



Anuran predators overcome visual illusion: dazzle coloration does not protect moving prey

Sara Zlotnik¹ · Geena M. Darnell¹ · Ximena E. Bernal^{1,2}

Received: 22 December 2017 / Revised: 19 May 2018 / Accepted: 13 June 2018 / Published online: 19 June 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Predators everywhere impose strong selection pressures on the morphology and behavior of their prey, but the resulting antipredator adaptations vary greatly among species. Studies of adaptive coloration in prey species have generally focused on cryptic or aposematic prey, with little consideration of color patterns in palatable mobile prey. Complex color patterns have been proposed to decrease the ability of visual predators to capture moving prey (motion dazzle effect). Most support for this hypothesis, however, comes from experiments with human subjects and simulated prey. We tested the motion dazzle effect using, for the first time, natural predators (cane toads, *Rhinella marina*) and live prey (house crickets, *Acheta domesticus*) with altered color patterns. We found no support for the motion dazzle effect as striped crickets did not fare better than solid colored ones. Crickets that spent more time moving, however, were more likely to be eaten. Our results suggest that motion specialized visual predators such as toads overcome the motion dazzle effect and impose stronger selection pressure on prey behavior than on coloration. These findings emphasize the importance of sensory specializations of predators in mediating antipredator strategies.

Keywords Motion dazzle · Camouflage · Antipredator adaptation · *Bufo marinus*

Introduction

Predators impose strong selection pressures on their prey, shaping the evolution of prey morphology and behavior (Ruxton et al. 2004). Many prey, for example, have evolved cryptic color patterns and a tendency to remain immobile when threatened (Stevens and Merilaita 2011). While camouflage can be an effective antipredator strategy for static prey, moving prey should rely on different color patterns as motion generally precludes crypticity (Hall et al. 2013). High-contrast color patterns, or ‘dazzle’ coloration, have been proposed to make moving prey more difficult to capture

by interfering with a predator’s perception of speed or direction (Thayer 1909). This motion dazzle effect has been invoked to explain seemingly conspicuous color patterns in a wide range of palatable moving animals (Stevens 2007). Although humans find striped stimuli harder to catch than certain solid colored stimuli (Stevens et al. 2008; Hughes et al. 2014), the motion dazzle effect has only been experimentally tested once in non-human predators (Hämäläinen et al. 2015), and never with live prey.

The effectiveness of motion dazzle coloration can be influenced by characteristics of prey movement such as speed (Scott-Samuel et al. 2011). Most experimental tests of this visual illusion, however, use simulated prey displaying constant or random motion (e.g. Hogan et al. 2016), and natural prey movement patterns have not been considered. Examination of both coloration and movement simultaneously when comparing escape strategies is critical for understanding how these traits evolve under predation pressure (Forsman and Appelqvist 1998). Certain color patterns in snakes, for example, tend to co-occur with specific types of antipredator behaviors, such as longitudinally striped species favoring rapid flight (Jackson et al. 1976; Pough 1976; Allen et al. 2013). Here, we investigate how these two factors,

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10071-018-1199-6>) contains supplementary material, which is available to authorized users.

✉ Sara Zlotnik
szlotnik@purdue.edu

¹ Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA

² Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama

coloration and movement, affect capture rate within a predator–prey system.

We tested the effects of motion dazzle coloration and prey movement using cane toads (*Rhinella marina*) presented with hand-painted house crickets (*Acheta domesticus*). Cane toads are an ideal group in which to investigate these effects as they are voracious predators that consume a wide range of invertebrate prey (Meshaka and Powell 2010). Based on the motion dazzle effect, we predicted that solid colored crickets would be caught more quickly than striped crickets. Furthermore, as toads are highly specialized to detect moving prey (Satou and Shiraishi 1991; Buxbaum-Conradi and Ewert 1999), we expected the proportion of time that crickets spent moving to be positively associated with their probability of being eaten. We discuss our findings in the light of the sensory specializations of visual predators.

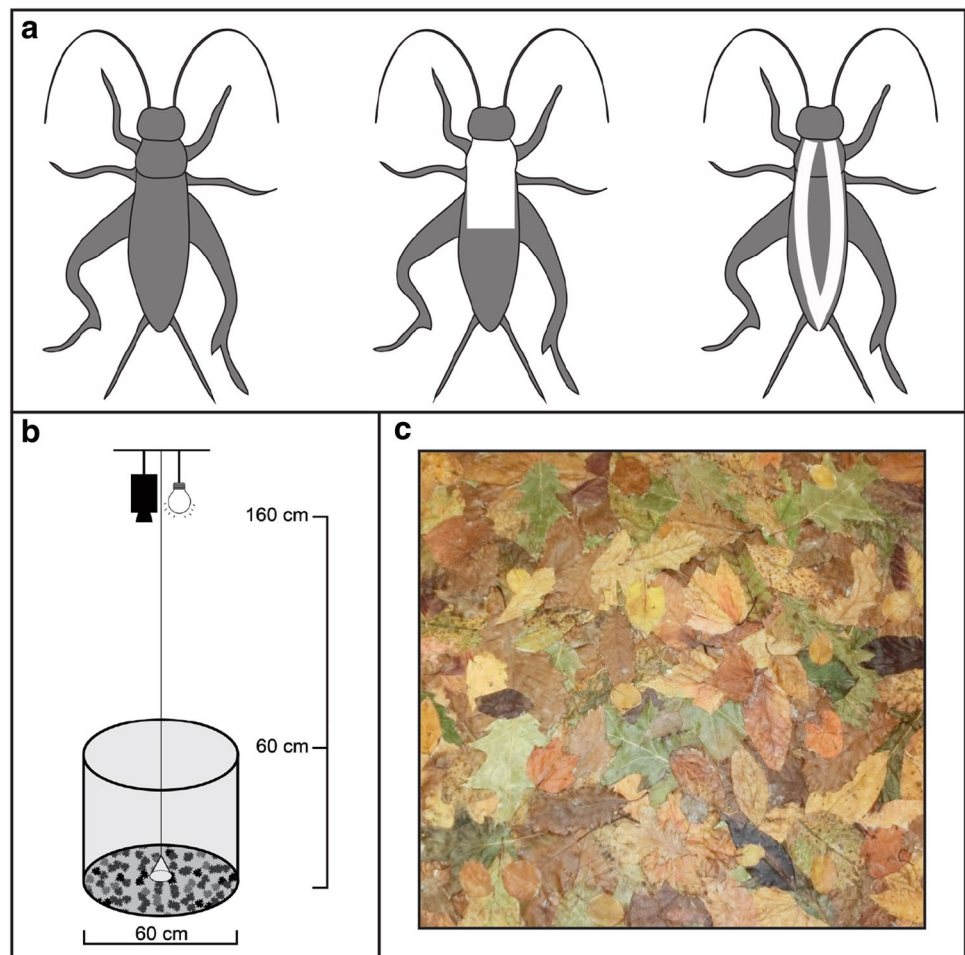
Methods

Study organisms

We collected 11 adult male cane toads in Fort Pierce, Florida, USA, and transported them to the animal facility at Purdue University in Indiana, USA. The toads were individually housed and allowed to acclimate to living in captivity and feeding on crickets for 2 months prior to testing. For their prey, we purchased house crickets and painted them in three ways (control, solid white, and white stripes, Fig. 1a) using nontoxic nail polish (Karma Organic Nail Polish). For the high-contrast striped treatment, we painted two white longitudinal stripes down the dorsum of each cricket. We compared this pattern with a solid white treatment, in which a white rectangle was painted over the dorsum, and a control treatment, in which we painted an equal-sized rectangle with clear nail polish. All treatments covered approximately the same proportion of the cricket's dorsum with nail polish.

To confirm high internal contrast between the white paint and the cricket dorsum, we measured the reflectance

Fig. 1 **a** Color patterns applied to crickets (left to right): control, solid white, and white stripes. **b** Set-up of the behavioral arena with a camera and light suspended above and a funnel to remotely release the toad. **c** Base of the behavioral arena covered with fallen leaves in shades of brown and yellow. (Color figure online)



spectra of the crickets using a StellarNet Black Comet portable spectroradiometer (StellarNet, Inc., Florida, USA). We took measurements of the white nail polish, the cricket dorsum, the cricket with clear nail polish, and, as a reference, a halon white standard (StellarNet RS50, > 97% reflectance). Detailed methods and a figure showing the reflectance spectra can be found in Online Resource 1. The cricket dorsum with and without clear nail polish yielded nearly identical reflectance spectra, indicating that the control treatment does not affect a cricket's visual appearance. The white nail polish had a similar reflectance spectrum to the white standard, although the nail polish was brighter within the 500–800 nm range (Fig. S1). Neither the cricket nor the white nail polish showed substantial reflectance below 400 nm, but above this wavelength the white nail polish had consistently higher reflectance than the cricket dorsum. Based on these spectra, we are confident that the white patterns would contrast strongly against the cricket dorsum for visually oriented predators.

Experimental protocols

We constructed a circular arena with an acrylic base (60 cm diameter) and walls made of paper-coated chicken wire (60 cm height, Fig. 1b). To create a complex background, we glued flattened leaves of various shades of brown and yellow to the base (Fig. 1c). At the start of each experimental trial, we placed a toad under an opaque funnel at the center of the arena and gave it 3 min to acclimate before remotely releasing it into the arena. For details on experimental conditions, see Online Resource 1.

We ran two behavioral experiments to account for differences among group sizes in the effectiveness of motion dazzle coloration for avoiding capture (Hughes et al. 2015). In Experiment 1, a toad was placed in the arena with nine crickets, three of each color treatment. After 6 min, we removed the toad and counted the number of each cricket type remaining. All 11 toads went through four to seven trials of Experiment 1 over the course of a month, for a total of 56 trials.

In Experiment 2, toads went through three randomly ordered trials, one for each color treatment. In each trial, one cricket was placed in the arena and the toad was given 10 min to eat it. Using videos recorded during these single cricket trials, two independent observers measured the time until each cricket was eaten, or until the trial ended, and the proportion of that time that the cricket spent moving. The crickets generally moved by walking along the edges of the arena and sporadically jumping longer distances. Ten toads completed Experiment 2, and some repeated the set of three trials on multiple days, for a total of 60 successful trials.

Statistical analyses

For each experiment, we ran a binomial generalized linear mixed effects model using package 'lme4' (Bates et al. 2015) in R 3.4.1 (R Core Team 2017). In Experiment 1, we tested whether each cricket's color treatment affected its likelihood of being eaten (Model: Eaten/Not ~ Treatment + (1|Toad/Trial)). In Experiment 2, we also included the proportion of time crickets spent moving as a predictor (Model: Eaten/Not ~ Treatment + Movement + (1|Toad) + (1|Order)). We then ran a Cox proportional hazards model using package 'coxme' (Therneau 2015) to examine how color pattern and movement affected the time until crickets were eaten (Model: Time Until Eaten ~ Treatment + Movement + (1|Toad) + (1|Order)). For all models, toad identity and either trial number (1–56; Exp. 1) or testing order (1, 2, 3; Exp. 2) were included as random factors. We used log likelihood ratio tests to determine whether each predictor had a significant effect on the dependent variable.

Results

Contrary to the predictions of the motion dazzle effect, color pattern did not affect the crickets' likelihood of being eaten either in Experiment 1 ($\chi^2 = 4.03$, $P = 0.133$) or in Experiment 2 ($\chi^2 = 0.94$, $P = 0.625$). In Experiment 1, the average number of crickets eaten per 6-min trial was 3.54 out of nine (SD = 1.63), and the averages were similar across color treatments (control 1.05 ± 0.94 , solid 1.36 ± 0.90 , striped 1.13 ± 0.83). In Experiment 2, toads ate the cricket within 10 min in 31 out of 60 trials: 10/20 control trials, 12/20 solid trials, and 9/20 striped trials. The color treatment of the crickets also did not affect the length of time they survived over the 10-min trials in Experiment 2 ($\chi^2 = 1.65$, $P = 0.438$; Fig. S2 in Online Resource 1). Of the crickets that were eaten within 10 min, the average time until death was 91.2 s (SD = 117.5 s) and was similar among color treatments (control 106.3 ± 173.1 , solid 84.6 ± 101.5 , striped 83.2 ± 58.9).

Crickets that spent a greater proportion of time moving, however, were both more likely to be eaten ($\chi^2 = 37.50$, $P < 0.001$; Fig. 2) and lived for a shorter time ($\chi^2 = 46.21$, $P < 0.001$). Overall, the crickets in Experiment 2 spent an average of 30.7% of their time moving (SD = 30.5%) and the amount of time devoted to this behavior did not differ much among color treatments (control $35.1 \pm 34.0\%$, solid $32.9 \pm 28.0\%$, striped $24.2\% \pm 29.6\%$).

Discussion

We found that prey capture success by cane toads is highly dependent on the amount of prey movement, with no detectable effects of color pattern complexity. Crickets that spent a greater proportion of time moving had a higher probability

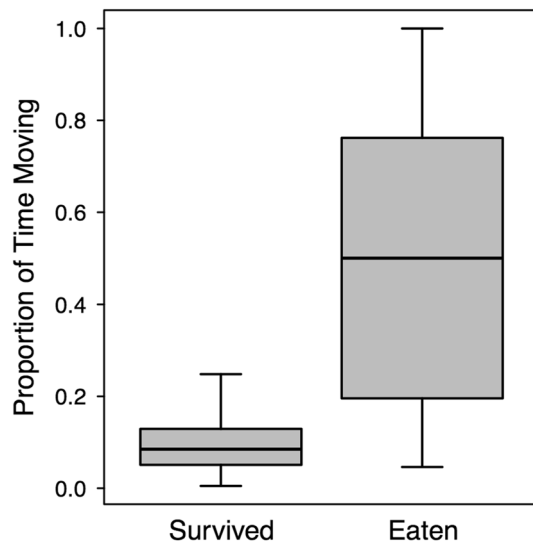


Fig. 2 Proportion of time crickets spent moving from the start of the trial until death if the cricket was eaten ($N=31$) or the end of the trial if the cricket survived ($N=29$). Box plots show minimum, median, and maximum values along with interquartile ranges

of being eaten, with no differences among control, solid white, and striped crickets in how often they were eaten. These results indicate that the color modifications made in the present study do not influence cane toads' ability to capture moving crickets. Anuran predators (frogs and toads) may therefore impose stronger selection pressure on prey behavior than on their color pattern.

Our experiment is the first to test the motion dazzle effect with living prey, which move in a more realistic manner than most computer simulated prey. Although house crickets are not native to the same geographic range as cane toads, these toads consume a wide range of arthropod prey, including many orthopteran species (Zug and Zug 1979; Meshaka and Powell 2010). The movement pattern of crickets is therefore likely to be recognized by cane toads as that of their natural prey. The generality of our results may be limited, however, if the movement patterns of house crickets are not representative of the patterns used by most prey species that benefit from the motion dazzle effect. Continuous linear movement, for example, may promote this effect more than the rapid jumps frequently displayed by crickets. Future experiments should use a diverse set of prey, including some with natural high contrast color patterns, as these species may move in ways that optimize visual illusions (Jackson et al. 1976; Allen et al. 2013). The motion dazzle effect has been invoked to explain the evolution of color patterns in a range of prey taxa (Thayer 1909; Stevens 2007; Hughes et al. 2014), but further experimental evidence is needed to evaluate this hypothesis.

This is also one of the first experiments testing the motion dazzle effect in nonhuman predators. Few other

species have been investigated in this context, and those that have, provided support for the effect. Wild caught great tits (*Parus major*), for instance, are more successful at attacking linearly moving prey that are solid colored rather than striped (Hämäläinen et al. 2015). Furthermore, locusts have weaker neural antipredator responses to high-contrast stimuli than to solid colored stimuli, indicating that predators may benefit from displaying motion dazzle coloration as well (Santer 2013). Certain color patterns, therefore, seem to impair visual perception in similar ways across distantly related taxa such as birds and insects. The generality of this phenomenon is, however, still unclear.

Lack of support for motion dazzle in our study suggests that cane toads, in contrast to other visual predators, are able to avoid succumbing to this visual illusion. Predators vary greatly in their sensory physiology, resulting in differences in how they detect and process sensory cues (Dusenbery 1992). While both birds and anurans use vision to detect prey, anurans are generally more specialized for detecting movement (Satou and Shiraishi 1991; Buxbaum-Conradi and Ewert 1999). Such specializations may optimize their ability to detect and localize rapidly moving prey and negate the effects of motion dazzle coloration. Our findings suggest that the sensory and perceptual systems of predators can play a role in modulating the adaptive value of prey color patterns and behaviors.

Acknowledgements We are grateful to J. Lam, N. Anderson, and C. Pantoja, for running experimental trials, R. Lim and E. Shank for coding videos, and J. Peniston for designing figures. We also thank H. Legett, B. Leavell, and F. Boyd for collecting the cane toads used in this study, and D. Pita for measuring the reflectance spectra of the crickets. Members of the Bernal lab provided suggestions that helped improve this manuscript.

Funding This study was funded by the Department of Biological Sciences at Purdue University. X.E.B. was funded by NSF IOS no. 1433990.

Data availability The datasets generated and analyzed during this study are available from the Dryad Data Repository: <https://doi.org/10.5061/dryad.gq6326t>.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Our experiments were approved by the Purdue Animal Care and Use Committee (Protocol #1405001073). This article does not contain any studies with human participants performed by any of the authors.

References

- Allen WL, Baddeley R, Scott-Samuel NE, Cuthill IC (2013) The evolution and function of pattern diversity in snakes. *Behav Ecol* 24:1237–1250
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Buxbaum-Conradi H, Ewert JP (1999) Responses of single neurons in the toad's caudal ventral striatum to moving visual stimuli and test of their efferent projection by extracellular antidromic stimulation/recording techniques. *Brain Behav Evol* 54:338–354
- Dusenbery DB (1992) *Sensory ecology: how animals acquire and respond to information*. W.H. Freeman, New York
- Forsman A, Appelqvist S (1998) Visual predators impose correlation selection on prey color pattern and behavior. *Behav Ecol* 9:409–413
- Hall JR, Cuthill IC, Baddeley R, Shohet AJ, Scott-Samuel NE (2013) Camouflage, detection and identification of moving targets. *Proc R Soc B* 280:20130064
- Hämäläinen L, Valkonen J, Mappes J, Rojas B (2015) Visual illusions in predator-prey interactions: birds find moving patterned prey harder to catch. *Anim Cogn* 18:1059–1068
- Hogan BG, Cuthill IC, Scott-Samuel NE (2016) Dazzle camouflage, target tracking, and the confusion effect. *Behav Ecol* 27:1547–1551
- Hughes AE, Troscianko J, Stevens M (2014) Motion dazzle and the effects of target patterning on capture success. *BMC Evol Biol* 14:201
- Hughes AE, Magor-Elliott RS, Stevens M (2015) The role of stripe orientation in target capture success. *Front Zool* 12:17
- Jackson JF, Ingram W, Campbell HW (1976) The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. *Am Nat* 110:1029–1053
- Meshaka WE, Powell R (2010) Diets of the native southern toad (*Anaxyrus terrestris*) and the exotic cane toad (*Rhinella marina*) from a single site in south-central Florida. *Fla Sci* 73:175–179
- Pough FH (1976) Multiple cryptic effects of crossbanded and ringed patterns of snakes. *Copeia* 1976:834–836
- R Core Team (2017) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Ruxton GD, Sherratt TN, Speed MP (2004) *Avoiding Attack: the evolutionary ecology of crypsis, warning signals, and mimicry*. Oxford University Press, Oxford
- Santer RD (2013) Motion dazzle: a locust's eye view. *Biol Lett* 9:20130811
- Satou M, Shiraishi A (1991) Local motion processing in the optic tectum of the Japanese toad, *Bufo japonicus*. *J Comp Physiol A* 169:569–589
- Scott-Samuel NE, Baddeley R, Palmer CE, Cuthill IC (2011) Dazzle camouflage affects speed perception. *PLoS ONE* 6:2–7
- Stevens M (2007) Predator perception and the interrelation between different forms of protective coloration. *Proc R Soc B* 274:1457–1464
- Stevens M, Merilaita S (2011) *Animal camouflage: mechanisms and function*. Cambridge University Press, Cambridge
- Stevens M, Yule DH, Ruxton GD (2008) Dazzle coloration and prey movement. *Proc R Soc B* 275:2639–2643
- Thayer GH (1909) *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries*. Macmillan, New York
- Therneau TM (2015) *coxme: mixed effects cox models*. R package version 2.2-5. <https://CRAN.R-project.org/package=coxme>. Accessed 20 Oct 2017
- Zug GR, Zug PB (1979) The marine toad, *Bufo marinus*: a natural history resumé of native populations. *Smithson Contrib Zool* 284:1–58