Report

Current Biology

Pattern and Speed Interact to Hide Moving Prey

Highlights

- The effectiveness of a pattern to camouflage moving animals is speed dependent
- High-contrast stripes are effective at hiding prey moving with sufficient speed
- Stripes make prey less visible than background-matching patterns as speed increases
- Combined with the appropriate pattern, movement can make, not break, camouflage

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In Brief

By presenting praying mantids with artificial moving prey, Umeton et al. show that the camouflage efficacy of a pattern depends on the speed at which an animal moves. Surprisingly, with increasing speed, high-contrast striped prey become better camouflaged than prey with a background-matching pattern.

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Report

Pattern and Speed Interact to Hide Moving Prey

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SUMMARY

Evolutionary biologists have long been fascinated by camouflage patterns that help animals reduce their chances of being detected by predators [1–4]. However, patterns that hide prey when they remain stationary, such as those that match their backgrounds [5, 6], are rendered ineffective once prey are moving [7–10]. The question remains: can a moving animal ever be patterned in a way that helps reduce detection by predators? One long-standing idea is that high-contrast patterns with repeated elements, such as stripes, which are highly visible when prey are stationary, can actually conceal prey when they move fast enough [11–14]. This is predicted by the "flicker fusion effect," which occurs when prey move with sufficient speed that their pattern appears to blur, making them appear more featureless and become less conspicuous against the background [2, 8]. However, although this idea suggests a way to camouflage moving prey, it has not been empirically tested, and it is not clear that it would work at speeds that are biologically relevant to a predator [13]. Combining psychophysics and behavioral approaches, we show that speed and pattern interact to determine the detectability of prey to the praying mantis (*Sphodromantis lineola*) and, crucially, that prey with high-contrast stripes become less visible than prey with background-matching patterns when moving with sufficient speed. We show that stripes can reduce the detection of moving prey by exploiting the spatiotemporal limitations of predator perception, and that the camouflaging effect of a pattern depends upon the speed of prey movement.

RESULTS

Using an established laboratory system [15–17], we compared the predatory behavior of African lined mantids toward five different prey types moving across a background chosen to resemble the statistics of natural images [18] (Figure 1). The mantid visual system is highly tuned to detect motion [15, 19–24] and is sufficiently well characterized to allow us to model when mantids should experience the "flicker fusion effect" and predict associated changes in the visibility of our moving prey [15, 17, 25] (see STAR Methods for full details). Whereas previous studies have suggested that certain patterns can cause predators to slightly misjudge the speed or trajectory of moving prey and make them more difficult to capture, we show how pattern and speed combine to reduce the visibility of the prey themselves.

Based on our calculations, we selected three different speeds (slow, medium, and fast) and two different striped prey (wide and narrow stripes; Figures 1B and 1C; Table 1), chosen such that the patterns of narrow-striped prey were predicted to increasingly blur through the flicker fusion effect at medium and high speeds, whereas the stripes of the wide-striped prey should remain resolvable across all three speeds. When flicker fusion occurs at these higher speeds, the loss of contrast in the pattern of the narrow-striped prey should effectively make them appear featureless and uniform gray, making them not only less visible than the wide-striped prey but also less visible than prey with patterns that match their background (see STAR Methods for full details). To test these predictions, we included uniform gray prey and prey whose texture matched the background (Figures 1D and 1E). We predicted that narrow-striped prey would become better camouflaged than both the wide-striped and background-matching prey with increasing speed. In addition, predators' responses toward narrow-striped prey should be the same as those toward gray prey at the higher speeds if blurring was indeed occurring. Finally, we included a uniform black prey (Figure 1F) as a control for the effects of speed independent of motion blur, which should remain visible at all speeds.

Overall, we found a significant interaction between prey type and speed ($\chi^2 = 26.312$, $p < 0.001$, degrees of freedom [df] = 8; Figure 2). Increasing speed had no significant effect on mantids' predatory responses toward our control black prey, which attracted a consistently high response rate across all three speeds ($\chi^2 = 5.546$, $p = 0.062$, df = 2). This rules out any effect of speed per se on the likelihood that mantids respond to our prey (for example, because they become harder to catch at higher speed), and ensured that any changes in the responses toward our patterned prey were due to speed-dependent changes in their visibility.

As predicted, speed differentially affected the detectability of wide-striped and narrow-striped prey: whereas speed had no significant effect on predatory responses toward wide-striped prey ($\chi^2 = 3.322$, $p = 0.190$, df = 2), responses to narrow-striped prey were reduced with increasing speed ($\chi^2 = 29.72$, $p < 0.001$, df = 2). Whereas mantids were equally likely to respond to narrow-striped and wide-striped prey at the slow speed ($\chi^2 = 2.270$, $p = 0.132$, df = 1), they were less likely to respond to narrow-striped than wide-striped prey at medium

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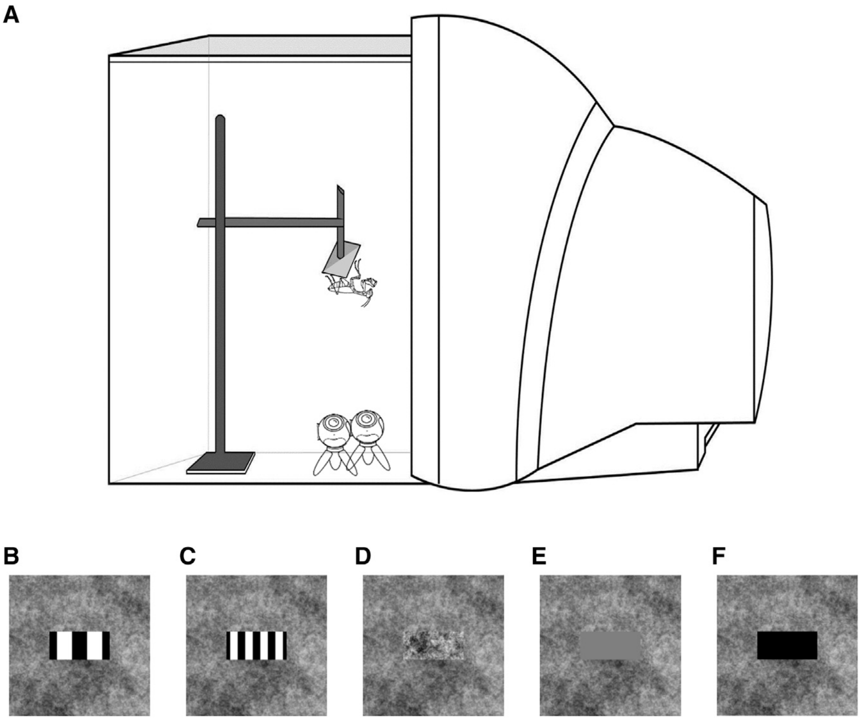

Figure 1. Mantids Viewed Moving Prey in the Laboratory

(A) The experimental setup, showing the position of the mantids to the monitor where prey were presented and the position of the cameras to record behavior.

(B–F) The five computer-generated prey types visualized against the natural textured background: wide-striped prey (B), narrow-striped prey (C), background-matching prey (D), gray prey (E), and black prey (F). Prey types (B)–(E) and the background had the same mean luminance.

(χ^2 = 10.49, p = 0.001, df = 1) and fast speeds (χ^2 = 24.49, p < 0.001, df = 1). Therefore, in line with our model and predictions, both kinds of striped prey were equally visible and attractive to mantids when moving slowly, but the narrow-striped prey became dramatically less detectable than the wide-striped prey when moving faster.

We also found that the narrow-striped prey were more camouflaged than background-matching prey at the two higher speeds. At the slow speed, background-matching and narrow-striped prey elicited similar levels of response (χ^2 = 2.16, p = 0.141, df = 1), but narrow-striped prey became less likely to elicit responses at medium and fast speeds (medium, χ^2 = 6.95, p = 0.008, df = 1; fast, χ^2 = 6.76, p = 0.009, df = 1). Whereas numerous studies of stationary prey have shown that background matching offers a simple and highly effective form of camouflage and that high-contrast stripes make prey extremely conspicuous (e.g., [2, 5, 7]; reviewed in [4, 7, 26]), we show that surprisingly, the reverse is true when prey move at sufficient speed.

If this reduction in visibility in the narrow-striped prey is indeed the result of the flicker fusion effect, the narrow-striped prey should appear isoluminant gray at medium and fast speeds and elicit responses similar to the gray prey at these two higher speeds. This was indeed the case: the mantids responded similarly to narrow-striped and gray prey when they were moving at the medium (χ^2 = 0.127, p = 0.722, df = 1) and fast speeds (χ^2 = 0.0597, p = 0.807, df = 1), but the narrow-striped prey were more likely than gray prey to elicit a response from a mantid when moving at the slow speed (χ^2 = 7.01, p = 0.008, df = 1), as would be expected if the stripes of the narrow-striped prey are appearing blurred to the predator through the flicker fusion effect.

DISCUSSION

We show that a moving animal can be patterned in a way that helps reduce detection by predators. Specifically, we find that the spatial features of patterns can interact with speed of movement to reduce predatory responses, and that even high-contrast patterns can effectively camouflage prey when moving with sufficient speed. Therefore, unlike other well-studied forms of camouflage pattern where movement makes prey more visible to predators [5, 7], we find that patterned prey can become less visible as their movement increases.

Our data are consistent with the idea that flicker fusion is the perceptual mechanism underlying the camouflaging effect: using

Table 1. Properties of the Two Striped Prey Patterns

Stripes	Width (px)	Period (px)	FSf (cyc/px)	LFSf (cyc/°)	Speed	Speed (px/s)	FTf (Hz)
Wide	16	32	0.0313	0.055	slow	129	4.0
					medium	259	8.1
					fast	501	16
Narrow	8	16	0.0625	0.108	slow	129	8.1
					medium	259	16
					fast	501	31

For wide- and narrow-striped prey: stripe width in pixels; spatial period in pixels; fundamental spatial frequency measured in cycles per pixel (FSf); lowest fundamental spatial frequency measure as cycles per degree at the center of the screen (LFSf); speed treatment; speed measured in pixels per second; fundamental temporal frequency measured in Hz (FTf).

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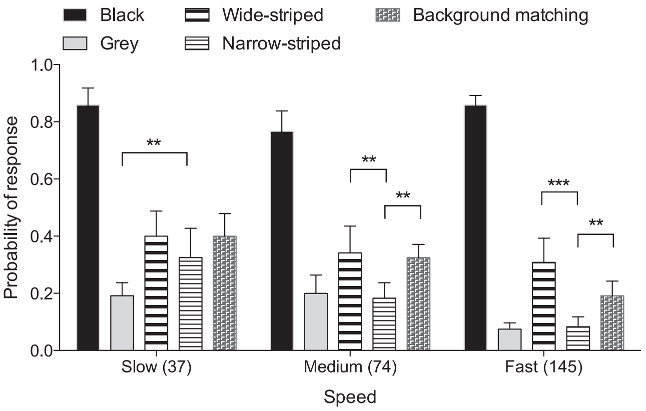

Figure 2. The Mean (+SEM) Probability that Praying Mantids (n = 12) Responded toward the Five Different Prey Types

Each prey type was presented 10 times to each mantid at each of the three speeds. $^{**}p < 0.01$, $^{***}p < 0.001$ for our planned pairwise comparisons between narrow-striped prey and the wide-striped, background-matching, and gray prey types.

empirical measures of mantid contrast sensitivity from their optomotor response [15], we were able to predict the responses to small prey targets surprisingly well. However, we currently cannot rule out that other perceptual mechanisms may be involved. For example, light and dark edges could interact antagonistically and disrupt the responses of motion-detecting visual neurons, if they occur closely enough together in space and time [27, 28]. Our study therefore opens up questions about exactly how speed and pattern of moving prey combine to camouflage animals from predators. The flicker fusion effect is particularly amenable to testing in natural predator-prey systems: it makes clear predictions about what specific combinations of patterns and movement speeds will help to hide moving prey [11, 13], based on the environmental and viewing conditions [13] and the spatiotemporal contrast sensitivity function (at least part of which, e.g., the critical flicker fusion rate, is available for a wide range of animals [29]). Similarly, it could be that the flicker fusion effect operates in other behavioral contexts, for example, where predators may hide their approach to prey, or in courtship or antagonistic displays. It is already well established that animals use visual illusions during courtship and mating displays [30], and the exploitation of such visual effects may be more widespread than previously thought.

Our novel finding that stripes can reduce the detection of moving prey by exploiting the spatiotemporal limitations of predator perception opens up new avenues of research in animal camouflage. Importantly, we have shown that these perceptual mechanisms can promote camouflage in moving prey at speeds that are ecologically relevant: our prey speeds were typical of those of small insects (e.g., [31–33]), and reliably elicit responses from mantids ([34–36]; see also Figure 2, black prey). In fact, our calculations predict that a bumblebee's stripes reduce its visibility to a praying mantid when the bee is in flight [13]. Demonstrating the ecological validity is an important principle to establish, and suggests that the benefits of pattern and speed interacting to reduce visibility may not be limited to very fast moving prey, as previously thought [11, 14, 37].

It is also likely that patterns could be selected to serve multiple speed-dependent defensive functions, potentially aimed at different types of predator. For example, a bumblebee's stripes could be a conspicuous aposematic signal deterring avian predators when stationary, yet help camouflage it from a hunting praying mantid when in flight [8, 13]. This idea has been suggested in previous studies on snakes [11, 38], but is theoretically possible for a range of other species [29]. Alternatively, stripes could be selected for signaling in different contexts: by moving in different ways, animals could change their appearance for different receivers, such as advertising to potential mates and avoiding would-be predators [2]. These intriguing possibilities not only offer ways in which stripes could evolve and enable camouflage at speed but also open up new perspectives in the study of animal patterns more broadly.

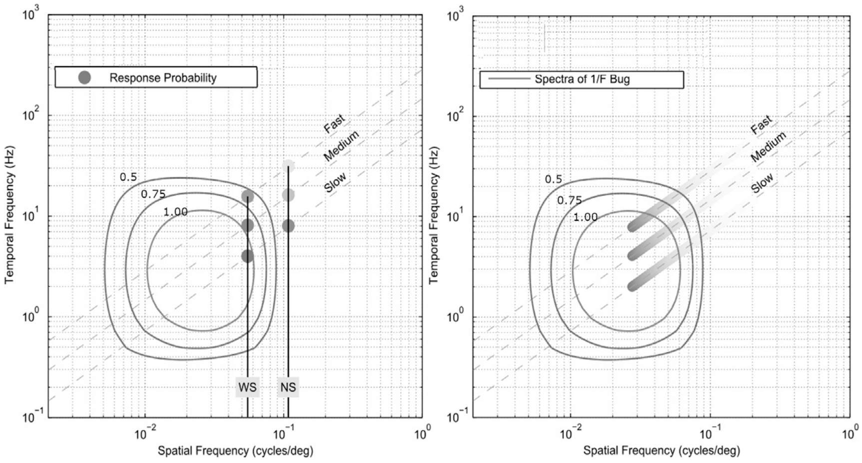

Figure 3. Visibility of Different Spatial and Temporal Frequencies, with Stimulus Content Indicated

The contour lines represent different levels of praying mantid contrast sensitivity, estimated by interpolation from the data of Nityananda et al. [15] on optomotor response to wide-field stimuli. Numbers on the contours represent the proportion of maximum sensitivity (sensitivity is estimated as maximal everywhere within the 1.0 contour).

(A) The dots represent the fundamental spatial and temporal frequencies of the wide-striped (WS) and narrow-striped prey (NS) when moving at the three different speeds. The dots' gray shades reflect the response rate observed during the experiment: darker gray dots correspond to higher rates, and lighter gray dots correspond to lower. As expected, more visible stimuli elicit more responses.

(B) The pattern of the background-matching prey contained a range of spatial frequencies, producing a range of temporal frequencies when they move, roughly indicated by the gray shading lines. Most power was at low frequencies. This means that at all speeds, the background-matching prey contain some frequencies to which the mantids are extremely sensitive, likely explaining why it remains relatively visible at high speeds.

Considering the perceptual processes underpinning motion detection also helps to explain why being uniform is so effective at reducing detection for moving targets, even more so than background-matching patterns [7, 9, 39]. Classical motion detectors respond to spatiotemporally correlated changes in luminance [40], which can occur from the moving edges of the prey across the background, and from the internal contrast of the prey's pattern. The uniformly gray prey are less likely to trigger motion detectors than background-matching prey on both counts: they offer no moving luminance features, and they contrast on average to a lesser degree with the background. Background-matching prey have patterns with dark and light parts that will trigger the predator motion detectors more when moving against opposing darker or lighter patches of the background. Natural scenes and textures typically have most variation at coarse spatial scales [18], so prey that match the background will necessarily have most variation at scales matching their body length (the longest scale available to them). These scales require much faster speeds to appear uniform than narrow stripes, which are much finer than the body length (Figure 3B). This likely explains why our background-matching prey were so much more visible than narrow-striped prey at the higher speeds, when we predict that the stripes had already exceeded the spatiotemporal limitations of the predator. This suggests that although static prey should match the background, moving prey may benefit from appearing unpatterned and matching the mean luminance of their background (e.g., [7, 9, 39]), an idea supported by evidence from studies of cuttlefish that reduce the physical contrast within their patterns when they move (e.g., [41]). Currently, little is known about how different selection pressures have shaped how animals move and are patterned [10], but our work highlights how natural selection is likely to act on the interaction of both.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

Conceptualization, D.U. and C.R.; Methodology, D.U., G.T., J.C.A.R., and C.R.; Software, G.T.; Formal Analysis, D.U., J.C.A.R., and C.R.; Investigation, D.U. and E.F.; Writing and Visualization, D.U., G.T., J.C.A.R., and C.R.; Funding Acquisition, D.U., J.C.A.R., and C.R.; Supervision and Project Administration, J.C.A.R. and C.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Raw data and videos	This paper	https://doi.org/10.25405/data.ncl.8869919.
Software	This paper	https://github.com/m3project
Experimental Models: Organisms/Strains		
African lined mantids (*Sphodromantis lineola*)	Metamorphasis	N/A

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Candy Rowe (candy.rowe@ncl.ac.uk). This study did not generate unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We acquired adult female African praying mantids (*Sphodromantis lineola*) from a UK breeder. Mantids were housed individually in plastic boxes (17cm L x 17cm W x 19cm H), which were perforated to facilitate ventilation, and stored in an insect housing facility at 25°C on a 12:12 light/dark cycle. Mantids were fed a single cricket (*Gryllodes sigillatus*, 18-25mm) twice a week, and the individual boxes were cleaned and sprayed with a fine mist of water weekly.

METHOD DETAILS

Experimental set-up and procedure

The experimental set-up consisted of a metal stand holding a Perspex perch (5 cm x 5 cm), from which the mantids hung upside-down, and which was clamped 4 cm away from a CRT screen to ensure that each mantis had a viewing distance from the screen of 2.5 cm, which is the preferred distance for mantids to capture their prey [36, 42] (Figure 1). The CRT screen (Hewlett-Packard 21'' color monitor P1130) was 40.4 cm x 30.2 cm, with pixel dimensions of 1600 px x 1200 px, and subtended a visual angle of 165.9 degrees at the viewing distance of the mantis. The CRT monitor was gamma corrected using a Minolta LS-110 photometer (gamma = 2.0) and had a maximum luminance of 103 cd/m^2, which we call ‘white’. During experiments, the mean luminance of the stimuli was half this maximum, 51.4 cd/m^2, which we call ‘gray’. ‘Black’ means the minimum luminance of the monitor, < 0.5 cd/m^2. The monitor’s refresh rate was 80 Hz (mantids are reported to not perceive flicker above 50 Hz [19]), which was sufficiently fast to eliminate temporal aliasing (the highest temporal frequency in our experiments was 31Hz). Two cameras (Kinobo USB B3 HD Webcam, Point Set Digital Ltd, Edinburgh, Scotland) were placed below the metal stand and next to the CRT monitor. One of these was an observation camera, which was connected to a computer (DELL OptiPlex 9010) and positioned so that the experimenter could use it to check alignment and to score response behavior blind to the stimulus being presented on the screen. The second camera had a broader field of view, including of the stimuli being presented, and was used to record the experiments for any potential follow-up (this was not necessary in this experiment). The set-up was enclosed to avoid mantids being visually distracted by the experimenter or by other movements in the experimental room. All experiments were run with the lab lights turned off, so the only light came from three computer monitors: the CRT monitor in front of the mantis and the two LCD monitors used by the experimenter.

Once an individual mantis was positioned on the viewing platform, it was left to acclimatize for 10 minutes. After that, a simulated ‘fly’ stimulus was presented which consisted of a black fly-shaped stimulus spiralling at a decreasing speed from the edge to the center of the screen against a high contrast black-and-white chequer background. The simulated fly attracted the mantid’s attention toward the center of the screen. If further centring was required, the high contrast full-screen chequer pattern could be moved left and/or right to elicit the optomotor response to ensure that the mantid was looking toward the center of the screen. Once the animal was fully aligned and responsive, the experiment began. Sometimes during the experiment, it was necessary to re-center a mantid’s attention toward the center of the screen, which we did by using the simulated fly and chequerboard pattern. Animals that stopped responding or vacated the viewing platform, for any reason, were returned to their housing box for a minimum of 30 minutes before being replaced on the platform for continuation.

As the experiment was performed, an observer recorded whether or not a mantid responded to each prey stimulus presented, blind to the prey type being shown on the screen. A mantid's response to a detected prey included: tracking (moving the head and/or the prothorax to follow the moving prey) and any other body and leg movements indicative of prey detection [43].

Subsequently, these judgments were independently confirmed by two naive observers. These observers viewed the videos recorded by the second webcam, after these had been masked with a black rectangle covering the whole video above a boundary chosen to ensure that the moving stimulus was never visible, and recorded whether or not they believed the mantis had responded to a stimulus. Despite the fact that these observers were not experienced with mantis behavior and were viewing different videos from those available during the experiment, scores were extremely consistent. Cohen's kappa was 0.83 between the two naive observers, and 0.78 and 0.88 respectively between each naive observer and the original experimenter. A kappa of 0.75 is generally taken to show excellent agreement.

Eighteen female mantids were given an experimental session consisting of 150 prey presentations, 30 of each of the five prey types, with each prey type being presented 10 times at each of the three speeds. Each presentation was separated by a variable inter-stimulus interval (from 15 to 90 s), and prey types were presented in pseudo-random order. Experimental data from a mantid were only included in our analyses if all 150 trials were completed, and the response rate to the black prey presentations was at least 50%. We employed these criteria to ensure that each mantid was sufficiently responsive to our prey types to allow us to test our hypothesis (female mantids require fewer nutrients and become less responsive to prey as they age). 12 mantids completed all 150 trials with a response rate above 50% toward the black prey.

Computer-generated stimulus background

All stimuli were programmed and rendered using Psychophysics Toolbox 3 for MATLAB (Mathworks, Massachusetts, US) [44–46]. Prey moved across a textured background which filled the screen. The background had a $1/f^2$ spatial frequency power spectrum, chosen because it resembles that of natural scenes [18]. Specifically, to generate the pattern, the Fourier amplitude of the component with spatial frequency f was $|FT| = 0.05 / (f + 10^{-10})$. The phase of each Fourier component was random, and generated uniquely for each prey presentation (the phase was taken from the Fourier phase spectrum of a white noise pattern where the value of each pixel was picked from (0,1) with a random uniform distribution). The pattern was then multiplied by a value such that its mean value was 0.5, the pixel value corresponding to the monitor mean luminance of 51.4 cd/m^2. The contrast was then made as high as possible without bringing the value of the highest pixel above 1, corresponding to the monitor's maximum luminance, or the value of the lowest pixel below 0, corresponding to its minimum. This produced an RMS contrast (standard deviation of the pixel values) of 0.12.

Computer-generated prey stimuli

Simulated prey consisted of a rectangle (dimension: 64 × 30 pixels, corresponding to 1.6 × 0.76 cm) moving horizontally across the screen, either from left to right or vice versa (equal numbers of each occurred in both directions in a randomized sequence). The prey speeds were 129, 259 and 501 pix/s, corresponding to 3.3, 6.5 and 12.7 cm/s. The prey size and speeds were both ecologically relevant [13, 31–34], and established as eliciting mantis responses in pilot work. Given that the speeds used are below those that elicit the strongest strike responses in mantids [34–36] and flicker fusion becomes more likely the faster prey moves, our study is likely to underestimate the capacity for the flicker fusion effect to work against these predators.

The conversion of prey size and speeds to angular units is complicated by the extremely close viewing distance (2.5 cm from the planar monitor). For instance, the instantaneous angular speed of the 'fast' prey, moving at 501 pix/s, ranged from ~50 deg/s at the edges of the screen to ~300 deg/s when it was at the center. The average across the central 1200 px window was 145 deg/s. Table 1 specifies the fundamental spatial frequency of the narrow and wide stripe patterns, averaged across one period when the prey is at the center of the screen [15]:

$$SF[\mathrm{cpd}] = \left(2 \times arctan\left(\frac{Period[px]}{2 \times Screenresolution[pix/cm] \times Viewingdistance[cm]}\right)\right)^{-1} \qquad \text{(Equation 1)}$$

There were five different prey types used in testing: wide- and narrow-striped, background matching, gray and black (Figures 1B–1F). Striped prey had either two (wide-striped) or four (narrow-striped) cycles of vertical square-wave alternations between black and white. In each case, a black stripe was centered on the rectangle and two black quarter-cycles formed the vertical edges of the rectangle. The stripes were oriented perpendicularly to the motion vector to ensure that the elements could fully blur into uniformity while moving [13].

Background matching prey consisted of a rectangle cut from a background texture generated as described above. Grey prey were simply a uniform gray rectangle. Both of these, and both striped prey, had the same mean luminance as the background texture of 51.4 cd/m^2.

Finally, we included black prey as a control, with uniform luminance < 0.5 cd/m^2. Objects like this, darker than their background, are particularly visible and attractive to mantids (e.g., [20]) so this enabled us to ensure that mantids remained responsive during the experiment by requiring them to respond to at least 50% of the black prey. The luminance decrement of the black prey is unaffected by speed, so these also control for the effect of prey speed, independent of changes in pattern visibility.

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Spatio-temporal contrast sensitivity function and estimated prey visibility

As the striped prey move over a given location, the luminance flickers from black to white and back again. Flicker fusion occurs when the pattern elements alternate so fast in the visual field of the predator that it can no longer visually resolve them [13, 14]. This effect has been well studied in the field of visual psychophysics [47, 48], making it possible to predict when flicker fusion should occur in the eyes of a predator, and consequently, when we should see lower detectability of patterned prey. Depending on the stimulus contrast and spatial frequency, flicker fusion for a given stimulus may occur at much lower temporal frequencies than the critical flicker fusion of photoreceptors, reflecting spatiotemporal interactions elsewhere in visual processing. This is quantified by the predator's spatio-temporal contrast sensitivity function.

Narrow-striped patterns are predicted to blur into uniformity at lower temporal frequencies than wide-striped [47], for two reasons. First, the fundamental temporal frequency depends on the width of the stripes and the speed of the prey:

$$TF[Hz] = Speed[px / sec] \times SF[cycle / \mathrm{px}] \quad \text{(Equation 2)}$$

where SF is specified by Equation 1. TF is the lowest temporal frequency associated with the alternation between black and white. Since the transition was abrupt, higher harmonics were also present (odd-integer multiples of the fundamental). Table 1 specifies the fundamental temporal frequencies for our striped prey.

Equations 1 and 2 show that, at a given speed, temporal frequencies are higher for narrower stripes. Furthermore, flicker fusion occurs at lower temporal frequencies for lower contrast and finer spatial scales. Both these factors mean that flicker fusion is predicted to occur earlier for the narrow-striped than the wide-striped prey.

Data on the contrast sensitivity function of *S. lineola* were available from our previous paper [15], although this assessed visibility using the optomotor response to wide-field stimuli and thus may not accurately predict the visibility of small prey objects. Using the Curve Fitting toolbox for MATLAB, we interpolated our previous contrast sensitivity data using the interp2 function with the spline method. This enabled us to calculate the contour lines corresponding to 0.5, 0.75 and 1 normalized contrast sensitivity (Figure 3).

In Figure 3A, we have superimposed on these contours the fundamental frequency of our wide and narrow-striped prey. The spatial frequency is fixed for each prey type, but the temporal frequency depends on speed. If the contrast sensitivity estimated from optomotor response applies to prey, we would expect the wide-striped prey to be visible at all three speeds, since its fundamental frequency lies within the contour of half-maximal sensitivity at all three speeds (blue line in Figure 3A). Conversely, even the lowest spatial frequency of the narrow-striped prey pattern is toward the upper end of mantis spatial resolution as estimated from the optomotor response, and its temporal frequency is also shifted toward higher frequencies that mantids perceive less well. Thus, despite the pattern's high contrast on the screen, its effective contrast for the mantis visual system is low, especially at high speeds (Figure 3A).

Since the background-matching prey had a $1/f^2$ power spectrum, most of its contrast power is at the lowest frequency consistent with its size, i.e., half the frequency of the wide-striped prey (Figure 3B). Thus, while background-matching prey had low internal contrast compared to the striped prey, most of that contrast occurred at frequencies to which the mantis is very sensitive, for all three speeds (Figure 3B).

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analysis were performed using R (version 3.5.2, ''Eggshell Igloo''), https://CRAN.R-project.org/. Models were fitted using function glmer of package lme4. All models used logistic regression with a binary outcome variable (whether or not a stimulus elicited a response) and a random effect of mantid. To analyze the full dataset, we included two categorical fixed-effect predictors: one representing prey type (five levels: black, wide-striped, narrow-striped, gray, background-matching) and one speed (three levels: slow, medium, fast). To assess the significance of the speed and pattern interaction, we performed ANOVA comparing the model with versus without interaction terms (df = 8). To examine the effect of speed on a particular prey type, we used a similar model of the data for that prey type only, with speed as the only fixed-effect predictor (df = 2). To assess the significance of speed, we performed ANOVA comparing this model to a model with only the intercept term. To carry out pairwise comparisons between two prey types at a particular speed, we analyzed the data for that speed and those two prey only, and performed ANOVA comparing a single two-level categorical predictors for prey type versus only the intercept (df = 1). All ANOVAs used the likelihood ratio test for significance ($p < 0.05$).

DATA AND CODE AVAILABILITY

Experimental software is available via https://github.com/m3project. The accession number for the original videos and datasheets generated through this study have been deposited to Newcastle University data repository: https://doi.org/10.25405/data.ncl.8869919.