BIOLOGY
LETTERS

rsbl.royalsocietypublishing.org

Review

Cite this article: Umeton D, Read JCA, Rowe C. 2017 Unravelling the illusion of flicker fusion. *Biol. Lett.* **13**: 20160831.
http://dx.doi.org/10.1098/rsbl.2016.0831

Received: 21 October 2016
Accepted: 9 January 2017

Subject Areas:
behaviour, biophysics, ecology, neuroscience

Keywords:
flicker fusion effect, camouflage, motion, deimatic display, startle, dazzle coloration

Author for correspondence:
Diana Umeton
e-mail: diana.umeton@gmail.com

THE ROYAL SOCIETY
PUBLISHING

Animal behaviour

Unravelling the illusion of flicker fusion

Diana Umeton[1,2], Jenny C. A. Read[2] and Candy Rowe[2]

[1]Department of Biology, Ecology and Earth Sciences, University of Calabria, Cosenza, Italy
[2]Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle NE2 4HH, UK

DU, 0000-0002-7204-952X; JCAR, 0000-0002-9029-5185; CR, 0000-0001-5379-843X

For over 150 years, researchers have investigated the anti-predator function of animal patterns. However, this work has mainly focused on when prey remain still, and has only recently started to incorporate motion into the study of defensive coloration. As motion breaks camouflage, a new challenge is to understand how prey avoid predators while moving around their environment, and if a moving prey can ever be camouflaged. We propose that there is a solution to this, in that a ‘flicker fusion effect’ can change the appearance of the prey in the eyes of their predators to reduce the chances of initial detection. This effect occurs when a high contrast pattern blurs at speed, changing the appearance of the prey, which may help them better match their background. Despite being widely discussed in the literature, the flicker fusion effect is poorly described, there is no clear theoretical framework for testing how it might reduce predation, and the terminology describing it is, at best, rather confusing. Our review addresses these three key issues to enable researchers to formulate precise predictions about when the flicker fusion effect occurs, and to test how it can reduce predation.

1. Introduction

Prey use an incredible array of different strategies to avoid predators [1]. These include signalling defences to predators using warning coloration [2,3], avoiding detection by predators through camouflage [4], and mimicking inedible objects in the environment to avoid being recognized [5]. These defensive strategies have been largely studied in the context of how a prey’s appearance enhances its survival when it is stationary. However, given that many prey need to move around their environment (e.g. to find resources and mates), or use movement as part of their defensive display, there is increasing interest in how defensive coloration and movement interact to reduce predation [6–10]. Incorporating motion into the study of defensive coloration is important because not only can it change the efficacy of a defensive strategy [6], but also it raises novel questions about how defensive strategies function and are defined [7–11].

One of the major challenges for understanding the anti-predator function of colour patterns of moving prey stems from the fact that ‘motion breaks camouflage’ [10]: if moving prey cannot conceal themselves through camouflage, what kind of patterns could help reduce predation? One possibility is that colour patterns elicit visual illusions in predators when prey are moving, making them hard to capture. For example, high contrast visible patterns could elicit ‘motion dazzle’, impairing predators’ judgements of speed and/or trajectory of moving targets [12–16].

However, there is another visual illusion that has received much less attention, but which could in fact help moving prey defend and possibly conceal themselves rather than just make them tricky to catch. The ‘flicker fusion effect’ can cause a change in a prey’s appearance if it moves sufficiently quickly that its pattern becomes blurred [17]. If that change in appearance enables prey to better match their background, it could reduce the chances that they are

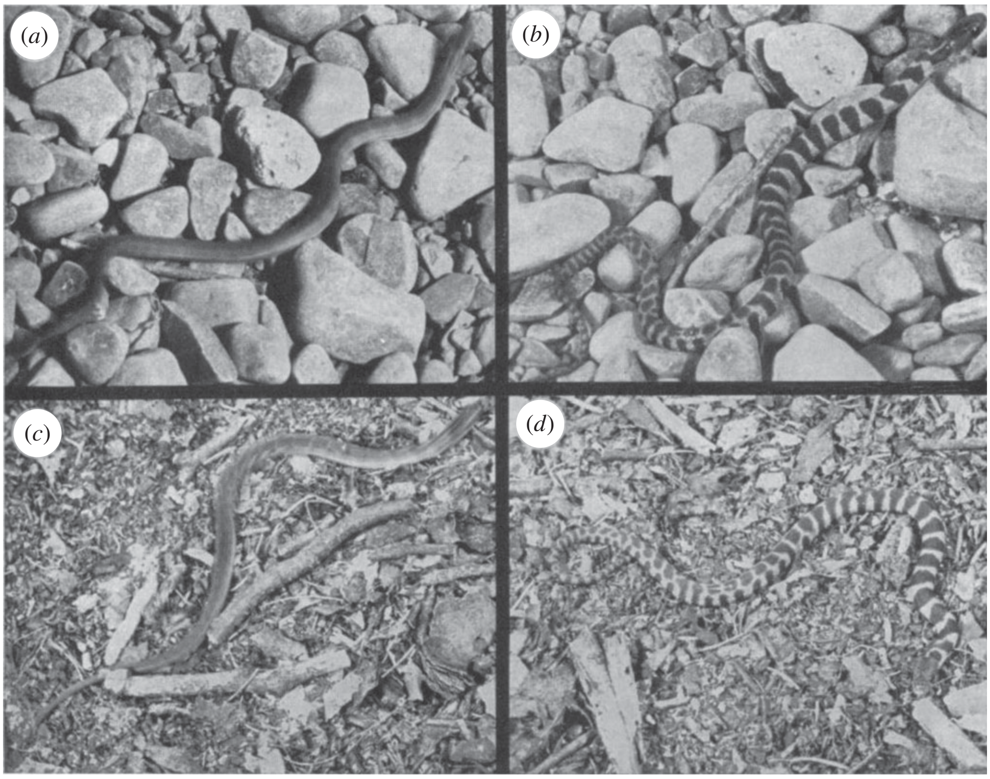

Figure 1. Newborn water snakes moving (left images) and stationary (right images) on coarse gravel (top images) and plant matter (bottom images) taken from Pough [17]. (Reproduced with the permission of the American Society of Ichthyologists and Herpetologists.)

detected by a predator. Despite anecdotal reports by researchers of this change in appearance occurring in the wild [17,18], it is still not known if, or how, it might work to deter natural predators. As a consequence, the flicker fusion effect remains poorly defined and understood, despite it having the potential to be a unique way to reduce predation across a wide range of prey species [19].

Our review will address three main issues. The first is to explain the psychophysics behind the illusion of flicker fusion effect so that we can precisely predict when it is found in nature, and what factors affect its occurrence. The second is to disentangle the putative functions of the flicker fusion effect. Enhanced concealment through background matching is not the only possible function, and we discuss other functions suggested in the literature. Finally, we will clarify the terminology surrounding the flicker fusion effect to avoid confusion, particularly with other strategies involving movement and coloration. We aim to facilitate the study of the flicker fusion effect in the context of prey defences, and particularly, to highlight its potential role in enhancing concealment of moving prey.

2. What is the mechanism underlying the flicker fusion effect?

It was 40 years ago that Pough [17] wrote about prey changing their appearance when in motion compared with when they were static. He observed striped newborn northern water snakes (*Nerodia sipedon*) producing sudden bursts of rapid movement in response to a threat which meant that their stripes blurred together to make them appear uniformly coloured (figure 1). He suggested that this change in appearance, from striped to uniform, was due to the fact that snakes' pattern elements were alternating faster than the observer's critical flicker fusion frequency (CFF), hence the name 'flicker fusion effect' [18].

The CFF is a measure of a visual system's ability to resolve rapid stimulus change, and is defined as the maximum temporal frequency at which a light can flicker before being perceived as continuous [20]. But how does this relate to a predator's ability to resolve the stripes of a moving prey? When a striped prey moves across a predator's visual field, the pattern elements locally alternate between light and dark (figure 2*a*). If the prey moves fast enough, the frequency of alternation, known as the temporal frequency, will exceed the maximum frequency that the predator can temporally resolve, and the stripes will blur and no longer be perceived. The temporal frequency at which the stripes alternate depends on the stripe width and on the speed at which the prey moves, and increases as either the stripes get thinner or the speed increases.

In principle, by knowing the stripe width and the speed of the prey, along with the CFF of the predator (which varies across species, see [21]), it should be possible to predict when the primary visual effect of blurring will occur in the eyes of a predator [18,22]. However, it is not quite that simple. The CFF is generally measured using a whole field flickering stimulus, which means that it is measured with a visual stimulus that has no internal pattern. By contrast, Pough's striped water snakes represent patterned visual stimuli, which are characterized by their pattern spatial frequency: spatial frequency is the number of cycles of alternating dark and light stripes per degree of visual angle (figure 2*a*). For patterned stimuli, this is substantially above zero, while for uniform ones, it is equal to zero. Empirically, flicker fusion occurs at lower temporal frequency for patterns having higher spatial frequencies [23]; this means that the temporal frequency at which the stripes of a patterned prey will completely blur is not fixed, but decreases as stripe

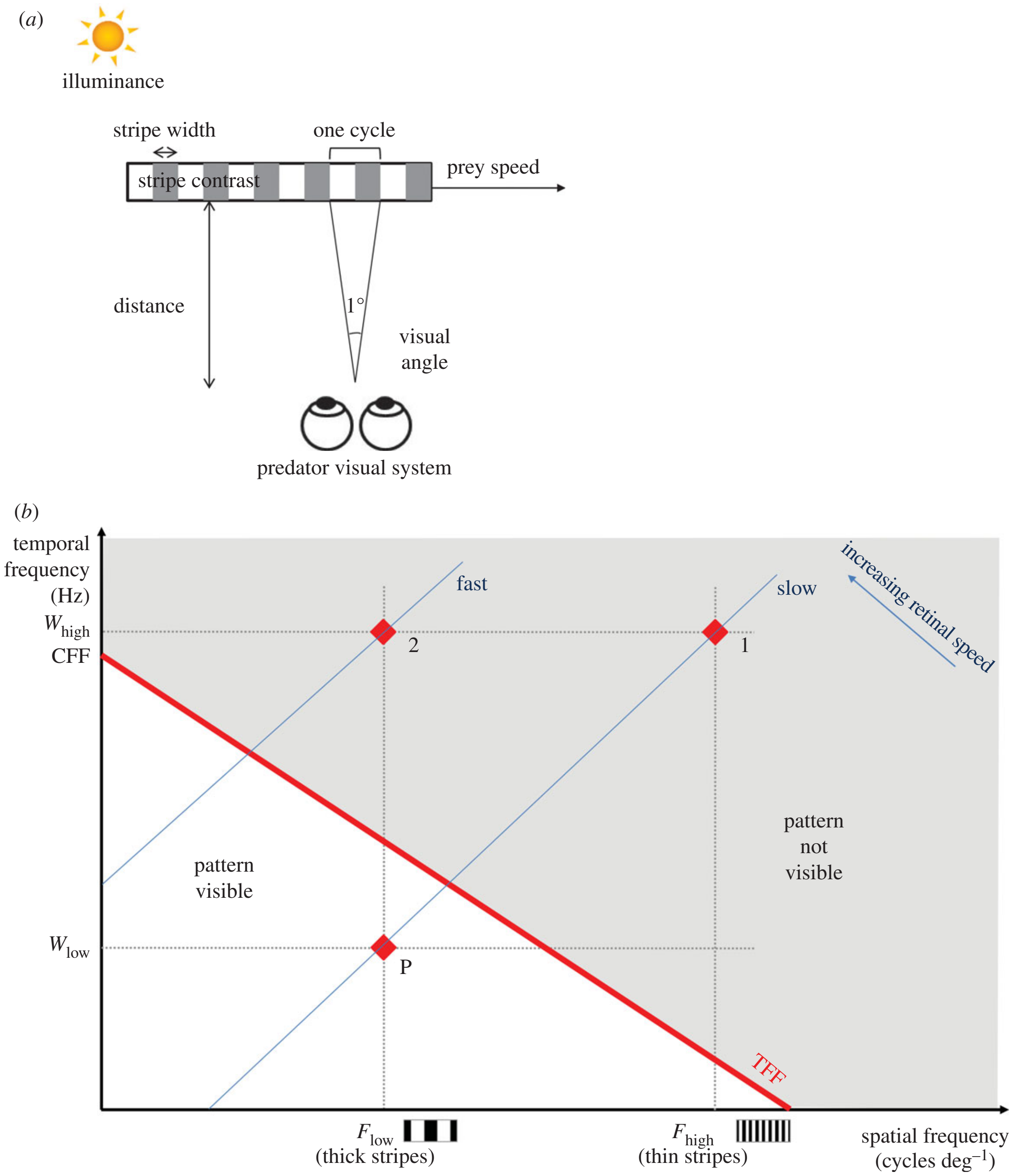

Figure 2. The psychophysics behind the flicker fusion effect. (*a*) The perception of a moving striped prey by a visually hunting predator, and the factors that affect whether or not the predator sees a flicker fusion effect. The spatial frequency of the pattern is measured in cycles per degree, and in this example is 1 cycle per degree (one pattern cycle occurs in one degree of visual angle). (*b*) How reducing stripe width or moving faster blurs the pattern in the eyes of a predator. Any moving prey with a particular pattern can be characterized by the spatial and temporal frequencies perceived by a predator's retina. The blue lines are isolines for speed on the retina. The red line is the TFF for a given contrast, illumination and species (note that the CFF is the same as the TFF when it meets the *y*-axis, i.e. the spatial frequency is zero). When a moving prey has a spatio-temporal frequency below the TFF, its patterns can be resolved (P); however, if the prey has thinner stripes (F_{high}) or moves faster, its pattern will blur and no longer be perceived by the predator (1 and 2, respectively).

width decreases. We will call this the threshold for flicker fusion, or the TFF (shown by the red line in figure 2*b*). Complete blurring occurs above the TFF, although patterns will start to blur below it. The TFF is the same as the CFF only when the stimulus is uniform (i.e. where the TFF intersects the *y*-axis and spatial frequency is zero); the CFF is the upper limit of resolvable temporal frequency. To help visualize this, imagine a striped moving prey with a defined spatial (F_{low}) and temporal frequency (W_{low}); when slow moving, its pattern remains visible to a predator (P; figure 2*b*). However, if the prey has thinner stripes (1; figure 2*b*) with a higher spatial frequency (F_{high}), or moves faster (2; figure 2*b*), resulting in a higher temporal frequency (W_{high}), its stripes will alternate faster than the predator's threshold for flicker fusion (i.e. $W >$ TFF). Consequently, it will no longer be possible for the predator to distinguish the pattern elements and the striped prey will appear uniform.

Besides the TFF, there are other factors that also influence the occurrence of the flicker fusion effect (table 1). In particular, the viewing conditions are critical. If the prey is further away, its stripes will appear thinner to the predator, i.e. the spatial frequency increases, and the flicker fusion effect will occur at lower prey speeds. In addition, as ambient luminance decreases, the TFF also decreases because animals' eyes visually sample their environment less frequently and integrate photon capture over longer periods in order to try

Table 1. Factors affecting the flicker fusion effect.

factor		impact
viewing conditions	distance from the prey	increasing viewing distance increases the spatial frequency of the pattern as seen by the predator, making the flicker fusion effect more likely to occur
	ambient light	at lower illumination, animals integrate visual information over longer times and TFFs decrease more rapidly: the flicker fusion effect can occur at lower speeds
prey pattern and movement	speed	adequate speed is required for blurring of pattern elements to occur
	stripe width	thinner stripes will blur at lower speeds as they produce more rapid temporal frequency
	pattern internal contrast	low contrast patterns blur at lower speeds than high contrast ones
	orientation of pattern elements	blurring occurs when elements are repeated along the vector of motion
predator vision	spatio-temporal acuity	increasing spatio-temporal acuity of the predator requires higher speeds for the flicker fusion effect to occur (in figure 2*b*, TFF will shift towards higher temporal and spatial frequencies)
	contrast sensitivity	the more sensitive the predator is to contrast at the relevant luminance level, the harder the flicker fusion effect is to achieve (in figure 2*b*, TFF shifts upwards and declines more steeply)
	fixation	if the predator tracks the prey to stabilize it on the retina, the effective speed of the prey will be reduced, weakening or abolishing the flicker fusion effect

and gather sufficient visual information from their environment [24]. When animal eyes become adapted to low lighting conditions, spatial acuity can also decrease [25]. This means that the flicker fusion effect is more likely to occur under dim compared with bright conditions [22], because prey do not need to be moving as fast for blurring to occur. While for a given speed, finer stripes will produce faster alternation (and more likely exceed the TFF), other things being equal, the speed necessary for the flicker fusion effect will always be lower for prey patterns of lower internal contrast. The same principles discussed so far can be applied to prey having non-striped patterns, e.g. zigzag or spotted, if the elements are repeated along the vector of motion. When the temporal frequency at which these elements alternate exceeds a predator's TFF, the prey will appear uniform or even differently patterned while moving.

Ultimately, the speed necessary for the flicker fusion effect to occur depends upon the predator's contrast sensitivity function. Contrast sensitivity is defined as 1/contrast threshold, where the threshold is the minimum contrast required for the predator to detect a pattern. The contrast sensitivity function describes how contrast sensitivity varies as a function of spatial and temporal frequency. The red 'TFF' line in figure 2*b* corresponds to a line of constant contrast sensitivity; for predators with more sensitive vision, the TFF line will be shifted upwards and decline less steeply with spatial frequency [23]. And of course, flicker fusion only occurs if the predator's eyes remain stationary as the prey moves: if it tracks the prey and stabilizes it on the retina, blurring will not occur.

Given this complex interaction of factors affecting the occurrence of the flicker fusion effect, how often might it occur in the wild? To date, the evidence is limited to striped coral snake mimics (*Lampropeltis triangulum campbelli* and *L. elapsoides*), which are calculated to move fast enough when in flight for their patterns to blur in the eyes of some potential predators (raptors), particularly in dim light [22]. Indeed, the effect may be particularly prevalent in low light intensity environments, including deep water or forest environments. However, while demonstrating the feasibility of the flicker fusion effect, these calculations are likely to be conservative as they were based on predators' CFF values, and prey do not need to move as fast to blur based on the TFF. Blurring through the flicker fusion effect may be occurring more often in nature than previously thought (e.g. [22]), and occur in slower moving prey, not just those performing a rapid escape.

Although calculations for the flicker fusion effect have been made predominantly with avian predators in mind, other species of predator (e.g. insects [26]) have lower visual acuities. This means that the flicker fusion effect could be occurring more often in the eyes of these predators. Based on praying mantis' visual acuity [26], we calculate that a bumblebee's pattern will certainly be perceived as blurred at a typical viewing and strike distance of 5 cm [26] when the insect flies at $0.25\ \mathrm{m\,s^{-1}}$ (*Bombus terrestris* maximum flying speed is $6\ \mathrm{m\,s^{-1}}$ [27]). Consequently, the flicker fusion effect could be more widespread than it initially would appear, and not restricted to striped snakes. In the same way that UV colours were ignored for a long time because we could not see them [28], blurring through the flicker fusion effect may also have been an underappreciated feature of animal coloration because of our own visual biases.

3. What defensive function might the flicker fusion effect have?

The second issue to address is what anti-predator function the flicker fusion effect may have. While changes in appearance caused by the flicker fusion effect have been widely assumed to be an adaptation to reduce predation (e.g. [29,30]), the problem is that there have been no tests with actual predators. So far, the evidence for the anti-predator function of the flicker fusion effect comes from indirect observations in snakes [22,31]. For example, the 'zigzag' morphs of

Table 2. How the flicker fusion effect might reduce predation.

function	how this is achieved
camouflage the moving prey	the uniform coloration from blurring helps prey match general features of their background, and enhances concealment [19,30]
alter the perception of motion	the change in appearance during movement alters the prey's perceived speed or trajectory, making it difficult to capture [18,30]
hide the final resting location	a sudden change in appearance from the moving to the static prey pattern makes it difficult for a predator to locate resting prey [17,22,29]
deter predators	a sudden change in appearance caused by the flicker fusion effect may cause the attacking predator to show neophobia or hesitate, giving the prey an increased opportunity to escape

Vipera berus appear to have a higher survival advantage compared with other morphs, but there is no evidence that this results from reduced predation, and if it does, how that occurs [31]. Therefore, it could be argued that the flicker fusion effect is simply the by-product of rapid movement that has been selected to escape a predator, rather than part of a defensive strategy. It is important to identify how the flicker fusion effect might work in order to conduct experiments with predators to distinguish among functional hypotheses. We have attempted to disentangle the proposed explanations to provide a theoretical framework for the future study of how the flicker fusion effect could help reduce predation (table 2).

As already mentioned, the flicker fusion effect could help prey to become more camouflaged during movement [19,30]. Pough's [17] original observations included how the uniform appearance generated by the flicker fusion effect in the escape responses of snakes made them appear to blend into their environment. This could happen, for example, if prey's coloration matches the mean luminance of the background, even though it has a high contrast visual texture (e.g. stripes); such prey might be highly conspicuous when remaining still but could become camouflaged when moving fast enough for the flicker fusion effect to occur [19]. If the flicker fusion effect does indeed improve background matching, it would be the basis for a unique form of camouflage in moving prey: rather than concealing the speed or trajectory of the prey's motion once detected (like motion dazzle; [13]), the flicker fusion effect would reduce the chances of initial detection.

However, it is possible that the flicker fusion effect could help prevent capture by 'confusing' predators, and making it difficult for them to track and effectively capture the prey; for example, pattern blurring could cause predators to lose internal reference points [15]. The effect of blurring could also lead to additional illusory effects, such as altering prey's perceived speed due to the loss of internal contrast in the pattern or reduced contrast against the background [30,32,33]. While this latter idea could be considered a form of motion dazzle [30], the idea and study of motion dazzle has thus far relied upon the prey's pattern being visible to the predator when it is moving [1,13–16]. Therefore, if the flicker fusion effect also changes the speed and/or trajectory of prey through pattern blurring, it must be due to different perceptual mechanisms than those already proposed (e.g. [13,16]) and not through the pattern 'dazzling' predators.

A third way that the flicker fusion effect could help reduce predation is by hiding the final resting place of a moving prey, making it difficult to locate once it becomes stationary again [17]. This idea is perhaps similar to the idea of 'flash coloration', where an otherwise camouflaged prey suddenly reveals a conspicuous body part when it flees a predator, only to hide it again before or as it comes to rest [1,34]. Although the benefits of flash coloration are not established, it is thought that if a predator tracks the moving prey using its conspicuous coloration, it will subsequently be less able to detect cryptic features of the prey's camouflage pattern (perhaps through loss of a search image; [35]). In the case of the flicker fusion effect, when the prey suddenly becomes stationary with a cryptic pattern, the predator would continue to look for the prey based on its appearance when moving. The problem of finding the stationary cryptic prey could be further exacerbated if the predator predicts the movement of the prey along the perceived trajectory, and searches in the wrong place, either because it looks further along the path than where the prey has actually stopped [17], or less far because of misjudging the speed [33].

Finally, the flicker fusion effect could simply be a way to deter predators: a novel dynamically changing appearance could elicit neophobia or an avoidance response, similar to that of warning signals (e.g. [36,37]). Alternatively, perhaps the sudden change in coloration is a deimatic display eliciting a startle or fear response in its predators [11], that gives prey an advantage to escape. In these cases, the flicker fusion effect simply performs a well-established defensive function.

We acknowledge that this may not be an exhaustive list, and of course, differences in hunting strategies or visual systems among predator species means that the flicker fusion effect could serve more than one defensive function, even for a single prey species. However, what is clear is that we need to know how it works, and particularly if it is a form of camouflage or a deterrent. We think it is particularly important to establish if it is a unique form of concealment, where blurring of an internal pattern at speed could reduce the initial detection of prey. The question of whether any pattern can reduce the detection of moving prey is one of the major unanswered questions in the study of defensive coloration. Currently, only the flicker fusion effect offers a possible solution.

4. How is confusion arising through current terminology?

To investigate the flicker fusion effect, we need to be clear about what it is we refer to when using this term. This is because the flicker fusion effect has not just been used to describe the mechanism by which the appearance of a prey's pattern changes (e.g. [14,30,31,38]), but has also given its name to a hypothesis [29–31], and been used to describe a camouflage strategy [4,12,30]. This has led to what we see as some confusion in the literature.

For example, some researchers refer to a 'flicker fusion hypothesis'; however, it is not clear what this is. Sometimes, it refers to the mechanism and whether or not it is possible that blurring occurs through the flicker fusion effect [22,30], while other times it refers to whether or not the blurring could confer a survival advantage [29,31]. While this is confusing in itself, there is of course the additional problem that there are multiple functional hypotheses relating to how it might reduce predation (table 2). The use of the term 'flicker fusion hypothesis' has the potential to lead to considerable confusion about what the hypothesis actually is, and we suggest that it is abandoned altogether.

The flicker fusion effect has also been used to describe a specific defensive strategy, 'flicker fusion camouflage' [12,30], which describes the situation when the effect helps prey better match their backgrounds by making prey 'uniformly camouflaged' [12]. The problem with the use of this term is that it suggests that the function of the flicker fusion effect is to camouflage the prey, while several other possible functions exist (table 2). While calling motion dazzle a form of camouflage works because its only possible function is to hide the movement of the prey ('dazzle camouflage'; [13,14]), the same logic cannot be applied to the flicker fusion effect, because it might instead deter predators. Unless we know that patterns have evolved to elicit the flicker fusion effect to enhance concealment, we suggest that it is best not to use this term.

However, we do still need terminology that allows us to study flicker fusion, so what terminology should we be using? Our view is that the flicker fusion effect should be limited to describing the visual illusion that alters the perceived pattern of a prey when it moves sufficiently quickly to exceed the predator TFF. This definition accurately describes how pattern and speed interact to produce a change in appearance in the eyes of the predator, and does not ascribe any particular function to the effect. Avoiding using flicker fusion effect in relation to any functional role reduces any implicit bias in understanding how it works. By clearly separating the mechanism (the perceptual effect) from the function (how it deters predators), our proposed terminology allows researchers to study one or the other, or both. Only once functions are better explored and identified should we start to use flicker fusion in ways that align it to particular defensive strategies.

5. Conclusion

For a long time, the flicker fusion effect has been thought to confer a selective advantage to several snake species fleeing from putative predators. By exploring the psychophysical principles behind the effect, we hope to have highlighted how widespread the effect could be. Striped patterns in particular, but also other patterns types, common across many taxa, could blur at speed given what we know about the visual capabilities of different species of predators.

It is clear that we need more studies of the flicker fusion effect in order to understand when it occurs, and what its effect(s) are on predators. Understanding how the flicker fusion effect works is likely to be solved by a combination of approaches. Field observations will be important for establishing how the effect might function and if it could be involved in contexts other than predation (e.g. signalling to mates). Nonetheless, psychophysics experiments in the laboratory are likely to provide valuable insights into its perceptual basis, and tests with computer generated targets can be readily conducted with predatory species, such as birds and mantids (e.g. [26,39]).

Despite these challenges to fully understand when and how it works in the wild, the study of the flicker fusion effect, to our eyes, offers an exciting opportunity to discover new ways in which a prey's appearance and behaviour have evolved to reduce predation. Notably, the flicker fusion effect fundamentally differs from other defensive strategies involving movement and patterning, because it allows prey to look different when moving and when stationary. Crucially, it has the potential to conceal an animal during motion, reducing the chances of it being detected by a predator. Perhaps, when combined with the right pattern, motion need not always break camouflage.

Competing interests. We have no competing interests.

Funding. J.C.A.R. is supported by a Leverhulme Trust Research Leadership Award (RL-2012-019), and D.U. by a Best Erasmus Traineeship for Jobs Scholarship.

Acknowledgements. We would like to thank Christina Halpin, Matthew Wheelwright, Robert Elwood, Adam Kane and an anonymous reviewer for helpful comments on the manuscript.

References

1. Cott HB. 1940 *Adaptive coloration in animals*. New York, NY: Oxford University Press.
2. Mappes J, Marples N, Endler JA. 2005 The complex business of survival by aposematism. *Trends Ecol. Evol.* **20**, 598–603. (doi:10.1016/j.tree.2005.07.011)
3. Rowe C, Halpin C. 2013 Why are warning displays multimodal? *Behav. Ecol. Sociobiol.* **67**, 1425–1439. (doi:10.1007/s00265-013-1515-8)
4. Stevens M, Merilaita S. 2009 Animal camouflage: current issues and new perspectives. *Phil. Trans. R. Soc. B* **364**, 423–427. (doi:10.1098/rstb.2008.0217)
5. Skelhorn J. 2015 Masquerade. *Curr. Biol.* **25**, R643–R644. (doi:10.1016/j.cub.2015.02.069)
6. Stevens M, Searle WTL, Seymour JE, Marshall KLA, Ruxton GD. 2011 Motion dazzle and camouflage as distinct anti-predator defenses. *BMC Biol.* **9**, 81. (doi:10.1186/1741-7007-9-81)
7. Umbers KDL, Mappes J. 2016 Towards a tractable working hypothesis for deimatic displays. *Anim. Behav.* **113**, E5–E7. (doi:10.1016/j.anbehav.2016.01.002)
8. Bian X, Elgar MA, Peters RA. 2016 The swaying behavior of *Extatosoma tiaratum*: motion camouflage in a stick insect? *Behav. Ecol.* **27**, 83–92. (doi:10.1093/beheco/arv125)
9. Srygley RB. 1999 Incorporating motion into investigations of mimicry. *Evol. Ecol.* **13**, 691–708. (doi:10.1023/a:1011046202928)
10. Hall JR, Cuthill IC, Baddeley R, Shohet AJ, Scott-Samuel NE. 2013 Camouflage, detection and identification of moving targets. *Proc. R. Soc. B* **280**, 1785. (doi:10.1098/Rspb.2013.0064)
11. Skelhorn J, Holmes GG, Rowe C. 2016 Deimatic or aposematic? *Anim. Behav.* **113**, E1–E3. (doi:10.1016/j.anbehav.2015.07.021)

12. Stevens M, Yule DH, Ruxton GD. 2008 Dazzle coloration and prey movement. *Proc. R. Soc. B* **275**, 2639–2643. (doi:10.1098/rspb.2008.0877)
13. Scott-Samuel NE, Baddeley R, Palmer CE, Cuthill IC. 2011 Dazzle camouflage affects speed perception. *PLoS ONE* **6**, e20233. (doi:10.1371/journal.pone.0020233)
14. Von Helversen B, Schooler LJ, Czienskowski U. 2013 Are stripes beneficial? Dazzle camouflage influences perceived speed and hit rates. *PLoS ONE* **8**, e61173. (doi:10.1371/journal.pone.0061173)
15. Hughes AE, Troscianko J, Stevens M. 2014 Motion dazzle and the effects of target patterning on capture success. *BMC Evol. Biol.* **14**, 1. (doi:10.1186/S12862-014-0201-4)
16. Kelley LA, Kelley JL. 2014 Animal visual illusion and confusion: the importance of a perceptual perspective. *Behav. Ecol.* **25**, 450–463. (doi:10.1093/beheco/art118)
17. Pough FH. 1976 Multiple cryptic effects of crossbanded and ringed patterns of snakes. *Copeia* **4**, 834–836. (doi:10.2307/1443481)
18. Jackson JF, Ingram W, Campbell HW. 1976 Dorsal pigmentation pattern of snakes as an anti-predator strategy. *Am. Nat.* **110**, 1029–1053. (doi:10.1086/283125)
19. Endler JA. 1978 A predator's view of animal color patterns. In *Evolutionary biology* (eds MK Hecht, WC Steere, B Wallace), pp. 319–364. Boston, MA: Springer US.
20. Talbot HF. 1834 XLIV. Experiments on light. *Phil. Mag. Series 3* **5**, 321–334. (doi:10.1080/14786443408648474)
21. Healy K, McNally L, Ruxton GD, Cooper N, Jackson AL. 2013 Metabolic rate and body size are linked with perception of temporal information. *Anim. Behav.* **86**, 685–696. (doi:10.1016/j.anbehav.2013.06.018)
22. Titcomb GC, Kikuchi DW, Pfennig DW. 2014 More than mimicry? Evaluating scope for flicker-fusion as a defensive strategy in coral snake mimics. *Curr. Zool.* **60**, 123–130. (doi:10.1093/czoolo/60.1.123 123-130)
23. Watson AB, Ahumada AJ. 2016 The pyramid of visibility. In *IS&T International Symposium on Electronic Imaging, 2016, Human Vision and Electronic Imaging 2016*, pp. HVEI-102.1–HVEI-102.6. Springfield, VA: Society for Imaging Science and Technology. (doi:10.2352/ISSN.2470-1173.2016.16HVEI-102)
24. Tyler CW, Hamer RD. 1990 Analysis of visual modulation sensitivity. IV. Validity of the Ferry–Porter law. *J. Opt. Soc. Am.* **7**, 743–758. (doi:10.1364/JOSAA.7.000743)
25. Van Nes FL, Koenderink JJ, Nas H, Bouman MA. 1967 Spatiotemporal modulation transfer in the human eye. *J. Opt. Soc. Am.* **57**, 1082–1088. (doi:10.1364/JOSA.57.001082)
26. Nityananda V, Tarawneh G, Jones L, Busby N, Herbert W, Davies R, Read JCA. 2015 The contrast sensitivity function of the praying mantis *Sphodromantis lineola*. *J. Comp. Physiol. A* **201**, 741–750. (doi:10.1007/s00359-015-1008-5)
27. Ellington CP. 1999 The novel aerodynamics of insect flight: applications to micro-air vehicles. *J. Exp. Biol.* **202**, 3439–3448. (doi:202:3439-3448)
28. Bennett ATD, Cuthill IC. 1994 Ultraviolet vision in birds: what is its function? *Vision Res.* **34**, 1471–1478. (doi:10.1016/0042-6989(94)90149-X)
29. Ruxton GD, Sherratt TN, Speed M. 2004 *Avoiding attack*. Oxford, UK: Oxford University Press.
30. Stevens M. 2007 Predator perception and the interrelation between different forms of protective coloration. *Proc. R. Soc. B* **274**, 1457–1464. (doi:10.1098/rspb.2007.0220)
31. Lindell LE, Forsman A. 1996 Sexual dichromatism in snakes: support for the flicker-fusion hypothesis. *Can. J. Zool.* **74**, 2254–2256. (doi:10.1139/Z96-256)
32. Blakemore MR, Snowden RJ. 2000 Textured backgrounds alter perceived speed. *Vision Res.* **40**, 629–638. (doi:10.1016/S0042-6989(99)00214-X)
33. Thompson P. 1982 Perceived rate of movement depends on contrast. *Vision Res.* **22**, 377–380. (doi:10.1016/0042-6989(82)90153-5)
34. Edmunds M. 2005 Flash colors. In *Encyclopedia of entomology*, p. 1466. Dordrecht, The Netherlands: Springer.
35. Troscianko J, Lown AE, Hughes AE, Stevens M. 2013 Defeating crypsis: detection and learning of camouflage strategies. *PLoS ONE* **8**, 8. (doi:10.1371/journal.pone.0073733)
36. Roper TJ, Cook SE. 1989 Response of chicks to brightly colored insect prey. *Behaviour* **110**, 276–293. (doi:10.1163/156853989X00510)
37. Roper TJ, Wistow R. 1986 Aposematic coloration and avoidance-learning in chicks. *Q. J. Exp. Psychol.* **38**, 141–149. (doi:10.1080/14640748608402225)
38. Niskanen M, Mappes J. 2005 Significance of the dorsal zigzag pattern of *Vipera latastei gaditana* against avian predators. *J. Anim. Ecol.* **74**, 1091–1101. (doi:10.1111/j.1365-2656.2005.01008.x)
39. Dittrich W, Gilbert F, Green P, McGregor P, Grewcock D. 1993 Imperfect mimicry—a pigeon perspective. *Proc. R. Soc. Lond. B* **251**, 195–200. (doi:10.1098/rspb.1993.0029)