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Rapid colour change by the spider, *Tylorida striata* (Thorell, 1877) (Araneae: Tetragnathidae)

Timothy C. Hawes

Abstract. Although it has been known since the 19th century that the tetragnathid spider *Tylorida striata* has the capability of rapidly changing colour, descriptions of this to date have been limited to simply noting that it darkens in response to disturbance. The process of rapid colour change by this species is described here formally, both qualitatively and quantitatively, for the first time. Submergence in ethanol elicited no rapid colour change – demonstrating that the colour change is induced by a perceived environmental signal rather than a received physiological stress. This is also consistent with observations of modification of the response as a result of familiarisation. It is hypothesised that, in association with web-dropping escape behaviour, rapid colour change probably serves a cryptic function.

Key words. colouration, crypsis, guanocyte, spider

INTRODUCTION

The colour of a spider may have a number of forms and functions. Although function is not implicit, functions have generally been supported by experiment and investigation. In communication terms, colours predominantly serve either interspecific signal systems like crypsis, mimicry, and prey-attraction (how it is perceived by other species) (e.g., Heiling et al., 2003; Peng et al., 2003; Tso et al., 2006; Chuang et al., 2007; Insausti & Casas, 2008), or intraspecific signal systems like some salticid sexual dimorphisms in colouration (how it is perceived by its own species) (e.g., Lim & Li, 2006; Lim et al., 2007). Although for most species such signal systems appear to select for the stabilisation of the signal (and therefore its communicated meaning), this is far from universal. Signal variability takes four main forms in spiders: (1) genetic polymorphisms; (2) ontogenic changes between instars; (3) background matching by pigment synthesis or degradation; and (4) rapid colour change. This paper concerns the latter: the fourth form of colour variability, rapid colour change – this is the least reported type of variability and involves colour changes ('rapid morphing') that occur almost instantaneously. Although its adaptive credentials seem fairly explicit, its functional significance remains poorly defined and both its mechanisms and the nature of its expression require much greater and more resolved quantification.

Rapid colour change in spiders has been known since the end of the 19th century (Bell, 1893). It appears to be primarily observed in the Araneidae (e.g., Sabath, 1969, Bristowe, 1976; Edmunds & Edmunds, 1986) and Tetragnathidae (e.g., Feng, 1990; Oxford & Gillespie, 1998), but has also been observed individually in other families like the Linyphiidae (Bristowe, 1941), Theridiidae (Uyemura, 1957), and Philodromidae (Ikeda, 1989). The key differences between it and the thomisid-type background matching are time and mechanism (Oxford & Gillespie, 1998). The instantaneous or semi-instantaneous responses of rapid colour-changers excludes the possibility of synthesising or degrading pigment in the manner used by crab spiders to background-match, in which the timescale of changes is that of days.

Instead, it appears that the colour change is brought about somehow by the movement or manipulation of the distribution of pigment. With the exception of unusual examples of rapid colour change brought about by food ingestion (Gillespie, 1989), this seems to be a shared feature of these species' colour change. (Traditionally these two types of colour change have been classified respectively as 'morphological' and 'physiological' colour change but these designators seem less apt now: the synthesis and degradation of pigment is a physiological process; while the movement of pigment is probably largely facilitated by sub-dermal architecture). How exactly the distribution of pigment is moved or manipulated in rapid colour changers is a more complicated question. More research needs to be done in this area, but studies carried out so far emphasise changes occurring around the guanocytes, the specialised sub-dermal spherical compartments which house the white-rendering biochrome, guanine (Blanke, 1975). Edmunds & Edmunds (1986) found no evidence of contractile elements in the guanocytes themselves. Wunderlin & Kropf (2013) provided a few micrographs to suggest the contraction of muscle tissue that occurs in association with the guanocytes is responsible for the colour change in the linyphiid, *Floronia bucculenta*.

190/12 Moo 16 Srimaarat Road, Khon Kaen, 40000, Thailand; Email: timothyhawes@hotmail.com

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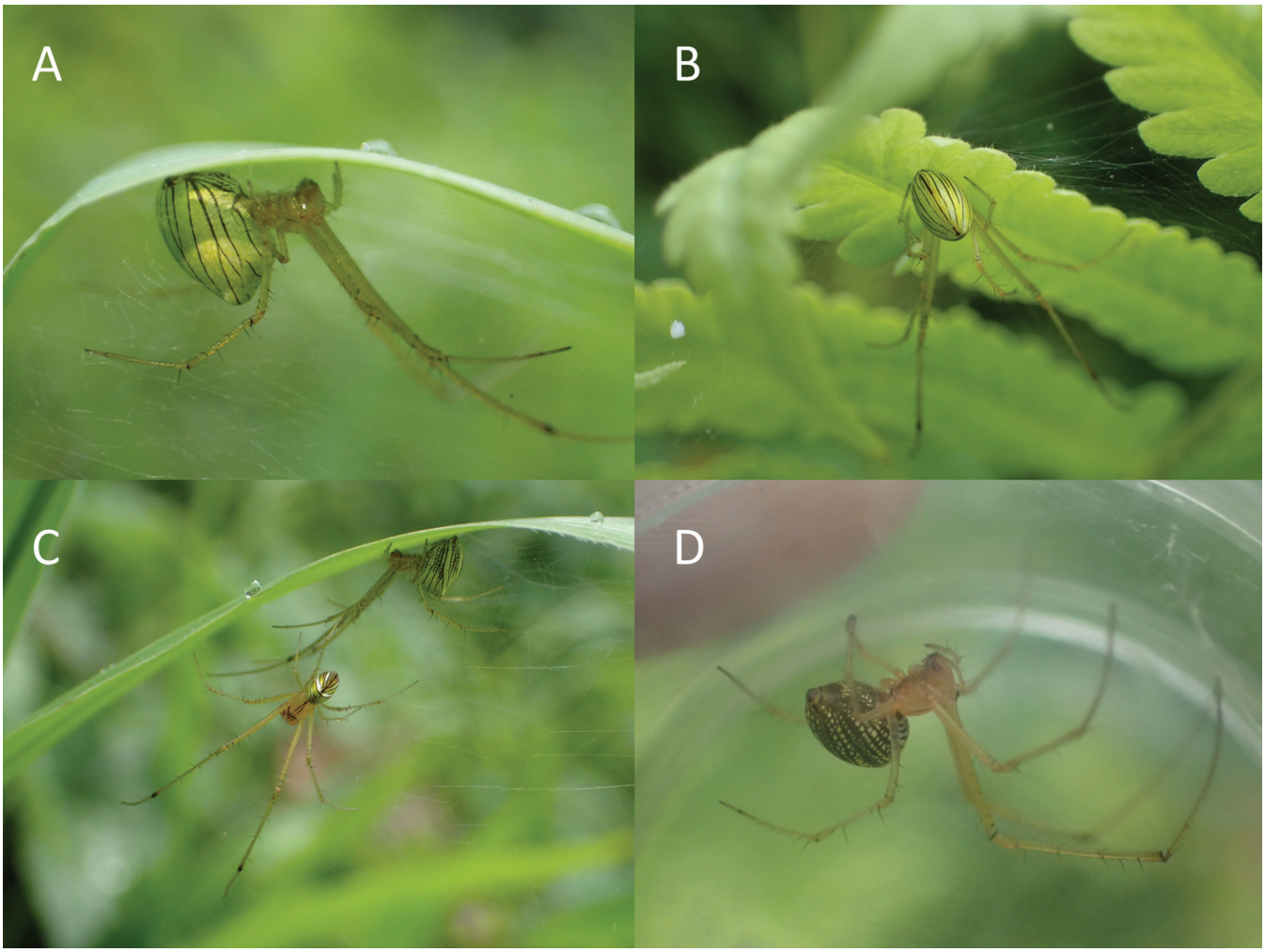

Fig. 1. *Tylorida striata* habitus in situ. A, female at web; B, dorsum of female; C, male and female at web; D, darkened female immediately after capture showing rapid colour change.

The Asian tetragnathid species, *Tylorida striata* (Thorell, 1877) is a good model of the phenomenon: its process of colour change is striking, reasonably readily elicited and observed. Even establishing relatively controlled and replicable conditions for elicitation can be extremely complicated in spiders – although studying *T. striata*'s responses is not without its own complications, it is relatively more amenable to experimental examination and therefore a good model for examining rapid colour change in spiders. *T. striata*'s response was first observed by the Irish clergyman and spider enthusiast, the Rev. Thomas Workman in Malaysia (Workman & Workman, 1894: 19): "I also noticed that this species of Spider has the power of darkening down its brilliant colouring when frightened." The response has since been independently illustrated by Feng (1990), and photographed by Koh & Ming (2014). However, despite being potentially such a good model, *T. striata's* rapid colour change response remains anecdotal. This paper attempts to remedy this omission with a more formal description and quantification of the response.

MATERIAL & METHODS

Study site and sample collection. *Tylorida striata* (Thorell, 1877) was identified with reference to Song et al. (1999) and Koh & Ming (2014). Systematic nomenclature follows the current organisation of the Tetragnathidae in the World Spider Catalog (World Spider Catalog, 2017). Research was carried out in April–May 2015. A cluster of *T. striata* webs was found in low-lying shrub thicket just above the river banks of Nam Song, Laos. Species records were provided previously by Jäger & Praxaysombath (2011). Although widely distributed across Southeast Asia, the species is usually encountered as singletons or lone pairs. The discovery of a small 'population' provided an unusual opportunity for examining its well-known colour-changing capabilities within a quantitative framework. As they are not commonly encountered, the presence of males, in particular, represented a fortuitous coincidence of reproductive phenology with the research visit and a chance to study the response in both genders. Spiders were collected by hand-searching shrubs over a 2-hour period each morning.

Induction of rapid colour change. Field pilot observations were made after discovering the *T. striata* population to confirm the existence of the response and test its relative ease of elicitation. Spiders were captured and tested individually in small transparent plastic pots (diameter = 3 cm; h = 2.5 cm). The pots are large enough to allow movement of the spider and therefore a more natural colour change response,

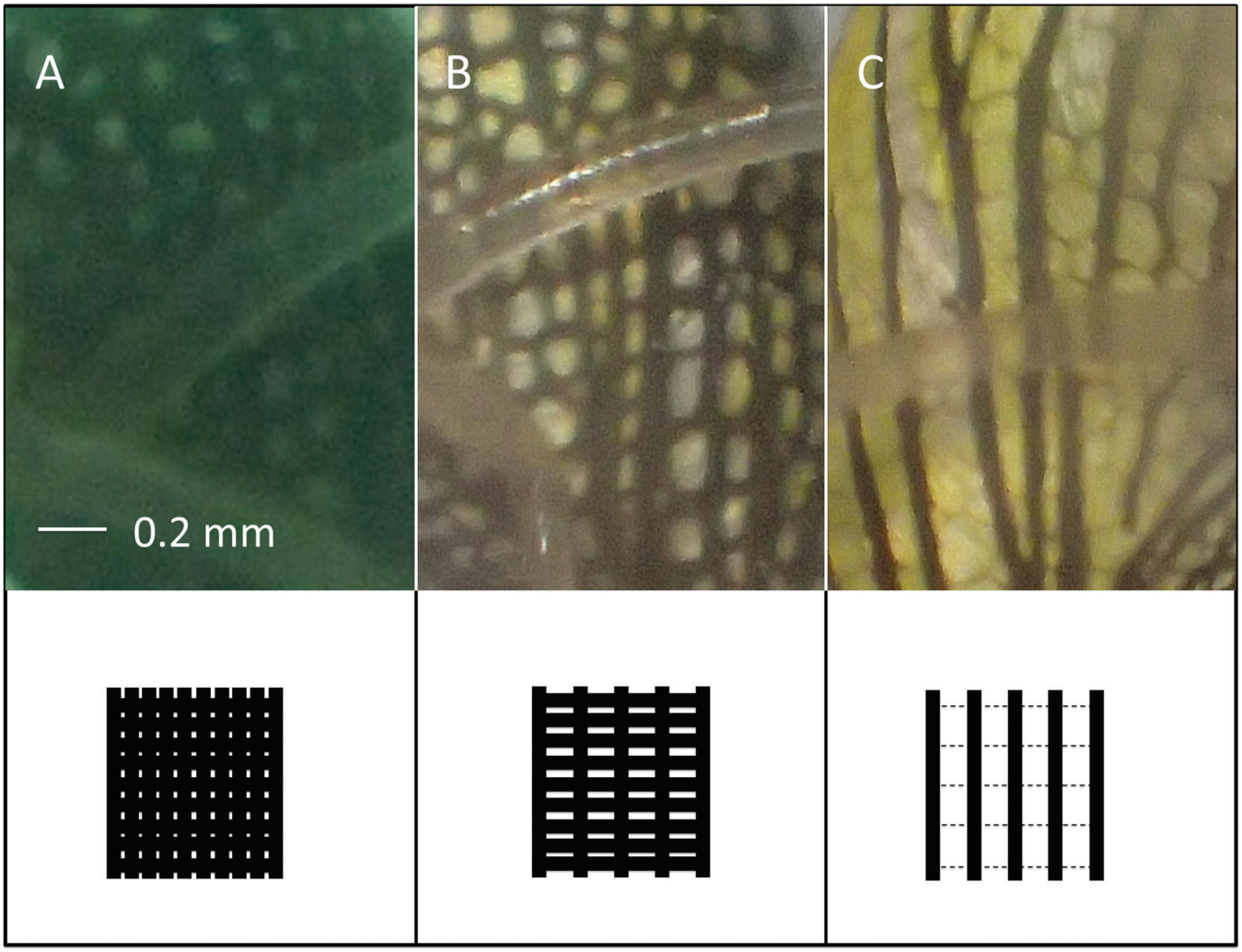

Fig. 2. Close-up of cuticular colour changes on the opisthosoma of *T. striata* female during rapid colour change with schematic representation of compartmentalised changes in: A, dark phenotype; B, transitional phenotype; and C, yellow phenotype.

but as observations of rapid colour change require the ability to observe the opisthosoma, movement is limited to relatively narrow spatial axes to facilitate better observation. The response was observed immediately after capture in all specimens. The response was also readily repeated in pilot specimens by holding the container between the thumb and index finger and shaking it. Having established the behaviour's amenability to testing, samples were collected and transported to a room being used as a make-shift laboratory. Field temperatures were maintained by the avoidance of air conditioning. Spiders were placed on a shelf and allowed to acclimate to their transport and capture pots for 24 hours with a moistened ball of tissue paper, then tested. After examination of the macrophotography of pilot observations, the response was categorised into three stages (described in Results). For the experiment, the response was elicited in most instances very simply just by removing the lid of their capture pot. Instances where this did not work are discussed in the context of familiarisation (below, Results). A stopwatch (resolution = 0.1 ms) was used to note the starting time of each stage of colour change from induction to reversal. In the cases where a familiarisation effect was present, the container was closed and given a vigorous shake (5 up-down movements), put back down, and the stopwatch started when they changed colour. If this elicited no change, no further disturbance was introduced and the individuals were noted as non-changing. A camera with a macro lens was used to both observe the changes through a view finder at the appropriate resolution and document the changes. Light conditions for both experimental and field observations and photography were uniform: external observations were made in bright sunlight without canopy or cloud cover (Fig. 1); internal observations were made during the day under ambient electrical lighting with all macro-photographs taken using identical illumination from the camera's macro-light (Fig. 2).

Non-induction of rapid colour change. A separate experiment was conducted to test whether the response was or was not elicited by changing the environment of the spider to one that exposed them to a mortal danger 'disguised' as a non-threatening change in environment, i.e., the opposite of the induction response. Many tetragnathid spiders are closely associated with water to some extent, building their webs near or often over water bodies. *T. striata* webs are constructed close to water and if they are dropped in water they readily swim and climb out again. The experiment used this 'non-threatening' environmental signal to test whether the colour

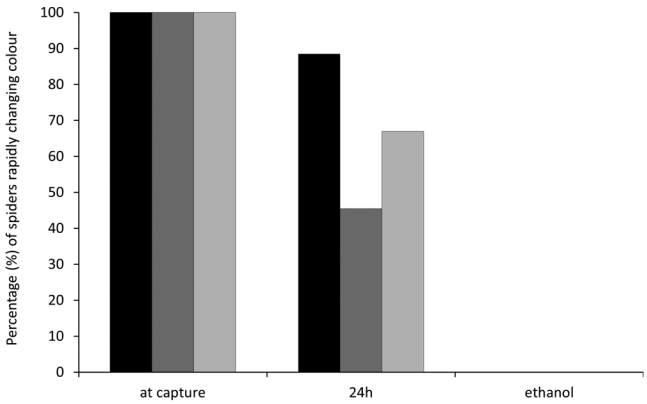

Fig. 3. Comparison of the induction and non-induction of the rapid colour change response after capture, after 24 hours, and when submerged in ethanol (black bars = females; dark grey bars = males; light grey bars = combined).

change response would be elicited by an environment with mortal danger but without its signal. *Tylorida striata* were dropped into 70% ethanol and observed for colour change behaviour. Of course, in that it has a smell, the alcohol is an imperfect mimic of water, but as they have no experience of this smell, they have no reason to associate it with danger (or the liquid environment); whereas they will readily recognise the visual appearance of and tactile experience of a liquid physical environment and should have no reason to associate it with danger when they are dropped in it. Even if one assumes aversive behaviour to novel noxious smells, they were not given time to process (or perhaps even receive) such informational stimuli (or connect it to the liquid) since they were dropped immediately into the liquid, with the process taking only a few seconds. Upon submergence, their very first movements were an attempt to 'swim' and were not obviously stressed. This obviously changed quickly but indicates that the environmental transfer is not in itself perceived as initially life-threatening. The procedure mimics that of standard specimen preservation so introduces no new or unusual stresses that are not normally experienced by study specimens. Mortality takes c. <60 seconds (much longer than the colour change takes to elicit artificially).

Familiarisation. Familiarisation is defined here as a reduction in the novelty of an environment — which may be either static or dynamic — particularly with regard to its perceived danger, through either repetition of, or extension of the duration of, an experience. In the context of rapid colour changing spiders, familiarisation represents a lessening of the perceived danger represented by disturbance treatments. This effect was examined and demonstrated in two ways. The first of these is described above as the 'non-induction' experiment and was used to distinguish between signal and physiological stress as response cues. The second method looked at the ways in which the rapid colour change response varied among individuals. Two sources of variation were identified: (1) loss of the response as a result of repetition; and (2) comparative variance in the timing of the different stages of the response. The first is an index of response decay due to greater familiarisation. The second is based on the hypothesis that if there is greater variance in the

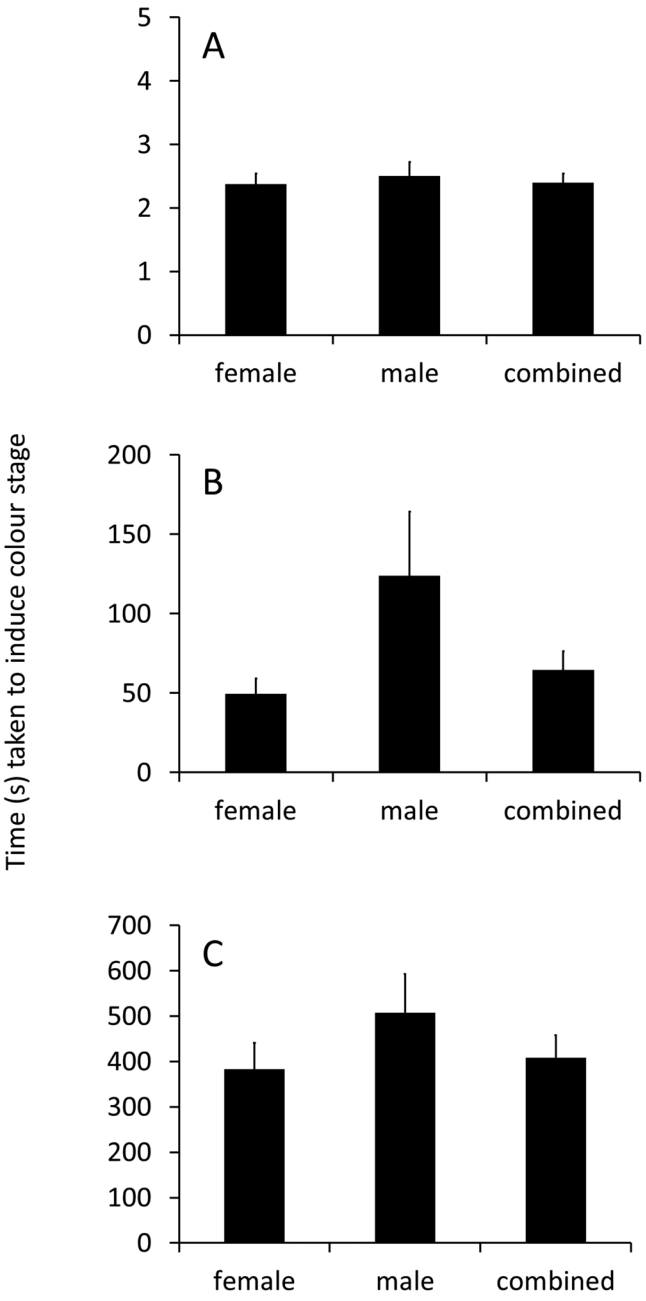

Fig. 4. Comparison of the time taken (s) for the onset of each colour stage after experimental induction. A, dark phenotype; B, transitional phenotype; C, yellow phenotype. (Error bars = ±1 S.E.).

reversal than the onset of rapid colour change this represents perceptual, rather than physiological, differences between individuals. This is based on the idea that while physiological responses should roughly correspond to a species' general physiology, physiological responses mediated by perception will show greater variation. This is because perceptual (in this case: threat/disturbance) assessments will be based on prior experiences of threat, which are necessarily different for every individual.

Data analysis. A chi-squared test was used to compare differences in elicitation success between the induction and non-induction treatment. Mann-Whitney Tests were used to compare differences between males and females and the time it took for the induction of each of the three stages of

Table 1. Temporal variance in the stages of the rapid colour change behaviour in *Tylorida striata*.

Colour Stage	Female (n=27)	Male (n=11)	Combined (n=38)	Statistical Comparisons	Levene's Test Statistic	p-value
I: Dark phenotype	0.7	0.3	0.6	Female:		
				I vs. II	16.05	<0.001
				I vs. III	43.31	<0.001
				Male:		
				I vs. II	5.81	0.037
				Combined:		
				I vs. II	20.93	<0.001
				I vs. III	67.50	<0.001
II: Transitional phenotype	2154	9778	4311	Female:		
				II vs. III	30.78	<0.001
				Combined:		
				II vs. III	38.53	<0.001
III: Yellow phenotype	81584	44365	74895			

the rapid colour change response. Differences in variance were compared for gender response and for response stage using Levene's Test.

RESULTS

Fig. 1 shows *T. striata* in situ (Fig. 1a–c) and darkened immediately after capture (Fig. 1d). Under magnification, the rapid colour change is revealed to occur in between the vertical striations that are normally visible on the spider's opisthosoma when it is undisturbed. Colour changes occur as a result of the appearance of dark 'cells' in these spaces. These 'cells' are rendered dark by their borders within which the presence of yellow is enclosed to greater or lesser degrees depending on the stage of colour change. At the extreme end of darkening at onset, the yellow colouration is almost completely occluded; as the colour change reverses the dark boundaries of these 'cells' become thinner and thinner, allowing the re-emergence of the yellow and producing a 'veiny' network of darkened lines. After the fully darkened stage, close-ups reveal a regular lattice of boundary lines, which suggest that the cell boundaries are all orientated horizontally across the opisthosoma (perpendicular to the striations). The space in between the striations is occupied by either one or two 'cells'. The striations seem to provide the general scaffold for the 'cell' network. Fig. 2 shows the compartmental changes under magnification and in schematic form.

On the basis of these observations, three stages of colour change were identified and used to delineate and quantify the process (Fig. 2): (I) dark phenotype: dark margins of 'cells' dominate and reduce yellow to specks (Fig. 2a); (II) transitional phenotype: dark margins of cells shrink but are still clearly discernible, yellow is more prominent as patches within the 'cell' network (Fig. 2b); (III) yellow phenotype: spider has returned to bright-yellow, the 'cells' are either invisible or linger only as a faint outline (Fig. 2c).

All spiders changed colour when they were captured (Fig. 1d). Fig. 3 compares the proportions of spiders that exhibited rapid colour change at capture, after 24 hours and when submerged in ethanol. No spiders changed colour when submerged in ethanol. Chi-squared comparisons found a significant difference between the proportions of spiders rapidly changing colour in the induction and non-induction treatments (χ^2= 4.239, DF = 1, P = 0.040). There was some reduction of the response after 24 hours, particularly among males, but this was not significant. Fig. 4 compares the rates of response induction for each of the three stages of rapid colour change. The induction of the response takes <5 seconds but the reversal of the phenomenon can take from 1–2 minutes to nearly 20 minutes. There were no significant differences between males and females. Table 1 compares the variance for each of the three stages of the change behaviour and delineates the significant differences found between stages. For females and combined male and females, variance was significantly different between all stages.

DISCUSSION

Rapid colour change in *T. striata* was readily demonstrated by both males and females. Its visual effect is a dramatic change from bright yellow to dark brown. Even using the basic magnification provided by photographic equipment it is clear that the overall visual effect is the product of subdermal morphological changes involving the boundaries of the 'cells'. Localised muscular action — involving the expansion and contraction of these areas — seems to be indicated, but further examination will be required to elucidate the mechanism properly. Given that the mechanism is clearly achieved morphologically, the most useful objective description of the colour change may not be 'colour' itself which varies with field of view and magnification and is obviously extremely transient during the change process, but morphological – i.e. the changing shape of the colour compartmental system. Colour is how the change is perceived

and how any intended signal is communicated, but the change itself is more correctly understood as one of rapid sub-dermal re-orientation.

The process itself takes <5 seconds to initiate, but can take minutes to reverse. Variability in reversal time, in association with delayed response induction and non-induction of the response in some individuals, support the hypothesis that the response is mediated by perception of threat and lessened as a result of familiarisation. This agrees with separate evidence from the experimental comparisons of response induction environments: a relatively mild physical disturbance from a 'potential predator' elicited almost universal change behaviour compared to none from a genuine mortality-inducing physiological stress disguised as a 'non-threatening' disturbance. There were observed, but non-significant, differences in familiarisation between males and females (Table 1): these may seem counterintuitive at first glance given that females are much larger and stronger, however this difference may stem from the need for males to be less sensitive to perceived signals during mating (threat, rebuff, etc.) – the aggressiveness of females being well known in spiders.

All observations of the phenomenon have been associated with disturbance (Oxford & Gillespie, 1998). However, as a response to disturbance, rapid colour change may have several possible display functions, including 'startling', warning, crypsis, fear, or a combination of some or all of these. In the case of *T. striata* both the submergence experiment and evidence of familiarisation from variance in spiders changing back to their normal colour, provide a slightly more concrete perspective on one aspect of its manifestion, at least in this species: the response is elicited by a change in its perceived environment, not in its actual material environment. This supports a 'fear'-as-eliciting-signal interpretation of the response.

Isolating the functional significance of the change needs further examination. However, examination of the response in the context of how it occurs in the natural environment may offer a few clues. When *T. striata* — and to my knowledge all, or most, other known rapid colour-changers — change their colour in situ, they do so in association with dropping out of their web onto the substrate. In tandem with the switch to less bright colours, this probably rules out a 'startling' function. The visual change in fact would, in most cases, not be witnessed by a disturbing agent as the change occurs in free fall, induction occurring within an equivalent timescale to that of the spider's vertical movement. Such dropping is common in many non-colour changing orb-weaving spiders and is usually followed by some form of 'playing dead'. In colour-changers, the behaviour is the same. This context would also appear to rule out warning as a display function – warning signals generally operate to enable the signaler to stay where they are: 'fight' (or pretend to) rather than take 'flight'. Although utilising a warning signal from a retreat position on the ground is not impossible, again the choice of colours argues against this as warning colours are also typically bright.

Although 'fear' seems to be an elicitor of the behaviour, it is difficult to see any evolutionary advantage in it as a signal. Certainly, although it is not impossible to envisage the existence of physiological responses which unintentionally signal vulnerability (e.g., blushing by humans), it would, as such, represent a response that seems antithetical to increased survival. In such a scenario the response would have to be seen as the opposite of an adaption – a trait which evolution has failed to select against. One could then argue, presumably, that this may be why the response is quite rare in spiders. (Although I am inclined from my own field observations — see below also — to think that it is certainly less rare than previously envisaged). However, given the evolutionary sophistication of spiders generally, this argument, although it cannot be ruled out at this stage, seems unlikely.

If rapid colour-changing has a function, the function that, on available evidence, seems most consistent with spider biology and the context of the response is crypsis. This is far from a definitive explanation but agrees with a number of scenarios. Changing from a conspicuous bright colour to a dark less bright colour is a match for a change to the ground substrate. Crypsis is usually also enhanced by immobility, which in turn matches the 'playing dead' behaviour common to web-droppers. Likewise, the rate of change is coincident with the rate of change involved in the transfer to a new background environment. Crypsis may co-occur with both 'flight' and 'fight' responses, but in association with 'flight', a defensive function seems strongly indicated. Further investigations into the functional significance of rapid colour changing might usefully examine the drop response in relation to substrate camouflage.

But further general descriptions and documentations of the response are perhaps of even more fundamental importance – my own field observations have found the response is not limited to 'known' rapid colour changers by any means, but reporting of such phenomena is complicated by a range of problems – uncertain taxonomic identity; species abundance; difficulties of establishing replicable conditions for elicitation; interactive effects of other polymorphisms, interactions with familiarisation, etc. The subject is ripe for revisiting using both more quantitative and hypothesis-driven approaches, but not unproblematic.

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