those from comparative analyses on reptiles suggesting that prey size constrains the evolution of motion dazzle markings (Allen et al. 2013; Murali and Kodandaramaiah 2018). In nature, motion dazzle markings may be more likely to evolve in smaller prey because, in larger prey, any benefit of the markings through the motion dazzle effect is negated by high conspicuousness of the markings, and high capture rates of larger prey. We predict that stripes are less likely to be found in larger prey in general. More comparative analyses on non-reptilian taxa along this direction are needed to test the generality of this prediction. Furthermore, since the type of predator varies among prey animals, the evolution of stripes may be influenced by the prey–predator size ratio rather than by absolute prey size, which will be interesting to test.

Effect of Object speed

The speed of target movement should be an important determinant of capture success, and of the effectiveness of protective patterns (Van damme and Van dooren 1999; Clemente and Wilson 2015). Stevens et al. (2008) found that striped targets were more difficult to capture at higher speeds than at lower speeds. In our study, stripes were just as effective as uniform black at low (Figure 5a) and high speeds (Figure 5c), while being more effective than uniform black at intermediate speeds (Figure 5b). The intermediate speed in this experiment equaled the speed in the other experiments in our study. The absence of a benefit at high and low speeds may be because of low and high capture success, respectively (Figure 5a,c), which negated any potential benefit of stripes. Although we found that the parallel targets (*Parallel-striped*) were perceived to move slower compared to uniform black ones (*Uniform-black*) across all absolute speed values, there was no clear increasing or decreasing effect of absolute speed on the matched speed (Figure 5d,e).

Nevertheless, comparative analyses (on lizards: Halperin et al. 2016 and Murali et al. 2018; on snakes: Allen et al. 2013) and empirical studies (Jackson et al. 1976; Brodie 1992; Rojas et al. 2014) suggest that stripes are more likely to be found in prey that are either more mobile or rely on rapid flight as an escape strategy. It is unclear how speeds in our experiment relate to those of prey under natural conditions. Moreover, selection by predators may not optimize speed to provide the maximal motion dazzle effect, because speed influences other factors such as maneuverability (Clemente and Wilson 2015; Wynn et al. 2015), and interacts with size (Hirt et al. 2017). Given that camouflage colorations might still be effective at very high speed (Brunyé et al. 2019), comparative studies of prey escape speed and color patterns (e.g., Jackson et al. 1976) may further expand our understanding of how prey may have optimized their escape speed in relation to body patterns.

Correlation between capture success and speed perception

Except when the pairwise comparisons involved target size differences (*1 × 2 cm-small rectangle* against *1 × 4 cm-large rectangle*, and *1 × 2 cm-small rectangle* against the two 2 × 2 cm prey), both stimuli in a given comparison moved at the same speed and were of the same size, but some stimuli were perceived to move slower or faster than others (Table 2). These results suggest that the coloration of the stimuli affected the perceived speed of the moving object. Stripes can interfere with capture accuracy if they either increase or decrease perceived speed. When a predator perceives a striped prey to move slower (underestimate speed) or faster (overestimate speed) than the prey's actual speed, the predator may misjudge the future position of the prey and hence direct its attack either "behind" (when it perceives the prey to move slower) or "in front" of the prey (when it perceives the prey to move faster). For example, Murali and Kodandaramaiah (2016) asked human participants to attack the anterior half of moving rectangular targets having uniformly colored posterior halves (i.e., "front") but either stripes or random patterns on the anterior halves (i.e., "behind"). They found that the striped targets were perceived to move slower, and thus reasoned that attacks on these targets were more often directed to the posterior halves compared to that on randomly patterned targets. Extrapolating the same argument to the current study, the target perceived to move significantly slower within a given target pair should consistently be the one more difficult to capture. However, the results do not indicate such a correlation. There were several target pairs where one was perceived to move slower, but there was no difference in capture success between the targets (Table 2). For example, in experiments comparing the influence of target size, although the large target (*1 × 4 cm-large rectangle*) was perceived to move slower, it was caught more often when to compared to the smaller target (*1 × 2 cm-small rectangle*). One explanation is that the

Table 2

Comparison of results from the speed perception (second column) and capture experiments (third column)

	Target that was perceived to move slower	Target with lower capture success
Effect of orientation (Figure 2)		
Uniform-black vs. *Uniform-white*	No difference	No difference
Uniform-black vs. *Parallel-striped*	*Parallel-striped*	*Parallel-striped*
Uniform-black vs. *Perpendicular-striped*	*Uniform-black*	*Perpendicular-striped*
Parallel-striped vs. *Perpendicular-striped*	N/A	No difference
Uniform-white vs. *Parallel-striped*	N/A	*Parallel-striped*
Uniform-white vs. *Perpendicular-striped*	N/A	*Perpendicular-striped*
Effect of contrast (Figure 3)		
Uniform-black vs. *Parallel-striped*	*Parallel-striped*	*Parallel-striped*
Parallel-striped vs. *Low contrast Parallel-striped*	*Parallel-striped*	No difference
Low contrast Parallel-striped vs. *Uniform-black*	*Low contrast Parallel-striped*	No difference
Uniform-white vs. *Parallel-striped*	N/A	No difference
Uniform-white vs. *Parallel-Low Contrast*	N/A	No difference
Uniform-white vs. *Uniform-black*	No difference	No difference
Effect of size (Figure 4)		
1 × 2 cm-small rectangle vs. *1 × 4 cm-large rectangle*	*1 × 4 cm-large rectangle*	*1 × 2 cm-small rectangle*
1 × 2 cm-small rectangle vs. *2 × 2 cm-square 3 striped*	*2 × 2 cm-square 3 striped*	*1 × 2 cm-small rectangle*
1 × 2 cm-small rectangle vs. *2 × 2 cm-square 6 striped*	No difference	*1 × 2 cm-small rectangle*
1 × 4 cm-large rectangle vs. *2 × 2 cm-square 3 striped*	N/A	No difference
1 × 4 cm-large rectangle vs. *2 × 2 cm-square 6 striped*	N/A	No difference
Effect of speed (Figure 5)		
Uniform-black vs. *Parallel-striped* (Low speed)	*Parallel-striped*	No difference (but high capture success overall)
Uniform-black vs. *Parallel-striped* (Medium speed)	*Parallel-striped*	*Parallel-striped*
Uniform-black vs *Parallel-striped* (High speed)	*Parallel-striped*	No difference (but low capture success overall)

N/A indicates that speed perception comparison was not performed.

deviance between actual and perceived speeds was not always large enough to decrease capture rates significantly. In this case, however, we believe that target size influenced the capture success more strongly (because larger targets are easier to catch, see Murali and Kodandaramaiah (2018)), but in the opposite direction to that expected based on perceived speed. Although we found pattern characteristics (e.g., contrast, orientation etc.) to affect perceived speed, we suggest that the lack of a strong correlation between the capture success and speed perception experiments could be because the target characteristics (e.g., speed and size) may have stronger, sometimes opposing, effects on capture success.

On the other hand, when a target was significantly more difficult to capture than another, and we had directly compared the perceived speeds of the target pair, the target that was difficult to capture was always the one that was perceived to move slower (Table 2). An exception was the perpendicular striped target (*Perpendicular-striped*) that was perceived to move faster but attacked less frequently compared to uniform black. We did not record whether attacks were directed “behind” or "in front" of the targets, so we cannot rule out the possibility that perpendicular striped target was caught fewer times because attacks were missed in front of the target. Although we did not test how the target and pattern features affected the perceived direction (Hughes et al. 2017), the fact that we found the target that was difficult to capture was generally the one that was perceived to move slower or faster, suggests that for the given conditions, dazzle stripes mostly work by hindering accurate speed perception. However, stripes may also distort perceived direction. Motion direction was kept constant in the current study, and experiments wherein the targets move erratically will be better suited to test the effect of direction perception distortion. Overall, we conclude that misjudgment of speed per se (both underestimation and overestimation) by prey markings is sufficient to reduce attack accuracy but features of the prey may be important factors determining the efficacy of dazzle colorations.

SUMMARY AND CONCLUSIONS

Results from previous studies on motion dazzle markings have been highly inconsistent, often strongly conflicting with each other, and this inconsistency is partly due to differences in target speed, size, attributes of the stripes, and experimental procedures. We found that stripes, both parallel and perpendicular in relation to the direction of motion, can benefit prey by reducing capture during motion. However, stripes were beneficial only compared to conspicuous uniform colors, but not compared to uniform gray which matched the average luminance of the background. The effectiveness of stripes was dependent on characteristics of both the target (speed and size) and the patterns (contrast and orientation), suggesting that the effect of motion dazzle stripes is conditional. A difference in speed perception between target types did not always correlate with a difference in capture rates. We argue that dazzle markings that distort speed may not necessarily decrease predation rates in nature, and therefore, studies that only test differences in perceived speeds of target types may not be able to confidently make inferences about the fitness benefits of such markings. Thus, we recommend that capture rates should always be incorporated into studies on motion dazzle patterns. Our results shed light on what features of the prey may have affected the evolution motion dazzle stripes, and what aspects of these stripes may be under selection by predators. We believe future studies testing the motion dazzle hypothesis will benefit by considering the above factors. Although experiments with human predators attacking virtual stimuli on touchscreens are popular, they have limitations. For instance, human vision may not accurately mimic that of real predators, and the computer screens cannot replicate the effects of color patterns on three-dimensional prey. Therefore, studies also need to focus on evolution of patterns of real prey animals through experiments (e.g., Hämäläinen et al. 2015; Zlotnik et al. 2018) and comparative analyses.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided Kodandaramaiah et al. (2019).

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