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Alfakih, A. orcid.org/0000-0001-8463-2088, Watt, P.J. and Nadeau, N.J. orcid.org/0000-0002-9319-921X (2022) The physiological cost of colour change: evidence, implications and mitigations. Journal of Experimental Biology, 225 (10). jeb210401. ISSN 0022-0949

https://doi.org/10.1242/jeb.210401

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REVIEW

The physiological cost of colour change: evidence, implications and mitigations

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ABSTRACT

Animals benefit from phenotypic plasticity in changing environments, but this can come at a cost. Colour change, used for camouflage, communication, thermoregulation and UV protection, represents one of the most common plastic traits in nature and is categorised as morphological or physiological depending on the mechanism and speed of the change. Colour change has been assumed to carry physiological costs, but current knowledge has not advanced beyond this basic assumption. The costs of changing colour will shape the evolution of colour change in animals, yet no coherent research has been conducted in this area, leaving a gap in our understanding. Therefore, in this Review, we examine the direct and indirect evidence of the physiological cost of colour change from the cellular to the population level, in animals that utilise chromatophores in colour change. Our Review concludes that the physiological costs result from either one or a combination of the processes of (i) production, (ii) translocation and (iii) maintenance of pigments within the colour-containing cells (chromatophores). In addition, both types of colour change (morphological and physiological) pose costs as they require energy for hormone production and neural signalling. Moreover, our Review upholds the hypothesis that, if repetitively used, rapid colour change (i.e. seconds–minutes) is more costly than slow colour change (days–weeks) given that rapidly colour-changing animals show mitigations, such as avoiding colour change when possible. We discuss the potential implications of this cost on colour change, behaviour and evolution of colour-changing animals, generating testable hypotheses and emphasising the need for future work to address this gap.

KEY WORDS: Physiological cost, Physiological colour change, Morphological colour change, Chromatophores, Behaviour, Phenotypic plasticity

Introduction

Colour change is a widespread strategy for many animals (Cott, 1940), which occurs during development (ontogeny) or throughout the animal's life as a form of phenotypic plasticity. Colour change performs several functions in changing environments, including thermoregulation (Smith et al., 2016), concealment (Duarte et al., 2017), signalling (Stuart-Fox and Moussalli, 2008; Ligon and McGraw, 2016) and protection from harmful ultraviolet (UV) radiation (Garcia et al., 2004). Colour change is generally mediated by colour-containing cells called chromatophores (see Glossary) (Bagnara and Hadley, 1973), and this change falls into two categories depending on the mechanism and speed (Bagnara and Hadley, 1973; Duarte et al., 2017). Morphological colour change is mainly defined by quantitative and qualitative changes in chromatophores (Thurman, 1988; Stuart-Fox and Moussalli, 2009), based on the synthesis and degradation of pigments (Bagnara and Hadley, 1973) occurring over long periods, ranging from days to months (Thurman, 1988; Umbers et al., 2014). In contrast, physiological colour change is the redistribution of pre-existing pigments in the integument and occurs over shorter time frames, from milliseconds to hours (Duarte et al., 2017) (Box 1). Both types of colour change can be under hormonal and neural control or a combination of the two (reviewed in Sköld et al., 2016; Duarte et al., 2017).

Growing interest in colour change has yielded a better understanding of the cues, mechanisms and benefits of this plastic trait. However, although plastic traits have clear benefits to organisms, through optimising their fitness across different environments, they also incur costs (DeWitt et al., 1998; Relyea, 2002). Generally, the costs of colour change have had minimal attention. The physiological cost associated with colour change was debated in the 1950s, but was restricted to the energy requirements of the mechanism pertaining to pigment dispersion and aggregation in the integument (see Horowitz, 1958, and references therein). Yet, the most discussed physiological cost of coloration in the literature is the cost of pigment and colour production, but not colour change per se (see Webster et al., 2018).

Recently, changing colour has been appreciated to carry some physiological (i.e. energetic and metabolic) costs based on a number of assumptions. First, there is a cost associated with pigment production, as synthesising pigments may require energy and can depend on dietary components (Sköld et al., 2016; Stevens, 2016), making pigment utilisation energy demanding or resource limited (Hill, 1996; 2000). Some pigments used for colour change, such as carotenoids, might be more costly than others (Hill, 1996) or may be used for other internal functions such as the immune system (Sköld et al., 2016; Duarte et al., 2017), and thus a cost emerges from trade-offs of allocating resources, which would ultimately affect the physiological state (Polo-Cavia and Gomez-Mestre, 2017). Furthermore, the catabolism of pigments is also suggested to carry some cost (Polo-Cavia and Gomez-Mestre, 2017). Second, intracellular translocation of pigments (Kang et al., 2016) and neuromuscular-mediated colour change (see Glossary) are considered energy-depleting activities (Sköld et al., 2012). Finally, maintaining physiological and morphological colour change can be a costly process, as it necessitates continuous monitoring of the environment and hence continuous optimisation of coloration depending on the changing circumstances, such as changes in visual properties (Hanlon et al., 1999; Stuart-Fox and Moussalli, 2009; 2011; Stevens and Ruxton, 2019).

Generally, colour change may drain energy during neural processing in rapidly changing animals, as encoding and

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Glossary

Chromatophores
Colour-containing cells that are classified broadly according to the colour of the pigment they contain.

Neuromuscular-mediated colour change
A change in the chromatophore organs (not cells) found in cephalopods, which is regulated via a neural pathway, by which relaxation and contraction of radial muscles surrounding these chromatophore organs causes a colour change.

Melanophore
A type of chromatophore containing the pigment melanin, which is generally black or brown and packaged within organelles called melanosomes.

Background matching
The situation where an animal bears a general resemblance to the colour, brightness and patterns of the background.

Disruptive coloration
The situation where an animal possesses markings that generate false edges that make the observer unable to detect or recognise the animal.

Masquerade
The situation where an animal resembles the shape of an uninteresting or inedible object in its environment (such as a stick) to make the observer unable to recognise it.

transmitting information is expensive (Stevens, 2013), and hence a considerable amount of energy is depleted during neural signalling (Laughlin, 2001; Niven and Laughlin, 2008). Also, hormones are essential components in motility and the increase and decrease in chromatophore number in both types of colour change (Leclercq et al., 2009; Bertolesi and McFarlane, 2020; Yang et al., 2021), and thus production and maintenance might ultimately pose energetic costs. However, current knowledge of the physiological cost of colour change has not advanced beyond these assumptions, and a number of questions remain unresolved (Sköld et al., 2016; Stevens, 2016; Duarte et al., 2017). In this Review, we assess the direct and indirect evidence of the physiological cost of colour change, from the molecular to the population level, in a wide range of taxa. We also discuss the potential ecological and evolutionary implications of colour change being physiologically costly, generating testable hypotheses.

We limit our Review to animals that use chromatophores for colour change, meaning that the colour is contained within living cells and tissues (unlike in birds and mammals, where most colour is contained in dead integumentary structures of hair or feathers, and colour change requires moulting). We discuss evidence from a wide range of species including vertebrates, such as fish, amphibians and reptiles, as well as invertebrates, including crustaceans and cephalopods (see Table 1). Colour-change mechanisms differ between taxa, especially vertebrates and invertebrates (Umbers et al., 2014; Ligon and McCartney, 2016), and this may affect the associated costs, but we attempt to draw general conclusions that will be applicable across taxa.

Evidence for a physiological cost of colour change

Direct evidence

There are a few lines of direct evidence supporting the hypothesis that colour change incurs a cost. On the cellular level, a few studies have stated that molecular motors such as myosin, kinesin and dynein, responsible for translocating pigment organelles within cells, at least in melanophores (see Glossary), depend on energy from ATP hydrolysis to move pigments from and towards the centre of the cells (reviewed in Aspengren et al., 2009; Sköld et al., 2016). For example, the depletion of ATP from fish melanophores has been shown to cause complete cessation of pigment granule movement (Rodionov et al., 1998).

Rodgers and colleagues (2013) were the first to provide direct evidence of physiological costs associated with colour change from behavioural experiments on guppies (*Poecilia reticulata*). When fish were induced to change colour over a period of days, they were found to consume more food, which may imply compensation for the energy expended. Generally, diet per se acts as a constraint such that colour change is contingent upon the availability and acquisition of dietary-pigment sources. It may be that fish consumed more food to compensate for low pigment availability, where food represents a constraint (Duarte et al., 2017). If this is the case, we predict that fish that darken their body will require more food than individuals that lighten their bodies. However, it is also possible that the everyday alternation between black and white backgrounds in Rodgers et al.'s (2013) study might have caused a stress response (Duarte et al., 2017). It has been suggested that metabolic measurements would help quantify the energetic expenditure associated with colour change (Duarte et al., 2017), and using a waterborne hormone sampling approach to detect cortisol might be useful to determine whether a stress response occurs.

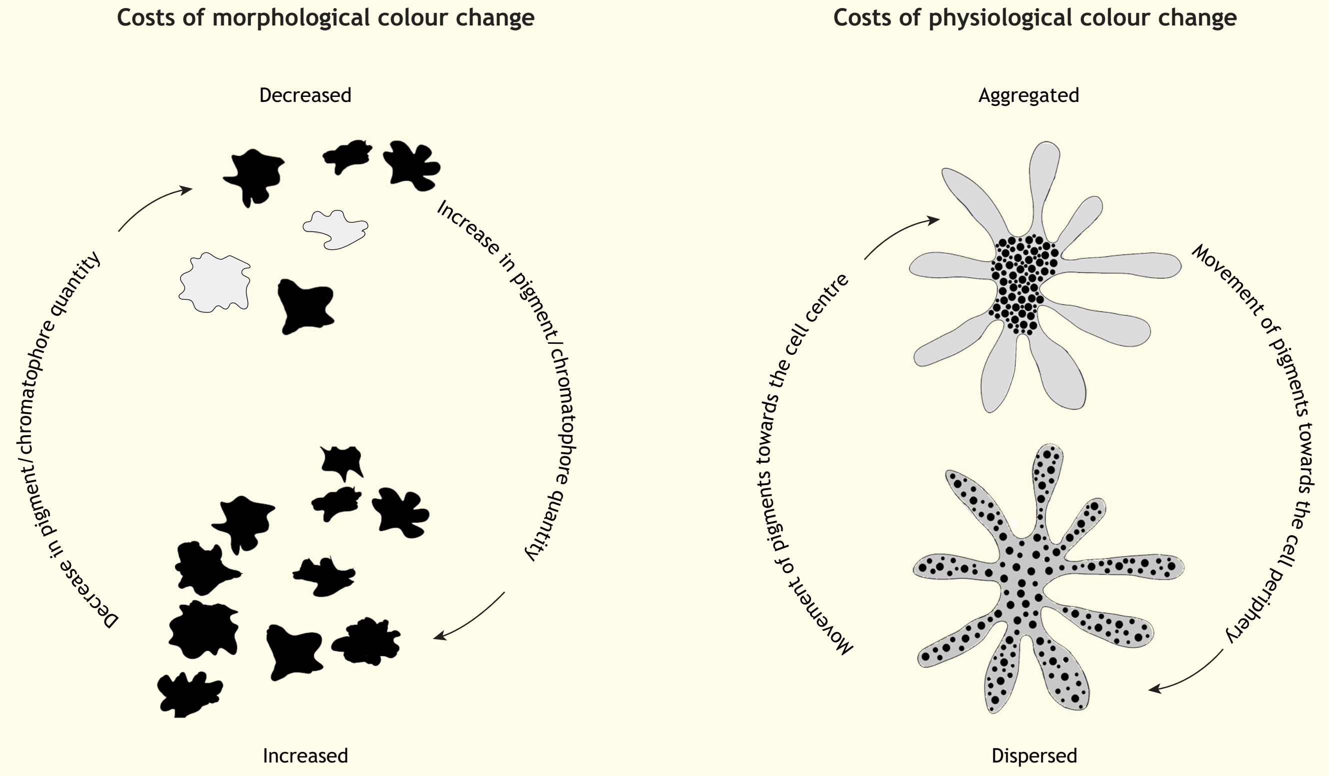
To the best of our knowledge, only one study has successfully determined a metabolic cost associated with colour change. Polo-Cavia and Gomez-Mestre (2017) showed that larvae of Bosca's newt (*Lissotriton boscai*) changed their colour with respect to the background on which they were placed over 2 weeks, and those that produced dark pigment when placed on black exhibited a higher metabolic rate than those placed on a white background, which reduced their pigment. This implies that changing colour in terms of producing pigments in the integument is accompanied by some physiological costs. However, this does not tell us about the costs of colour change per se, and it is still unknown whether the destruction of pigments during colour change poses a cost, or whether dispersion is more costly than the aggregation of pigments (Horowitz, 1958; Fan et al., 2014), though they both require energy (Iga and Bagnara, 1975; 1976). Thus, measuring metabolic rate in species changing colour morphologically and physiologically would be of help. For example, individuals could be assigned to a midpoint starting substrate with uniform colour and then allowed to change to dark and light backgrounds to demonstrate the costs in both directions.

Indirect evidence

Despite the small number of studies pertaining to the physiological cost of colour change, there is more indirect evidence. Observations of rapidly colour-changing octopuses have found that these animals do not show highly cryptic body patterns at all times, and it has been suggested that maintaining maximum crypsis in synchrony with heterogeneous backgrounds is neurophysiologically expensive (Hanlon et al., 1999). Further, studies on dwarf chameleons uphold this suggestion, as several species (*Bradypodion* spp.), rather than exhibiting and maintaining highly camouflaging patterns, seem to facultatively respond only when predators are present (Stuart-Fox et al., 2006; 2008; Stuart-Fox and Moussalli, 2009).

Many colour-changing animals preferentially select visually similar habitats that match their own coloration. For example, the rockpool goby (*Gobius paganellus*) can change colour rapidly, within 1 min, but is better able to match certain backgrounds than others (Stevens et al., 2014a; Smithers et al., 2018). These gobies were also shown to display a strong preference for backgrounds that

Box 1. Schematic diagram of the chromatophore changes in morphological and physiological colour change, and the potential causes of the costs for each.



Cause

(1) Production and destruction of pigments can be costly to colour-changing animals as they require energy and hormones as a prerequisite for synthesis and decomposition (e.g. α-MSH and MCH hormones).

(2) Utilisation process of dietary-derived pigments such as carotenoids is costly because, after the acquisition of food containing pigments, these pigments may need to be absorbed, transported, metabolically modified and deposited into colour-containing cells.

(3) Trade-offs of allocating pigment resources pose physiological costs when pigments or other compounds involved in the colour change are used in different internal functions at the same time, such as colour change versus immunity.

Cause

(1) Pigment translocation within chromatophores is costly because moving pigments from the cell centre towards the periphery and vice versa requires energy.

(2) Continuous changes of body coloration over a short time scale are energy depleting as a result of the repetitive processes of neural/hormonal signalling events and translocation of pigments within cells.

(3) Maintenance of coloration for a prolonged time during colour change might be costly (e.g. contracting the muscles that are responsible for expanding chromatophores in cephalopods).

Under morphological colour change, there is a decrease or increase in the quantity of the pigments or chromatophores in the integument. Under physiological colour change, pigments within the chromatophore change from aggregated to dispersed states.

are easier to match using colour change (Smithers et al., 2018). Slowly colour-changing taxa, such as fish (Rodgers et al., 2013), amphibians (Polo-Cavia and Gomez-Mestre, 2017) and crustaceans (Green et al., 2019), also show habitat preference that presumably maximises their camouflage. These findings suggest that the strong preference for certain backgrounds diminishes the need for costly colour change. Alternatively, certain colours might be more costly to exhibit than others, or matching the visual properties of the backgrounds of certain colours and textures could be beyond the ability of these animals and, therefore, using behavioural choice is a better option to improve their camouflage.

Some pigments needed for colour change cannot be synthesised *de novo*. Carotenoids, which vary in colour from red to yellow, are among the most common pigments found in plants, but most animals must obtain them through their diet (Bagnara and Hadley, 1973). These pigments can either be deposited in the integument directly or modified metabolically to other derivatives of carotenoids (Maoka, 2019). Important physiological costs

Table 1. Summary of the potential ways that animals can avoid or minimise the physiological costs of morphological and physiological colour change, with examples from different taxa

	How mitigation is achieved	Type of colour change	Example	Time to achieve colour change	Reference
Facultative colour change	Animals express body coloration that may or may not confer some degree of function but is less physiologically costly. Therefore, animals may change colour only when needed, such as when signalling for conspecifics or facing instantaneous threats.	Physiological	Octopus	Milliseconds	Hanlon et al., 1999
			Fish	Minutes	Burmeister et al., 2005
			Chameleons	Seconds	Stuart-Fox et al., 2006
					Stuart-Fox et al., 2008
					Stuart-Fox and Moussalli, 2009
Energy conservation	Animals can minimise the energetic costs resulting from colour change by:				
	(1) Changing to a less costly state in rhythmic patterns when the costly colours are not needed.	Physiological	Crabs	Hours	Powell, 1962b
					Darnell, 2012
					Stevens et al., 2013
			Salamanders		Garcia and Sih, 2003
					Garcia et al., 2004
	(2) Changing colour only in situations in which changing colour is affordable (condition dependent), causing variation in the colour change ability between and within individuals over time. However, the costly colour change may be selected against and lead to variation in the ability to change colour within populations.	Physiological	Shrimps	Hours	Siegenthaler et al., 2018
			Crabs		Stevens et al., 2014b
			Frogs		Kang et al., 2016
		Morphological	Prawns	Weeks	Duarte and Flores, 2016
			Frogs		Wente and Phillips, 2003
	(3) Deploying strategies that functionally replace colour change but are less costly, such as burying or decoration.	Physiological	Cuttlefish	Milliseconds	Allen et al., 2010
			Shrimps	Hours	Siegenthaler et al., 2018
			Fish	Seconds	Tyrie et al., 2015
		Morphological (ontogenetic, not reversible)	Crabs	Weeks	Hultgren and Stachowicz, 2008
					Hultgren and Stachowicz, 2009
Habitat selection	Animals may lessen the physiological cost of colour change by: (1) Avoiding mismatched habitats to prevent the need to change colour. (2) Choosing substrates that grant less costly colour change (i.e. choosing dark backgrounds when changing to/maintenance of dark colours is less costly). Selection of habitats is linked to the speed of colour change where slowly colour-changing animals show higher preference than rapidly colour-changing animals.	Physiological	Fish	Seconds	Smithers et al., 2018
					Tyrie et al., 2015
		Morphological	Prawns	Weeks	Green et al., 2019
			Fish		Rodgers et al., 2013
			Newts		Polo-Cavia and Gomez-Mestre, 2017
Shift mechanism	The above approaches constitute short-term solutions to avoid or minimise the costs of colour change. Animals that use physiological colour change may shift to morphological colour change (pigmentation or depigmentation) if they are under a relatively long-term pressure that causes repetitive colour change for prolonged periods.	Physiological	Crabs	Hours	Powell, 1962b
			Fish		Bergstrom et al., 2012
					Bertolesi and Mcfarlane, 2020
			Frogs and salamanders		Babák, 1913
					Bertolesi et al., 2016

associated with dietary-derived pigments are: (i) their acquisition (searching for and obtaining food), (ii) their utilisation (the internal processes from absorption to deposition in the skin) (Hill, 1996; 2000) and (iii) trade-offs with other processes that require these compounds (e.g. immune function) (Duarte et al., 2017).

Beyond the acquisition of pigment resources, which may require some energy, the utilisation process of these pigments may be more costly. The utilisation of pigments involves multiple stages, including absorption, transport, metabolic modification and deposition into colour-containing cells, each of which requires energy (Hill, 1996; 2000). The type of pigment derived from different foods might vary in costliness in colour-changing taxa relying on diet. For example, red carotenoids might be physiologically more costly to obtain than others (Hill, 1996).

Chameleon prawns (*Hippolyte varians*) display slower colour change when shifting from green to red colour than from red to green (Duarte et al., 2017; Mynott, 2019), especially in larger individuals (Green et al., 2019). This might be due to the utilisation of costly red carotenoids, particularly in larger individuals that require more. Many carotenoids found in aquatic animals are metabolites of other types of carotenoids present in food sources (Maoka, 2019). Lee (1966a,b) successfully isolated the pigments from green, brown and red individuals of two species of colour-changing isopods (*Idotea* spp.) and found evidence for the modification of red carotenoids; the final displayed red pigments in these taxa were derivatives of the original carotenoids found in the algal food source.

These examples together may imply that the red carotenoids involved in colour change are more energetically costly than the other types of pigments or could have pleiotropic effects on other internal functions. Thus, investigating non-changing and changing individuals in systems that rely on diet for colour change would highlight whether there is a pronounced differential physiological cost associated with the colour-change process or whether this is specific to one direction of colour change.

Implications

Depending on the time scale and frequency of colour change, there are several short- and long-term implications. At the individual level, these could be mitigated by physiological and behavioural strategies. At the population level, microevolutionary changes due to selection against costly colour change and in favour of alternative strategies could result in variation in colour change within and between populations and individuals (Table 1).

Facultative colour change

Changing colour is expected to be manifested only when the benefits, such as avoiding instantaneous threatening situations, outweigh the costs, including energetic (Stuart-Fox et al., 2008; Stuart-Fox and Moussalli, 2009) and social costs. Facultative colour change is stimulated by interspecific and intraspecific interaction between animals. As discussed, crypsis in octopuses and dwarf chameleons is not maximised at all times when predators are absent, which might be a less costly strategy compared with maintaining crypsis for long periods. Moreover, some species of dwarf chameleons adjust their coloration according to the perceived threat; for example, they respond to birds and snakes in a different way and invest more in colour change when faced with avian predators, which are thought to have better vision, by showing a better match to their backgrounds (Stuart-Fox et al., 2006; 2008; Stuart-Fox and Moussalli, 2009). Alternatively, although used for crypsis, changing colour facultatively might have evolved primarily to facilitate social interactions (Stuart-Fox and Moussalli, 2008) and can be used to signal to potential mates, or to avoid social costs such as receiving increased aggression from conspecifics when dishonestly signalling dominance, as in chameleons (Ligon and McGraw, 2016) and fish (Burmeister et al., 2005).

However, changing colour facultatively seems to be strategy dependent and might be confined to rapidly colour-changing organisms (i.e. those that change colour within seconds to minutes) faced with an immediate threat or higher social costs (Table 1), and is less relevant to slowly colour-changing animals. Studies on amphibians revealed that predator cues do not show clear effects on colour change (Garcia and Sih, 2003; Polo-Cavia and Gomez-Mestre, 2017). In theory, slow colour change for crypsis might have evolved to tackle temporally predictable fluctuations in microhabitats (Caro et al., 2016).

Energy conservation

One potential way to offset the physiological cost incurred during colour modification is to retract the process to a less costly state when pigments are not needed. This can be achieved via relaxing the muscles of chromatophore organs, as seen in cephalopods (Hanlon et al., 1999), or modifying the expressed colours, as seen in chameleons (Stuart-Fox and Moussalli, 2009), to reduce energy expenditure when predators are absent (Stevens, 2016). Many animals display a rhythmic form of physiological colour change (Abbott, 1973; Thurman, 1988; Darnell, 2012; Duarte et al., 2017). The day–night circadian rhythm in colour change may reflect a physiological cost resulting from the maintenance of the chromatophores in a dispersed or aggregated state (Darnell, 2012), and changing colour at night could be a way to conserve energy (Stevens, 2016; Duarte et al., 2017).

The shore crab (*Carcinus maenas*) can change colour in accordance with brightness of the background within ∼2 h (Powell, 1962a; Stevens et al., 2014b), but it has also been shown to undergo an endogenous rhythmic colour change, becoming darker during the day and lighter during the night (Powell, 1962b). A similar photoperiodic pattern was found in the subtropical fiddler crab (*Uca panacea*) (Darnell, 2012). The function of changing colour in these organisms may be to confer protection against potential harm from UV radiation during the day. For example, observations on salamander larvae (*Ambystoma* sp.) indicated that they are darker during the daytime and lighter at night (Garcia and Sih, 2003). When further examined, larvae were found to darken their body when exposed to UV radiation (Garcia et al., 2004). From these examples, blanching of pigments at night may offset the physiological cost of maintaining the dispersed state of colour cells when colour seemingly is not needed.

Although a darker appearance displayed during the day appears logical because it may protect animals against UV, rhythmic colour change is still perplexing because some animals show the opposite pattern. For instance, the horned ghost crab (*Ocypode ceratophthalmus*) becomes lighter during the day and darker during the night, a rhythmic change that might maximise camouflage over 24 h (Stevens et al., 2013). Regardless of what type of colour appears during the day or night, colour-changing species showing cyclic changes in colour are assumed to utilise this to save energy, but no studies have examined this (Stevens, 2016). However, some studies have argued over this point, with contrasting conclusions regarding whether dispersing or aggregating pigments is more energetically costly (Horowitz, 1958; Fan et al., 2014). Moreover, it remains undetermined whether chromatophores in a dispersed or aggregated state are active or passive (i.e. whether energy is required to maintain the chromatophores in a dispersed or aggregated state; see Parker, 1935).

Habitat choice

When colour change is likely to be physiologically costly, it is hypothesised that habitat choice will mitigate the potential cost by two means: (i) avoiding mismatched habitats to prevent the need to change colour (Rodgers et al., 2013; Polo-Cavia and Gomez-Mestre, 2017) and (ii) choosing habitats that meet the colour-changing ability of animals when forced to alter coloration (Polo-Cavia and Gomez-Mestre, 2017). Broadly, rapidly colour-changing animals are predicted to lack strong habitat preferences, as they can cope with the heterogeneity through fast colour change compared with slowly colour-changing animals (reviewed in Stevens and Ruxton, 2019).

To some extent, this prediction about habitat preference seems to be true when comparing dynamically colour-changing organisms that differ in their colour-changing ability as a consequence of morphological constraints (i.e. the types of patterns and colours they are able to produce). Cephalopods appear to lack a preference for particular habitats (Allen et al., 2010; Hanlon et al., 2011), and this may largely be the result of the repertoire of their patterns that serve different camouflaging strategies, such as background matching, disruptive coloration and masquerade (see Glossary) (Hanlon et al., 2009; Chiao et al., 2011), but the continuous changes are considered to be neurophysiologically costly (Hanlon et al., 1999).

Allen and co-workers (2010) studied the physiological cost of colour change in cuttlefish (*Sepia officinalis*) through sets of behavioural experiments to determine whether different body patterns – uniform, mottle and disruptive – differed in cost. They allowed individuals to change their coloration and choose between backgrounds that provoked the three types of patterns or a mixture of them. The researchers did not find support for the preference of cuttlefish for one type of background or body pattern over the others and concluded that the physiological cost of colour change between the three types of camouflage patterns was negligible. However, the time frame in this study was relatively short, ranging from 8 to 12 min. Thus, it is possible that the maintenance of certain pattern types for longer periods is more costly than the expression itself. In cephalopods, the expansion and retraction of chromatophores is governed by contracting and relaxing radial muscles around them (Bagnara and Hadley, 1973), which is likely to be an energy-consuming mechanism. The cost in these systems may be minimised in the absence of habitat preference through displaying conspicuous or moderately camouflaging patterns and/or through hiding inside dens (e.g. octopus; Hanlon et al., 1999) or beneath sand (e.g. cuttlefish; Allen et al., 2010) to avoid detection.

However, many rapidly colour-changing animals lack the exceptional capabilities of cephalopods. For example, the peacock flounder (*Bothus lunatus*) can change its pattern within 3 s, yet still actively chooses certain backgrounds that match the patterns it is able to produce, such as sand, rubble and dead corals (Tyrie et al., 2015). Moreover, the rockpool goby, *G. paganellus*, can adjust its colours within minutes and yet has limited ability to match some backgrounds (Stevens et al., 2014a; Smithers et al., 2018) and, when given a choice, prefers substrates that are easier to align with through colour change (Smithers et al., 2018). This may imply that some types of colours and patterns in habitats are difficult to replicate and are limited by physiological and morphological constraints (Stuart-Fox and Moussalli, 2011) or that some colours or patterns are more costly to produce than others; therefore, animals may choose substrates that grant less costly colour change or substrates that may allow them to dispense with colour change such as soft sands (Tyrie et al., 2015; Siegenthaler et al., 2018).

Behavioural choice of colour-matching substrates in slowly colour-changing taxa is crucial because it aids the efficacy of colour change given its slower pace. Selecting the appropriate microhabitats requires continuous modification of the choice as the colour changes (Stevens and Ruxton, 2019). For example, the chameleon prawn, *H. varians*, which shifts between green and red coloration within weeks, strongly selects a substrate to match its colour when given the choice (Green et al., 2019). As previously mentioned, changing to the red morph is slower – probably because of the utilisation of the red carotenoids – which would increase the mismatch intervals, potentially leading to higher predation risk.

In other slowly colour-changing animals, there are varying patterns of bias towards which background is chosen (see Stevens and Ruxton, 2019, for further details), which may indicate differences in strategies employed by animals to mitigate the physiological cost within and between species. For example, when guppies, *P. reticulata*, acclimatised to black and white backgrounds, they displayed a preference for black substrates but no clear choice of white (Rodgers et al., 2013). In contrast, larvae of the newt *L. boscai* preferred white over black substrates, with the latter proving more costly to change colour to (Polo-Cavia and Gomez-Mestre, 2017), as discussed earlier. Hence, the choices in these cases may be to mitigate the physiological costs incurred during the colour-changing processes, but in different directions.

However, there is still a need for studies to address how habitat preference would make up for the physiological costs incurred by colour-changing animals, in conjunction with measuring the metabolic rate, as done by Polo-Cavia and Gomez-Mestre (2017).

Individual variation

The physiological cost of maintaining a certain chromatophore state (e.g. fully dispersed pigments) in the integument may have an impact on the evolution of colour change. Variation in the capacity of colour change between individuals occurring in nature may be maintained by differential physiological costs within populations. Therefore, in a prey–predator context, the differences in cost may drive the evolution of other antipredator responses, such as having a fixed appearance with reliance on behavioural avoidance or other strategies. Intrapopulation variation in colour-changing ability has been documented in the Japanese tree frog, *Dryophytes japonicus* (Kang et al., 2016), and the shore crab *C. maenas*, which can change colour within an hour and over several hours, respectively, with some individuals easily changing colour and others showing almost no change (Stevens et al., 2014b).

The co-existence of colour-changing and non-changing morphotypes within populations has been documented in some species, such as Pacific tree frogs (*Pseudacris regilla*) (Wente and Phillips, 2003) and prawns (*Hippolyte obliquimanus*) (Duarte and Flores, 2016), and may possibly occur in other species (e.g. chameleon prawns, *H. varians*; Duarte et al., 2017). Although the literature seems lacking in studies on interpopulation variation in colour change, there is evidence of this from a few studies (e.g. Stuart-Fox et al., 2006; Whiteley et al., 2009; Cadena et al., 2017). Further investigation is warranted on whether and how physiological costs might maintain variation within and between populations. Euryhaline species, such as fish living in both saline and freshwater ecosystems, are excellent models for testing this given the substantial differences in abiotic and biotic components of their habitats.

There are two potential explanations for variation in colour-change ability within populations that would implicate physiological costs. It could be a consequence of opposing selection pressures for higher colour-changing capacity and reduced physiological cost (Kang et al., 2016). Alternatively, in the short-term, variation in colour change might be condition dependent (i.e. depend on energy availability), such that only individuals in optimal condition can undergo colour change (Stevens et al., 2014b). Equally, the presence of these changing and non-changing morphotypes and their frequencies may not necessarily reflect the involvement of a physiological cost of colour change as a selective pressure but, rather, they could be traded against other types of costs (e.g. opportunity cost) and linked to the locomotion patterns (i.e. mobile versus motionless) and other lifestyles such as habitat use (Duarte et al., 2016).

The extent to which these assumptions are met is not yet understood. There is evidence for trade-offs between anti-predator strategies in some closely related species of crabs (Hultgren and Stachowicz, 2008; 2009). These crabs can change colour according to the algal substrate over some weeks and can also camouflage themselves by utilising decoration within hours to days. Yet, there was a negative correlation between the magnitude of colour change and decoration within and between the crab species: species that showed little decoration had a higher capacity for colour change, while those that were more decorated exhibited less capacity for colour change; species that were moderately decorated were intermediate in their colour-change capabilities. Presumably, the driver of intraspecific and interspecific variation in camouflage strategies in these species of crab is the difference in physiological cost between decoration and colour change, in the sense that both strategies may be costly and hence there is a trade-off, with resources being allocated to one or the other (Hultgren and Stachowicz, 2008; 2009).

Fitness cost

Direct or indirect physiological costs resulting from colour change (Sköld et al., 2016) would ultimately affect animal fitness. Currently, there is almost no support for this assumption, though at least one study on coastrange sculpins (*Cottus aleuticus*) found a non-significant trend of decreased fitness with colour change (Bergstrom et al., 2012). In this study, fish were placed in three groups and assigned to three background treatments for 6 months. The control group was on a constant background, the physiological colour-change animals had a 2 day alternated background (either white or black) and the morphological colour-change individuals had a 2 month alternated background. After 6 months, they found that fish that underwent slow (morphological) colour change had higher mortality than those that underwent rapid (physiological) colour change, followed by the control group. These findings may suggest that the production and destruction of chromatophores (morphological) is more costly than maintaining the dispersed and aggregated pigments within colour cells (physiological).

Arguably, physiological colour change should pose a more challenging cost than morphological colour change (Duarte et al., 2017). Morphological and physiological colour-change processes are interlinked. The prolonged exposure to constant backgrounds can lead animals to shift from physiological colour change to the morphological type (Sugimoto, 1993), as the latter is often preceded by the former (Bagnara and Hadley, 1973; Sköld et al., 2016). For example, the shore crab *C. maenas* can physiologically change its colour according to the background within 2 h (Powell, 1962a; Stevens et al., 2014b) and in an endogenous rhythmic way becomes darker during the day and lighter during the night (Powell, 1962b). These crabs, after long-term adaptation to a black background over 35 days, were found to increase their dark coloration during the night compared with those on neutral backgrounds (Powell, 1962b).

It is unknown why both types of colour change operate in the one species. On the one hand, the shift might be linked to the temporal pressures where animals face both predictable and short-term unpredictable changes in habitats. On the other hand, we suggest that the shift could help animals minimise the physiological cost of maintaining colours (physiologically) in a fully dispersed/aggregated state of the chromatophores for a prolonged period. However, it is predicted that this shift comes with a potential concomitant reduction in the animals' mobility and activity patterns and an increase in behavioural preferences for substrates.

Although the shift from physiological to morphological colour change is seemingly observable in some groups of animals (e.g. crabs: Powell, 1962b; amphibians: Babák, 1913; Bertolesi et al., 2016; fish: Bergstrom et al., 2012; Bertolesi and Mcfarlane, 2020), it is poorly known, and the mechanisms linking the two types of colour change (Bertolesi et al., 2016; Bertolesi and Mcfarlane, 2020) and their adaptive values are not well understood.

Conclusion

Although changing colour is clearly a successful strategy in many animals, its costs – specifically the physiological costs – have received limited attention. Previous studies have occasionally assumed that changing colour could be physiologically costly, but only a few studies have attempted to investigate these costs. There is evidence that changing colour does incur physiological costs from the processes of producing, translocating and maintaining pigments within chromatophores. Although both rapid and slow colour change are costly, rapid colour change appears more costly if continuously employed. Moreover, the costs of rapid and slow colour change can be mitigated behaviourally and physiologically via some shared and slightly different mitigation approaches depending on the change strategy (i.e. rapid or slow; Table 1), and can be different at the individual, population and species level as well.

However, the physiological cost of changing colour is still ambiguous across many genera and many substantive questions must be resolved to fully understand the role that such a cost has on colour change. First, are the costs of colour change equal in all directions? For example, is the dispersion of pigments within chromatophores more costly than their aggregation in rapidly colour-changing animals? Is the production more challenging than the destruction of chromatophores in slowly changing taxa? What explains the differentials, if they exist? Second, are the chromatophores in fully expressed states active or passive? Third, does the physiological cost explain interspecific and intraspecific variation in colour change? Fourth, what type of colour change is more physiologically costly? Does the physiological cost differ mechanistically between reversible and irreversible colour change and does the cost differ phylogenetically among related colour-changing taxa? Finally, how does morphological colour change interact with physiological change in reducing the physiological cost of colour change, and how would it affect the efficiency of physiological colour change? At what point is the shift to morphological colour change triggered and what is the adaptive benefit of it?

Competing interests

The authors declare no competing or financial interests.

Funding

This work was supported by Albaha University, which granted a PhD scholarship to Ateah Alfakih (2019/40245343).

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