

**POTENTIAL STARTLING (‘DEIMATIC’) FUNCTION
OF THE WING COLOURATION OF THE RED
ADMIRAL BUTTERFLY *VANESSA ATALANTA*
(LEPIDOPTERA: NYMPHALIDAE)**

JAMIE C. WEIR^{1*} & DANIELLA DI PIRRO²

¹ *Institute for Ecology and Evolution, University of Edinburgh*
Email: JamieCWeir@outlook.com

² *The Royal (Dick) School of Veterinary Studies, University of Edinburgh*
**Corresponding author*

ABSTRACT

Startle colouration or ‘deimatism’ occurs when an organism is generally cryptic but can suddenly expose patches of conspicuous colouration in order to startle a potential predator, allowing the prey organism time to flee. Here, we recount an observation of a Red Admiral butterfly *Vanessa atalanta* (L.) apparently adopting this strategy effectively against a captive Sun Bear *Helarctos malayanus* (Raffles). We discuss this anecdotal observation in light of the evidence for startle colouration, and the function of concealed conspicuous colouration in Lepidoptera more generally. We note that, in the Lepidoptera in particular, potential displays of startle colouration are widespread, though of varying degrees of subtlety, and that a reliance on startling colouration may be adopted to some extent by more species than previously thought. We emphasise the need for the reporting of more field and experimental data on this topic, particularly when observations of this phenomenon in such well-known species are lacking.

INTRODUCTION

Many organisms which usually rely on crypsis to avoid predation also have patches of bright or contrasting colours on their body which are concealed when at rest, but which the individual can expose under certain conditions (Jenner Weir, 1869; Poulton, 1890). Exposure of these bright colours can be a deliberate act or a by-product of some other concurrent behaviour, for example flight. In his classic, systematic work on animal colouration, Cott (1940) distilled the phenomenon of concealed conspicuous displays into three different explanatory mechanisms:

(1) One, referred to as ‘flash colouration’ is a form of perceptual trick. The hypothesis is that an animal which is brightly coloured when moving, for example, will confuse a predator when it suddenly stops moving and that conspicuous colouration is abruptly concealed—from the predator’s perspective, the prey will have seemingly vanished. The sudden change in visual stimuli makes it more difficult for predators to locate the new resting site of the prey which they had been pursuing (Murali, 2018; Loeffler-Henry, Kang & Sherratt, 2021), and can also reduce the time taken for predators to give up the search without finding it (Loeffler-Henry *et al.*, 2018; Bae *et al.*, 2019) – if foraging as efficiently as possible, it makes sense to spend less time searching an area for an object which is believed to be conspicuous, and which should, if present, be readily noticeable. (2) Second, so-called ‘deimatic’ (Greek δειματῶσ, *deimatōo*, meaning ‘to frighten’; Maldonado, 1970) or ‘startle’ colouration, is a form of bluff, sometimes by an otherwise poorly defended prey item, where the sudden exposure of bright and vivid colours on an otherwise drab and inconspicuous animal serves to briefly frighten a predator, which hesitates,

allowing the prey animal to escape (Drinkwater *et al.*, 2022). (3) Finally, the sudden exposure of bright colour patches at a critical moment when under attack can serve to confuse a predator, misdirecting their attacks away from more vital parts of the prey's anatomy ('deflective marks'; Cott, 1940).

It will be apparent that these mechanisms need not be mutually exclusive and could equally well operate simultaneously to various degrees, as well as in isolation. Despite the extremely widespread occurrence of concealed conspicuous displays, these three mechanisms have received comparatively little research focus. Of the small literature which exists on startle colouration, much deals with the function of eyespots as threatening displays (reviewed in Drinkwater *et al.*, 2022). Here, we report a novel observation of the wing colouration of the Red Admiral butterfly *Vanessa atalanta* (L.) likely functioning as a startle display against a large omnivorous mammal, the Sun Bear *Helarctos malayanus* (Raffles). Particularly with reference to the Lepidoptera, we consider the role this functional mechanism may play more widely as a driving force for the evolution of concealed conspicuous displays.

OBSERVATION

On 30 July 2022 we visited Edinburgh Zoo, a zoological garden owned by the Royal Zoological Society of Scotland. The weather was sunny and warm, with temperatures of ~20°C according to forecasts, and a gentle breeze. We stopped at the enclosure housing the Zoo's two captive sun bears and observed for around thirty minutes. The Sun Bear *H. malayanus* is the smallest member of the Ursidae, and is found in the rainforests of Indochina, stretching into the Malay Archipelago (Fitzgerald & Krausman, 2002). The outdoor portion of their enclosure at Edinburgh Zoo consists of a high, rocky central area with vegetation (including *Buddleja davidii* Franch., attractive to butterflies), surrounded by a deep gulley and wall which separates it from the paths used by the general public. We noticed a single Red Admiral butterfly *V. atalanta* flying around the enclosure. It eventually chose to alight on a small plant at ground level at the edge of a path used by the bears around the perimeter of the enclosure. On landing, it oriented itself with its wings closed in the sunlight. The ventral and dorsal wing colouration of this species, like many of its close relatives, are quite distinct, with the ventral pattern (exposed when the wings are closed) being cryptic (Fig. 1).

The butterfly landed about a metre from one of the bears which was active in the outdoor area. The movement seemed to catch the bear's attention. It cautiously approached the spot where the butterfly landed, moving its nose to within 30 cm of it. At this point the butterfly suddenly flicked its wings open. Visibly startled, the bear recoiled and took a step backwards. The butterfly then immediately took flight and moved off to another area in the enclosure. It continued to move around finding different positions in which to bask in the sun for the remaining time during which we observed. We noted that it adopted resting postures in the sun both with its wings open (exposing the bright dorsal colouration) and closed (concealing that colouration), as is typical for this species. On landing in a given location however, it rarely switched between these two postures until it had moved to a new location. The butterfly received no further attention from the bear throughout this period, whether this was due to its not being noticed or being deliberately ignored. The bear did however come close to the butterfly on several other occasions, and at least once more inadvertently disturbed it as it moved about.

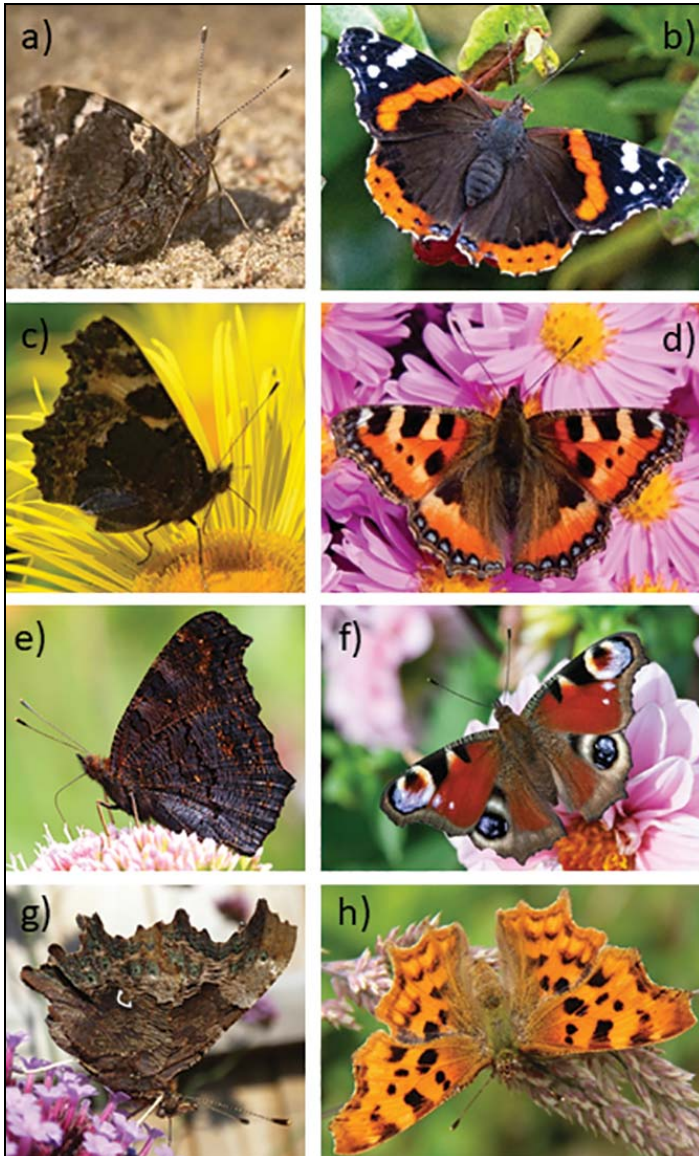


Fig. 1. Concealed conspicuous colouration in a suite of British nymphalid butterflies. The potentially startling dorsal colouration is concealed when the wings are closed and individuals display a more cryptic appearance and colour pattern. (a–b) Red Admiral *Vanessa atalanta*, (c–d) Small Tortoiseshell *Aglais urticae*, (e–f) Peacock *Aglais io*, (g–h) Comma *Polygonia c-album*. All images taken from Flickr.com and are used under an appropriate Creative Commons licence. Image credits (author, title): a) hedera.baltica, “Red Admiral”, b) Hindrik Sijens, “Atlanta”, c) It’s No Game, “Small Tortoiseshell”, d) Natural England, “Small Tortoiseshell butterfly”, e) Nick Goodrum, “peacock *Aglais io*”, f) Alexey Popov, “*Aglais io*”, g) Amanda Slater, “Comma”, h) Mark Hilditch, “Comma Butterfly”.

DISCUSSION

It seems reasonable to infer that in this particular case the sudden exposure of the conspicuous dorsal colour pattern of an otherwise cryptic butterfly likely functioned as startle colouration, with the combination of (a) rapid movement and (b) a change in appearance startling a potential threat and giving the insect time to escape. As far as we can ascertain, this is the first reported observation of the colouration of this species functioning in this way – indeed, there seems to be very little evidence relating to the defensive function of the colouration of *V. atalanta*. Also, this would seem to be the first record of this defensive mechanism being successfully deployed by a prey species against a bear. Previous work on adaptive colour patterns in insects, particularly Lepidoptera, mostly focuses on birds as the (natural) target predators (e.g. Stevens, 2005; Bond, 2007; though also see e.g. Olofsson, Jakobsson, & Wiklund, 2012). The sun bear is a solitary, predominantly diurnal omnivore, consuming plants, fruit, invertebrates, honey and occasionally small vertebrates (Wong & Servheen, 2002; Fredriksson, Wich & Trisno, 2006). Their diet is often particularly rich in insects – in a population in Eastern India, beetles, termites and bees were identified as the most abundant food items in the diet (Sethy & Chauhan, 2018). The taxonomic scope of the insect groups found in their diet suggests that they do not solely exploit colonies or nests of social insects, and may consume a range of species encountered during foraging, though there is no direct evidence for the consumption of butterflies.

In this particular observation, we can probably exclude the operation of flash colouration. If the colour patterning served to obscure the landing site of the insect it seems curious that the bear would have approached it so definitely after it had caught its attention. If, however, the sudden concealment of the bright colours visible in flight acted to make the bear uncertain as to the *exact* landing location, it might then make the sudden and unexpected exposure of those colours even more startling and perhaps more effective. These different defensive strategies almost certainly grade into one another – early authors did not observe any strict distinction between flash, startle, or deflective colours, and spoke of them interchangeably or as a single group of diverse tactics operating together (Jenner Weir, 1869; Poulton, 1890). If the colours of *V. atalanta* do serve a flash function, it is likely subordinate to the startle one. In fact, due to their generally dark colouration, nymphalids can be difficult to follow visually when flying during the day, particularly in low light conditions (Kettlewell, 1973).

A good example of the gradual continuum between the different mechanisms driving concealed cryptic colouration is to be found among some other closely related nymphalid butterflies (Fig. 1). Among these species there is consistently contrast between the ventral and dorsal colouration, suggesting that quite different selective pressures act on each wing surface. The Peacock butterfly *Aglais io* (L.), in particular, has been the subject of research into the function of its prominent dorsal “eyespot” display. These may actually mimic eyes (Blest, 1957; reviewed in Stevens, 2005), thus giving the insect the appearance of a much bigger animal. Alternatively, they may function as deflective marks (reviewed in Stevens, 2005) or, as is suggested by the weight of current evidence, they may have a purely startling, deimatic role (Stevens, Hardman & Stubbins, 2008). In a study of three British species – the Comma *Polygonia c-album* (L.), Small Tortoiseshell *Aglais urticae* (L.), and Peacock butterflies *Aglais io* (L.) – Vallin *et al.* (2006) found that it took birds longest to detect Commas, and least time to notice Peacocks. But, in contrast, wing flicking behaviour – rapidly opening and closing the wings so as to flash the dorsal colour pattern at a

predator, in the manner reported in our observation – occurred most frequently and readily in the Peacock, and least so in the Comma. In the Peacock, wing flicking which flashes the eyespots in the direction of a threat can be accompanied by a hissing or rasping stridulation, created by rubbing the basal parts of the wings (Blest, 1957), to increase the intimidatory nature of the display. All three of these species have crypsis as their primary defence, followed, where necessary, by a startling, deimatic display. However, the emphasis which each of these species place on the different defensive components varies. At one extreme, we have the Peacock which has a less cryptic display, and a more dramatic startling display; at the other, the Comma has a much more effective cryptic resemblance, using a less effective startle display only as a last resort (Fig. 2). Between these two ends of a continuum, the Small Tortoiseshell occupies a compromise position, with fairly effective cryptic and startle displays. The Small Tortoiseshell is similar to the Red Admiral in the nature of its colour and patterning, and it is reasonable to suppose we see a similar strategy adopted by this species.

The success of startle colours as an anti-predator device is reflected in the extent to which it is relied upon as a defensive mechanism – in the Peacock it is surprisingly effective. Vallin *et al.* (2005) found, for example, that the number of Peacocks killed

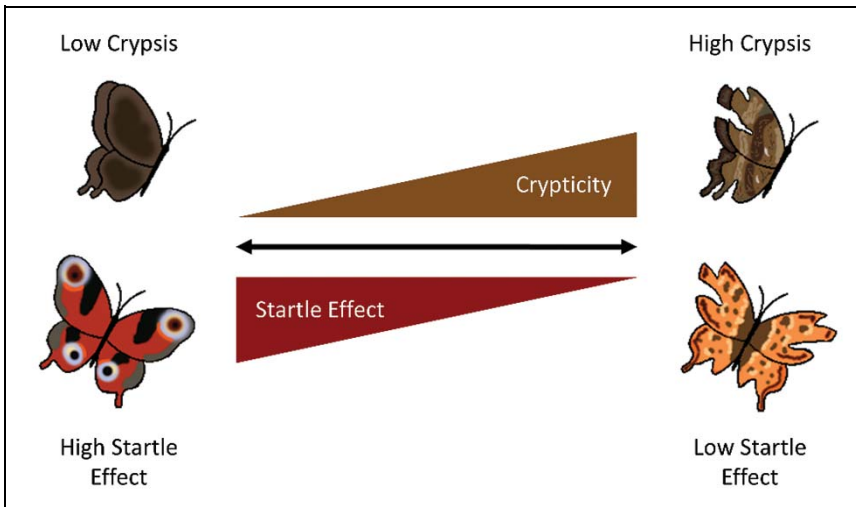


Fig. 2. Potential trade-offs in defensive colouration strategies in Lepidoptera. Different species appear to vary in the extent to which they rely upon particular defensive strategies. At one extreme, some (e.g. Peacock *Aglais io*) readily employ startling behaviours (e.g. wing flicking) and show highly effective startle colour patterns, but have less effective cryptic colour patterning. Others have a much more effective cryptic appearance and only employ startling behaviours as a final line of defence, after considerable provocation (e.g. Comma *Polygonia c-album*). Because butterflies typically rest with their wings closed dorsally, the ventral colouration is generally cryptic and the dorsal colouration shows startle colour patterns where these exist. Species such as the Red Admiral *Vanessa atalanta* or Small Tortoiseshell *Aglais urticae* seem to adopt a compromise strategy lying between these two extremes, of moderately effective cryptic appearance and moderately effective conspicuous startle displays.

when exposed to adult Blue Tits *Cyanistes caeruleus* (L.) increased from one out of 34 (3%) to 13 out of 20 (65%) when their eyespots were painted over. This highly successful deterrent display is almost entirely bluff, and the butterflies present no real threat to birds other than possibly being slightly distasteful relative to other butterfly species (Cott, 1940; Hagen, Leinaas, & Lampe, 2003; though see Möhl & Miller, 1976; Wiklund & Tullberg, 2004). This highlights the fact that startle displays may also serve as an aposematic advertisement (Drinkwater *et al.*, 2022). The extent to which the Red Admiral butterfly is palatable to predators is not yet known.

In the Lepidoptera, concealed conspicuous colouration of various degrees is widespread. This ranges from the spectacular, clearly intimidating eyespot flashing of the Peacock, through the brightly coloured hindwings of the underwing moths *Catocala* Schrank, to the more subtly contrasting pale or white hindwings of almost all noctuid moths (Skinner, 2009). Whether patterns all along this continuum of colouration function as startle colours is unclear, as is the relative benefit derived from each. In each species there is clearly a selective balancing act, where different strategies are prioritised and optimised based on the particular ecological circumstances of that organism (Drinkwater *et al.*, 2022). While the different explanatory mechanisms behind concealed conspicuous colours tend to be treated independently in the experimental literature, we would emphasise the need to discuss them collectively, as overlapping and perhaps multi-functional. To determine more widely the significance and function of putatively startling colour patterns, and the range of predators against which they may be effective, we also stress the need for more reporting of observations made by naturalists in the field, as well as systematic experiments. In spite of recent advances in theory (Drinkwater *et al.*, 2022), the fact that this potential defensive mechanism in such a well-known species as the Red Admiral is not widely acknowledged should serve to drive this message home.

REFERENCES

- Bae, S., Kim, D., Sherratt, T. N., Caro, T. & Kang, C. 2019. How size and conspicuousness affect the efficacy of flash coloration. *Behavioral Ecology* **30**: 697–702.
- Blest, A. D. 1957. The function of eyespot patterns in the Lepidoptera. *Behaviour* **11**: 209–256.
- Bond, A. B. 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics* **38**: 489–514.
- Cott, H. B. 1940. *Adaptive Colouration in Animals*. Methuen, London.
- Drinkwater, E., Allen, W. L., Endler, J. A., Hanlon, R. T., Holmes, G., Homziak, N. T., *et al.* 2022. A synthesis of deimatic behaviour. *Biological Reviews* **3**.
- Fitzgerald, C. S. & Krausman, P. R. 2002. *Helarctos malayanus*. *Mammalian Species* 1–5.
- Fredriksson, G. M., Wich, S. A. & Trisno. 2006. Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. *Biological Journal of the Linnean Society* **89**: 489–508.
- Hagen, S. B., Leinaas, H. P. & Lampe, H. M. 2003. Responses of great tits *Parus major* to small tortoiseshells *Aglais urticae* in feeding trials; evidence of aposematism. *Ecological Entomology* **28**: 503–509.
- Jenner Weir, J. 1869. On insects and insectivorous birds; and especially on the relation between the colour and the edibility of Lepidoptera and their larvae. *Transactions of the Royal Entomological Society of London* **17**: 21–26.
- Kettlewell, B. 1973. *The Evolution of Melanism*. Clarendon Press, Oxford.
- Loeffler-Henry, K., Kang, C. & Sherratt, T. N. 2021. The anti-predation benefit of flash displays is related to the distance at which the prey initiates its escape. *Proceedings of the Royal Society B* **288**.
- Loeffler-Henry, K., Kang, C., Yip, Y., Caro, T. & Sherratt, T. N. 2018. Flash behavior increases prey survival. *Behavioral Ecology* **29**: 528–533.

- Maldonado, H. 1970. The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Zeitschrift für Vergleichende Physiologie* **68**: 60–71.
- Möhl, B. & Miller, L. A. 1976. Ultrasonic clicks produced by the peacock butterfly: a possible bat-repellent mechanism. *Journal of Experimental Biology* **64**: 639–644.
- Murali, G. 2018. Now you see me, now you don't: dynamic flash coloration as an antipredator strategy in motion. *Animal Behaviour* **142**: 207–220.
- Olofsson, M., Jakobsson, S. & Wiklund, C. 2012. Auditory defence in the peacock butterfly (*Inachis io*) against mice (*Apodemus flavicollis* and *A. sylvaticus*). *Behavioral Ecology and Sociobiology* **66**: 209–215.
- Poulton, E. B. 1890. *The Colours of Animals: their meaning and use especially considered in the case of insects*. Kegan Paul, Trench, Trubner, & Co. Ltd., London.
- Sethy, J. & Chauhan, N. P. S. 2018. Dietary preference of Malayan sun bear *Helarctos malayanus* in Namdapha Tiger Reserve, Arunachal Pradesh, India. *Wildlife Biology* **2018**: 1–10.
- Skinner, B. 2009. *Colour Identification Guide to Moths of the British Isles*. Apollo Books, Stenstrup, Denmark.
- Stevens, M. 2005. The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biological Reviews of the Cambridge Philosophical Society* **80**: 573–588.
- Stevens, M., Hardman, C. J. & Stubbins, C. L. 2008. Conspicuousness, not eye mimicry, makes “eyespot” effective antipredator signals. *Behavioral Ecology* **19**: 525–531.
- Vallin, A., Jakobsson, S., Lind, J. & Wiklund, C. 2005. Prey survival by predator intimidation: an experimental study of peacock butterfly defence against blue tits. *Proceedings of the Royal Society B: Biological Sciences* **272**: 1203–1207.
- Vallin, A., Jakobsson, S., Lind, J. & Wiklund, C. 2006. Crypsis versus intimidation – anti-predation defence in three closely related butterflies. *Behavioral Ecology and Sociobiology* **59**: 455–459.
- Wiklund, C. & Tullberg, B. S. 2004. Seasonal polyphenism and leaf mimicry in the comma butterfly. *Animal Behaviour* **68**: 621–627.
- Wong, S. & Servheen, C. 2002. Food habits of Malayan sun bears in lowland tropical forests of Borneo. *Ursus* **13**: 127–136.

REVIEW

The Mind of a Bee by Lars Chittka. 304 pp. Princeton University Press, 2022. Cloth cover £25.00. ISBN 978-0-6911-80472.

For members of the RES Insect Behaviour SIG, Professor Lars Chittka and his students are familiar faces who have given entertaining talks over the years about the foraging behaviour of bumblebees and honey bees and insights into the difficult realm of how insects ‘think’. Chapter titles in his book include – Seeing strange colours; It’s Just Instinct or Is It?; The Roots of Bee Intelligence and Communication; Learning about Space and Flowers; the Brains behind It All; Personality differences; and Do Bees Have Consciousness? Quite different challenges of experimentation and analysis compared to those of species identification and recording species distributions which we usually concern ourselves with.

The author takes us deep into the sensory world of bees and explains how bee brains are unparalleled in the animal kingdom relative to the size of their nervous systems. Mostly conventional animal studies here. The shock comes in the last chapter when the author argues that a bee may have a ‘mind’ that thinks and feels. Invertebrates such as octopus have been added to this exclusive clan, and now possibly bees, and I have some sympathy as I think back to the 1950s while watching