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Review



Cite this article: Hughes A, Liggins E, Stevens M. 2019 Imperfect camouflage: how to hide in a variable world? *Proc. R. Soc. B* **286**: 20190646.
<http://dx.doi.org/10.1098/rspb.2019.0646>

Received: 2 April 2019

Accepted: 25 April 2019

Subject Category:

Evolution

Subject Areas:

behaviour, cognition, evolution

Keywords:

camouflage, vision, anti-predator coloration, disruption

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Imperfect camouflage: how to hide in a variable world?

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Camouflage is an important anti-predator strategy for many animals and is traditionally thought of as being tightly linked to a specific visual background. While much work focuses on optimizing camouflage against one background, this may not be relevant for many species and contexts, as animals may encounter many different habitats throughout their lives due to temporal and spatial variation in their environment. How should camouflage be optimized when an animal or object is seen against multiple visual backgrounds? Various solutions may exist, including colour change to match new environments or use of behaviour to maintain crypsis by choosing appropriate substrates. Here, we focus on a selection of approaches under a third alternative strategy: animals may adopt (over evolution) camouflage appearances that represent an optimal solution against multiple visual scenes. One approach may include a generalist or compromise strategy, where coloration matches several backgrounds to some extent, but none closely. A range of other camouflage types, including disruptive camouflage, may also provide protection in multiple environments. Despite detailed theoretical work determining the plausibility of compromise camouflage and elucidating the conditions under which it might evolve, there is currently mixed experimental evidence supporting its value and little evidence of it in natural systems. In addition, there remain many questions including how camouflage strategies should be defined and optimized, and how they might interact with other types of crypsis and defensive markings. Overall, we provide a critical overview of our current knowledge about how camouflage can enable matching to multiple backgrounds, discuss important challenges of working on this question and make recommendations for future research.

1. Introduction

Animal coloration has a wide range of functions, from signalling and communication through to strategies such as camouflage [1]. The efficacy of these signals is strongly linked to the environment, including promoting conspicuousness for communication in different habitats (e.g. [2]) and concealment (e.g. [3]). For the latter, background matching is perhaps the most archetypal form of camouflage, and describes cases where an animal's appearance matches the colour, lightness and pattern of the background on which it lives [4]. In recent years, much work has focused on rigorously analysing how animal coloration may provide background matching camouflage in natural environments from the point of view of their predators (e.g. [3,5–7]). However, animals live in a diverse and changing world, and thus background matching camouflage strategies may be less effective in providing concealment if the visual background changes in space and time [8]. While some species may encounter only relatively similar visual habitats throughout their lives, many others will be found against multiple different backgrounds, both because of their own movement patterns and also due to changes in the environment over their lifetime (e.g. [9–11]).

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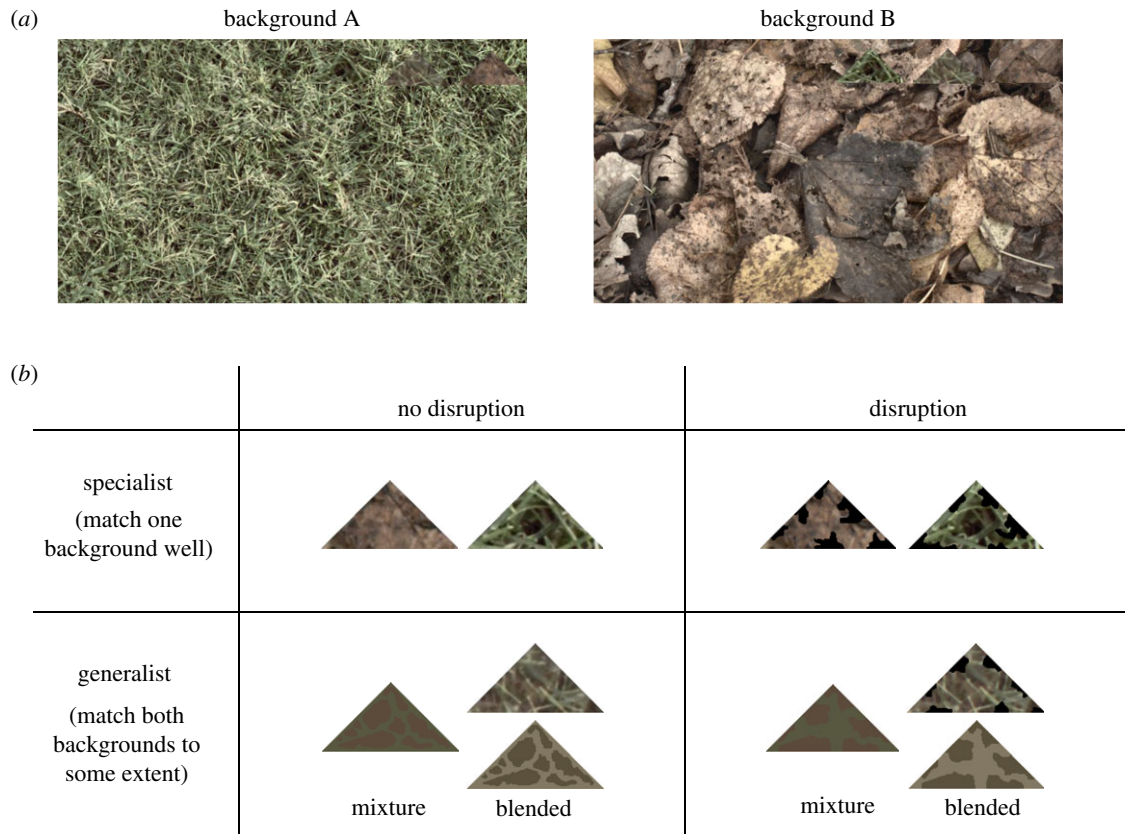


Figure 1. (a) Example imperfect camouflage strategies for two different backgrounds (background A, grass; background B, leaves) with example ‘moths’ in the top right-hand side of both backgrounds. (b) Coloration can be specialist (top row) or generalist (bottom row). Coloration can also be background matching (i.e. without disruption; left-hand side) or disruptive (i.e. with markings that break up the outline of the target; right-hand side). Finally, there are multiple ways to produce generalist camouflage, such as by using ‘blending’ methods where features are intermediate between two backgrounds (examples show two possible methods for generating blended targets: a target produced by Fourier blending, and a target where the colours are intermediate between the common background colours) or by using ‘mixture’ methods where discrete features from the two backgrounds are used (example shows a target where the colours are selected to be common background colours). (Online version in colour.)

There are several ways that camouflaging animals may reduce their visual predation risk while living in a heterogeneous and changing world. Some have the ability to change coloration to match different habitats; this is increasingly studied as a prevalent strategy found across many taxa [12]. However, in many species, the time scale of appearance change is too slow to cope with changes in the visual background caused by individual movement or environmental changes occurring over minutes to days [12,13]. Many animals can also rely on their behaviour, choosing visual habitats and substrates that most closely match their appearance [14]. However, there is another option: animals can adopt a form of camouflage that is not perfectly background matched to any one habitat, but instead offers a degree of resemblance on multiple backgrounds, and/or use types of camouflage that work somewhat independently of background matching. There is a growing collection of studies exploring these ideas, yet there remains a great deal unknown about the role of imperfect camouflage in determining animal coloration, and as yet no synthesis of these important concepts.

In this review, we explore what is currently known about imperfect camouflage, considering several key issues:

1. When do theoretical models predict imperfect camouflage should evolve?
2. What empirical evidence do we have to support these predictions?

3. How can we study imperfect camouflage in the wild?
4. What should an optimal compromise phenotype look like?
5. Can other types of camouflage provide protection in multiple habitats?
6. What are the broader implications of studying imperfect camouflage for our understanding of animal coloration more generally?

Throughout, we also provide suggestions for future research.

2. Theoretical modelling

The most widely considered type of imperfect camouflage is ‘compromise’ camouflage, where an individual partially matches, and therefore has some protection on, several backgrounds, but matches none perfectly. This contrasts with a specialist camouflage strategy, where the camouflage is fine-tuned for one background type [4] (see figure 1 for examples).

There is strong theoretical evidence supporting the notion of compromise camouflage under certain conditions. Merilaita and colleagues carried out an initial modelling study defining the conditions under which it might be expected to evolve [15]. Their model considered how background structure and prey habitat choice affected the optimal camouflage strategy for a prey animal living in a habitat consisting of two different microhabitats. One important conclusion was that the similarity between microhabitats is an important

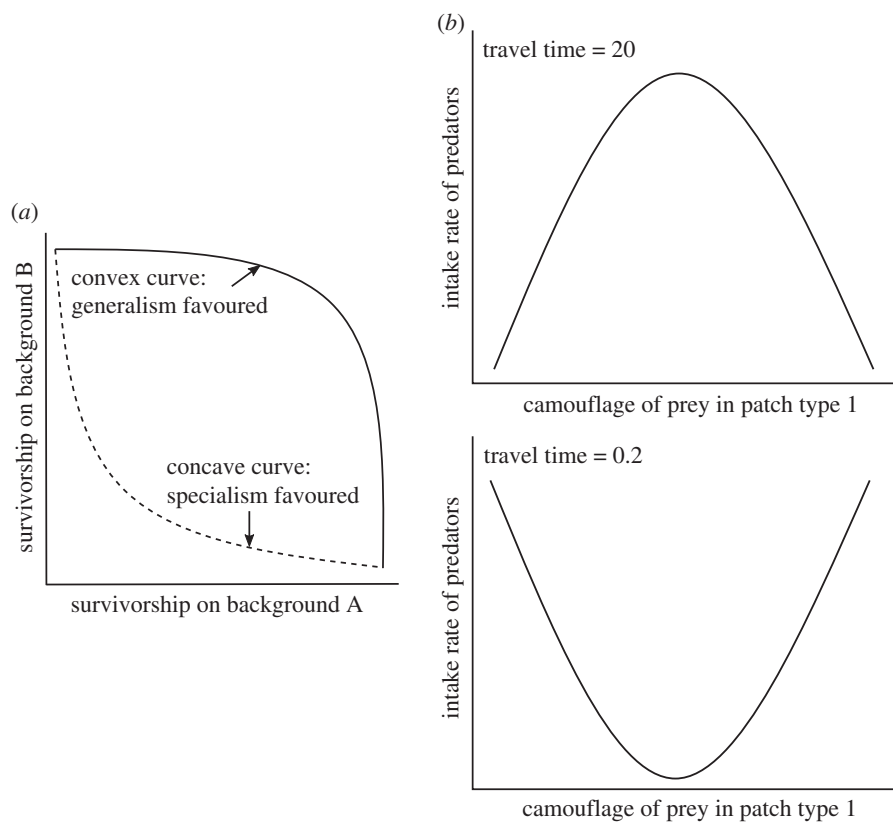


Figure 2. (a) Adapted from [16], showing how differential survivorship on two different backgrounds (*a,b*) can lead to the evolution of different camouflage strategies. (b) Adapted from [17], showing how different predator travel times can affect the optimal prey coloration strategy. If travel time between patches is long, specialization should be favoured (top); if travel time between patches is short, a generalist strategy instead minimizes the intake rate of predators (bottom).

factor. If microhabitats are similar, there is an optimum 'intermediate' that provides good camouflage on both backgrounds, maximizing fitness when prey are randomly choosing between microhabitats. However, if microhabitats are very different, prey should specialize on just one background. Yet the best crypsis strategy also depends on a range of other factors, including the microhabitat proportions, the habitat use pattern of the animal and the risk of encountering a predator in each microhabitat. For example, if predators are only found in one microhabitat, prey animals should specialize in this microhabitat, even if a generalist strategy could be possible. Figure 2*a* outlines how differential survivorship on two backgrounds should lead to the adoption of different camouflage strategies, in accordance with their results.

Later work has addressed some of the simplifications of this key model, which focused predominantly on prey behaviour. Houston and colleagues [17] considered optimal predator behaviour in more detail, asking how this would change the optimal prey strategy. They showed that the travel time of predators between different habitat patches can have a strong effect on prey camouflage strategy, with increased travel time favouring specialization and decreased travel time favouring compromise (figure 2*b*). If travel time is short, predators will encounter many microhabitats and thus are unlikely to specialize on any one prey type, meaning that there is an advantage for prey to have some degree of camouflage on a range of backgrounds. On the other hand, if the travel times between patches are long, predators are more likely to be specialists, and prey should therefore optimize their camouflage against one habitat. Similarly, low

prey dispersal rates are thought to favour local adaptation and specialization, while higher dispersal rates promote a generalist strategy. This result was found using an asexual, clonal model population, suggesting that it does not simply reflect an increased mixing of gene pools [18].

One of the benefits of theoretical work is that it generates testable hypotheses for empirical investigation. Further theoretical research into imperfect camouflage would therefore be valuable. For example, models should be extended to incorporate more than two types of microhabitat [19]. In this case, it might be predicted that selection for generalist strategies would be stronger, particularly if all microhabitats are visited regularly. More complex selection scenarios can also be envisaged, such as situations where the fitness of the background is also affected by the predator–prey interaction. This may be the case when flowers act as a background for camouflaged ambush predators, but also need to be pollinated by the prey species [20]. There has also been relatively little consideration of the possible opportunity costs of specialization, such as the limited range of resources available and the locomotion costs of finding a well-matched background. Considering some of these broader selection pressures would be valuable in understanding the evolution of generalist strategies.

Finally, since the original studies were conducted, there has been an increased emphasis on recognizing that different animals may have highly different visual systems and that a prey item that is conspicuous to one predator may in fact be well camouflaged to another [5,21,22]. Considering how multiple predators with different colour perception and visual acuity can affect the outcomes in these types of evolutionary

games is an important next step. For example, predators with inferior acuity may see two backgrounds as being more similar, making generalism a more effective strategy. Similarly, prey with dichromatic predators are likely to have a wider range of possible generalist camouflage than those with trichromatic or tetrachromatic predators, meaning that generalism might be more common in species with mammalian rather than avian predators.

3. Empirical tests of theoretical predictions

The theoretical prediction that the evolution of compromise camouflage should depend upon microhabitat similarity has since been tested experimentally. An initial laboratory experiment used avian predators and two backgrounds that differed in element size: the prey were either specialist on one background or had an intermediate, compromise element size [23]. The compromise prey had relatively high levels of survival on both backgrounds, suggesting that a generalist strategy was optimal. Similar results have also been found in a recent experiment using humans as model predators [24]. These results therefore fit well with the theoretical predictions, assuming that backgrounds that differ in element size to a limited degree can be considered relatively similar microhabitats.

Evidence has also been found for the superiority of specialist forms in some circumstances. One experiment used human predators, pseudo-uniform backgrounds that were either light green or dark green in colour, and prey with various degrees of colour matching to these backgrounds [16]. Here, the intermediate prey survived badly, suggesting that specialist forms would be favoured in these microhabitats. It is also possible to find cases where the specialist and generalist strategies have similar survival rates. This has been shown in a number of experiments with different sized background elements, where the size of the difference was such that specialists and generalists both performed relatively well [16,24].

The switch from generalist to specialist strategies has been more directly tested in an experiment using blue jays that were trained to hunt for artificial moths on computer screens to test the forms that evolved on three different backgrounds [25]. They found that specialist forms evolved on the disjunct and mottled backgrounds (which had relatively large patches), while the speckled backgrounds (with small patches) produced generalists. This also supports the prediction that highly similar microhabitats should favour the evolution of compromise prey, while more highly different microhabitats created by discrete patches favour specialism.

Despite these studies, it remains challenging to predict whether generalist or specialist strategies will be favoured in a given experiment. One issue is how to define similarity: to date, experiments have used 'bigger' or 'smaller' differences in a particular stimulus dimension without reference to the true perceptual size of these differences in the relevant viewer. Future research should consider stimulus differences with regard to just noticeable differences (JNDs) [21], as the amount a stimulus needs to change in order for a difference to be detected may vary depending upon the property considered. For example, animals may be more sensitive to colour differences than size differences, and thus specialists

may be more favoured in situations where the backgrounds differ in colour.

The importance of predator learning in understanding prey camouflage strategies is beginning to be recognized [26,27], and the efficacy of generalist strategies may also depend on predator learning. In a study using avian visual predators [28], search times were found to be longer for specialist prey compared with compromise prey on the first three prey presentations. However, for later presentations, the compromise and specialist prey were equally difficult. In a natural situation, this could suggest that generalist strategies will be more likely when predators repeatedly encounter the same prey types.

Overall, it is plausible that both compromise and specialist camouflage strategies can be good solutions, depending upon background properties, as predicted by theoretical modelling. There are still theoretical predictions that have not been directly tested (for example, how prey dispersal rate or predator travel time affect the balance between generalist and specialist types), and these would be interesting questions for future research. More fundamentally, the experimental results to date have mostly been obtained using artificial prey stimuli, often comprising unnatural geometric shapes and only a limited range of predator systems, frequently in a non-naturalistic set-up. In addition, the microhabitats used are often limited in number and may not resemble real-world habitats. It is also not necessarily clear that detection time is an adequate proxy for survivorship, and there may be a range of other constraints on coloration that are not accounted for by these experiments, such as the necessity of coloration to attract mates or for thermoregulation. For these reasons, it is crucial to address whether examples of generalist and specialist camouflage can be found in natural settings and more complex natural scenes.

4. Evidence in nature?

While several studies have tested the predictions of compromise camouflage in laboratory settings, there has so far been a little exploration of this question in wild animal populations. At least observationally, there are clearly many examples of excellent and highly specialized camouflage phenotypes [3,5,7,15]. Similarly, there are cases that have been suggested as examples of generalist camouflage, including the desert spiny lizard [9], some Aegean wall lizard morphs [29], shore crabs [30,31], and some moth [10] and grasshopper [32] species. These putative generalist species often seem to have relatively drab coloration, which is often greenish-brownish to human observers and appears as if it would broadly match more than one background (figure 3). However, these examples are predominantly suggestive rather than conclusive. In some cases, the measurement of background matching is limited, sometimes being based on little more than unquantified human perception. Similarly, even if the coloration has been quantified, it is rare to find examples where this has been directly linked to predation risk by behavioural experimentation. In general, a key issue is that there have been few dedicated attempts to test for compromise camouflage in wild populations.

Why has this important question been neglected? There are several factors that make generalist camouflage difficult

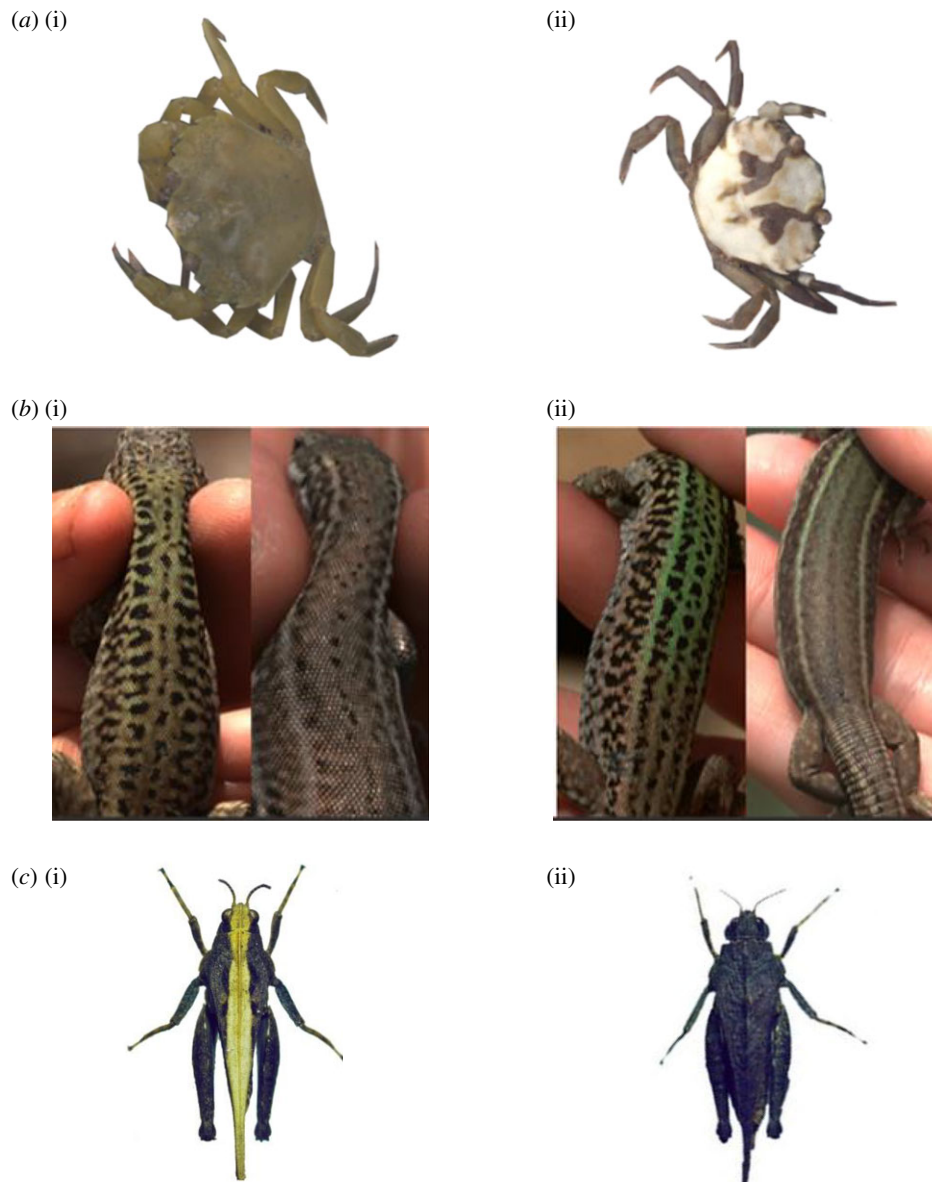


Figure 3. Examples of possible generalist and specialist camouflage found in nature. (a) Examples of shore crabs [31]. (i) An individual with putative generalist camouflage, from a mud flat environment. (ii) A younger and potentially more specialist individual, from a rock habitat. (b) Examples of Aegean wall lizards [29]. (i) Male and female lizards from the island of Santorini, where the population may show generalist camouflage, possibly due to a high frequency of volcanic eruptions, leading to a heterogeneous environment that may prevent more specialist camouflage. (ii) Male and female lizards from Folegandros, where the camouflage is considered more specialist. (c) Examples of pygmy grasshoppers [33]. (i) Striped morph, considered a more generalist strategy. (ii) Black morph, which seems to be more specialist (becoming better camouflaged with an increase in the percentage of the burnt substrate in the environment). All images reproduced with permission. (Online version in colour.)

to study in natural settings. One issue is simply experimental logistics. For many species, we still lack fine-grained information about the habitats they use and how often they move between different backgrounds. On a conceptual level, it is also difficult to define separate microhabitats, especially as the appropriate scale will be likely to depend upon the visual acuity and colour vision of the predator in question. An even trickier question is determining whether camouflage can really be described as generalist, or whether it is in fact simply a poor match, perhaps restricted by developmental constraints or competing evolutionary pressures. In some instances, a lack of a close match may simply reflect evolutionary lag. Behavioural studies are therefore crucial for determining if a camouflage pattern truly is equivalently effective at preventing capture on multiple backgrounds.

The ideal situation would be to study a polymorphic species that is easy to track where the patterning and coloration of both backgrounds and animals can be easily measured and where it is possible to record predation events. A generalist camouflage could then be defined as any morph that has similar camouflage across a range of backgrounds, either measured via image analysis techniques or by predation events, or ideally both. However, in the absence of this perfect option, one useful approach may be to combine studies in the wild with more controlled laboratory experiments. Work on pygmy grasshoppers has shown that different morphs are captured at different rates in the wild, and there is a strong relationship between these capture rates and detection times of humans searching for these targets on these backgrounds on a computer screen [34]. This validation of the laboratory data suggests it is possible to

extend these experiments to ask a wider range of questions that might be challenging in a natural situation. For example, in this study, the participants additionally viewed the morphs on images of other common habitats of this species, and the striped morph was found to be relatively difficult to capture on multiple backgrounds, suggesting that this could be a generalist strategy. We suggest future investigators try to use more realistic stimuli when designing laboratory experiments (such as calibrated images of natural backgrounds at an appropriate spatial scale) to help generalizability to natural systems.

Another approach is to test species that can change their colour to see how they respond to visually heterogeneous habitats. This has the advantage that it can be done in controlled laboratory settings but can also use realistic background types to investigate natural coloration strategies. Peppered moth larvae change their colour in response to the twig that they are resting on, but in a heterogeneous environment with multiple twig colours, they seem to adopt a specialist strategy rather than developing an intermediate colour [35]. By contrast, shore crabs adjust their appearance over moults and can change from pale and dark forms to converge on a more dark green/brown generalist appearance, regardless of the background they are placed upon, and these forms are highly camouflaged to human observers across a range of habitats [31]. Similarly, Japanese tree frogs can adopt intermediate forms when their background consists of two achromatic hues [36].

Finally, it would be valuable to attempt to disentangle generalist strategies from evolutionary lag. This could be tested in a species with two known resting sites, allowing the computation of an optimal compromise camouflage based on those backgrounds. The real appearance of the animal can then be compared with these different options. If it is a specialist, it should match only one of the backgrounds, whereas if it is a generalist, it should match the theoretical compromise. However, if the coloration reflects evolutionary lag, it should match none of the options well. These image analysis findings could then be corroborated with survival experiments testing the performance of the real prey phenotype against the other possibilities.

5. How should compromise camouflage be defined and optimized?

Another challenge of studying compromise camouflage is determining what an optimal compromise pattern should actually look like. Endler proposed that the optimal pattern for any form of background-matching camouflage should be a random sample of the background at the time and location of the highest predation risk [37], but this definition has recently been challenged. In a study using avian predators, background-sampled targets with different levels of subjective difficulty (easy and hard) were shown to have significant differences in capture time [38]. Thus, in a complex environment, some random samples of the background are likely to provide better crypsis than others. A subsequent study used more naturalistic stimuli and backgrounds and showed that it is better to match the most common colours and patterns of a background rather than a random sample [39]. However, both these studies considered only one background or a few highly similar background images. It

remains to be seen whether these principles extrapolate when animals must compromise between larger numbers of more different background types.

A further issue is that there are different interpretations of what is meant by compromise patterning, as evidenced by the fact that different experiments have adopted different ways of creating such patterns; in some cases, a sample of features is taken from each background, creating a 'mixture' stimulus [23,28,38], whereas others have used features that may not be found in either background, but are instead perceptually intermediate (blended) between the two backgrounds [16,24] (figure 1). As outlined above, both strategies can be successful for generating good compromise camouflage, but it is difficult to compare them meaningfully given the small number of studies to date. It remains possible that there are different optimal strategies depending on the type of compromise adopted, and therefore future work should test whether there are differences between putative compromise camouflage strategies. Now we are beginning to be able to quantify animal coloration and patterning effectively [40], one elegant approach would be to 'reverse engineer' these processes, measuring background parameters and using them to generate closely matching targets. This would also allow manipulation of each feature dimension independently, giving the ability to ask questions about which aspects of the target are most important for effective compromise camouflage. We can also use image analysis techniques to identify which forms of compromise camouflage we actually see in real animals.

The most appropriate forms of imperfect camouflage may vary in more realistic situations, such as when the complexity of the habitats varies. Predators in laboratory experiments find it harder to detect prey items against complex backgrounds compared to simpler (but still non-uniform) ones [41–44]. Artificial evolution experiments have also suggested that prey can evolve more effective crypsis against more complex backgrounds [45]. Recent work has shown that increased background complexity reflects an increase in the density or variance of the features of the background that are shared with the target [46]. We are also starting to be able to quantify complexity across the UV visible spectrum and therefore more accurately represent non-human visual systems [47]. These developments open up exciting new avenues for compromise camouflage research, which to date has only used similar backgrounds [38,39], therefore probably testing only one level of complexity. Future work should consider whether there are different compromise optima when animals are found among backgrounds with a varying range of complexities, as determined using appropriate image metrics and consideration of the viewer's visual system.

There has also been little work so far on how predator and prey constraints may influence optimal generalist camouflage. Predation experiments both in the laboratory and in the field have shown that increased pattern regularity [42] and symmetry [48,49] can make prey easier to find, and given that real animals often display highly symmetric and regular patterning due to developmental constraints, it would be instructive to consider how to optimize generalist patterning given this limitation.

One final challenge of determining the optimal camouflage strategy for a given set of conditions is that it can involve exhaustively testing many stimuli, which can be difficult even when using human participants. Artificial

evolution experiments are one way to focus on exploring only the most relevant areas of evolutionary space [25,45]. In addition, new methods are being developed that use generative adversarial networks to allow the evolution of camouflage to be automated, allowing the rapid testing of large numbers of potential prey patterns [50].

6. Alternative strategies for camouflage in multiple environments

Compromise camouflage is one possible method for generating imperfect camouflage, but there may be other strategies that allow some degree of concealment in multiple habitats. For example, animals may exploit the visual processing mechanisms of predators using so-called disruptive markings that create false boundaries, therefore making it difficult to identify edges and recognize the true shape of an object [4,51] (figure 1*b*, right-hand side). Conceptually, this strategy could act independently of background matching.

In support of this hypothesis, there is some evidence that disruptive markings may be effective even when targets do not match their background colour or luminance [52,53]. However, other research suggests that at least partially matching the average colour and luminance contrasts found in the background is important [54,55]. This suggests that disruptive coloration may have to work in tandem with at least some degree of background matching coloration, perhaps indicating it may not be a particularly effective imperfect strategy on its own. To resolve this debate, it may be productive to approach the question differently by testing how adding different types of disruptive markings alters the performance of a target displaying an optimal compromise pattern.

Another way to afford protection in multiple habitats is to reduce reliance on minimizing detectability. Masquerade is an anti-predator defence where prey resemble an uninteresting object and is thought to interfere with predator recognition mechanisms [4]. Some recent work has suggested that masquerade is most effective when prey (twig-mimicking caterpillars) are viewed in isolation from their models (twigs) [56], arguing that this strategy does not derive its effectiveness from background matching. However, the evidence base is currently limited, and it would be interesting to determine if masquerade can be considered a generalist strategy across a wider range of species.

Distractive camouflage offers another possible strategy for crypsis in multiple environments. Here, conspicuous markings on the prey animal act to direct the attention of the predator away from cues that would enable recognition, such as the body outline [4]. However, while there is some evidence from laboratory studies suggesting that high contrast markings may provide effective camouflage across a range of backgrounds [57], this has been debated, given that field studies with birds and computer experiments with humans have demonstrated that distractive markings are costly and reduce detection or capture times, and even promote predator learning [27,58,59]. A study of comma butterflies (*Polygonia c-album*) also reported support for a distractive effect of white comma markings [60], but in the laboratory experiments conducted, the butterflies were not actually camouflaged and the results are best explained by

avoidance of already-visible prey [27]. There was also no benefit of markings in field trials [60]. On balance, there is currently limited evidence that distractive markings can act as a form of imperfect camouflage. However, more work is needed with potentially distractive markings on other species and under more naturalistic conditions; it may be the case that they could work against more complex natural backgrounds and in certain field lighting conditions. Experiments presenting real prey with and without markings against known resting sites, alongside video recordings of predator behaviour, would be a good first step in addressing this.

A final putative route to imperfect camouflage is self-shadow concealment, where directional light is cancelled out by countershading, potentially leading to better concealment [4]. Optimal countershading appears to be strongly illumination dependent [61] and having suboptimal countershading seems to be almost as bad as having no countershading at all, at least in a study with highly different illumination conditions [62]. Future studies with a more gradual range of illuminations may help to determine if countershading has more general benefits, or if it is truly a strategy that is only effective in a specific light environment.

7. Broader implications

While the study of imperfect camouflage is valuable in its own right, it also has a number of important implications for other areas of biology. First, there is evidence that imperfect camouflage may be an important driver for the evolution of aposematic coloration. In an evolutionary simulation model where the prey population could evolve distastefulness as well as its coloration, aposematic coloration evolved more often in a situation where the habitat was visually variable, consisting of two different microhabitats, than when the habitat always remained similar [63]. Future work could investigate whether phylogenetic evidence supports this hypothesis and explore in real-world set-ups the extent to which imperfect camouflage can combine with aposematism and other signalling strategies (similarly to recent work on distance-dependent camouflage and aposematism [64]).

Studying how camouflage evolves in heterogeneous habitats also has important consequences for the understanding of the development and maintenance of polymorphism. Modelling work has shown that in addition to single habitat specialist and intermediate generalist strategies, it is possible for multiple specialist strategies to evolve (polymorphic crypsis). This is thought to be a stable evolutionary solution when prey have intermediate dispersal rates and a moderate amount of camouflage in multiple habitats, and predators have an intermediate attack rate [18]. Understanding polymorphic crypsis is particularly critical as it may lead to speciation, as specialization in conjunction with active background choice can create reproductive isolation. Work on polymorphism has also generated a long tradition of studying the cognitive strategies predators may use to forage for prey items, such as search image formation [65]. These ideas may be of importance in further understanding the evolution of imperfect camouflage; for example, future research could consider whether there are differences in predator search image formation ability for generalist and specialist strategies [27,28].

The study of imperfect camouflage also has parallels with imperfect mimicry. In particular, it has been proposed that mimicry may sometimes be imperfect because the mimic adopts a generalist strategy, bearing a degree of resemblance to multiple models [66]. While this hypothesis has received support from theoretical models [67], empirical evidence is still relatively scarce. Horsfield's bronze cuckoos (*Chrysococcyx basalis*) may lay eggs that bear some resemblance to all of its hosts, rather than specializing to host specific races [68]; however, there is also evidence that in hoverflies, imperfect mimicry may be better explained by relaxed selection for small species that are less profitable for a predator [69]. Again, we think there are many ways for these two research fields to productively interact: for example, a better understanding of how to define generalist strategies will benefit both. Similarly, studies on imperfect mimicry highlight the importance of considering alternative hypotheses for the persistence of generalist forms [69] and the role that predator cognition may play [70].

Understanding how animals respond to living in different habitats is also crucial for conservation. It is possible to imagine a 'knife-edge' fitness landscape where a very small change in the environment can change the optimal strategy from specializing in one background to specializing in another. However, it may be difficult for an animal to evolve to its new optimum, particularly if this might involve lower fitness intermediates [19]. Understanding which animals are likely to be vulnerable to these pressures may be extremely important as environments are altered as a result of climate change and other human activity. There are also occasions where animals may need to be translocated to a new habitat (e.g. due to habitat destruction), and it is important to assess the suitability of their new habitats for providing camouflage. One study assessed the effect of translocation on shore skinks and showed that the variability in patterning drastically reduced after the animals had been moved to their new habitat, and the morph that remained was the best colour match to the release site [71]. This translocation therefore potentially reduced genetic diversity, which may have important consequences for conservation, particularly in cases where populations are already small. Similarly, work on snowshoe hares has identified that mismatch with snow cover affects mortality differently in different habitats [72]. These findings suggest that improving our understanding of the situations in which imperfect

camouflage can offer protection may help conservationists decide how best to protect threatened species.

In this review, we have focused on the role of coloration in crypsis, but many animals also have conspicuous colour signals that are thought to be involved in sexual and social communication. Similarly to camouflage, these conspicuous colour signals can also be considered within a generalist or specialist adaptation framework. For example, in some lineages of African dwarf chameleons, male display coloration is specialized to its specific habitat in order to maximize visibility, while female display coloration may be more generalist, offering maximal detectability across all habitat types [2]. This highlights that studying generalist strategies could potentially help us to understand the whole range of animal coloration found in nature.

8. Conclusion

We propose that the future study of imperfect camouflage requires an interdisciplinary, mixed methods approach. Evolutionary games will help us understand more fully the situations under which imperfect camouflage might be expected to evolve. Laboratory studies using carefully controlled experiments may be particularly useful for testing predictions of theoretical models, or for validating observational findings in the field. Ideally, future research should also try to test for the presence of imperfect camouflage in natural settings or at least using more naturalistic backgrounds, despite the many challenges of this approach.

We further suggest that there are many questions about imperfect camouflage that deserve more attention. Predator cognition has been little studied in the context of generalist or specialist strategies. Similarly, defining and testing optimal compromise forms in different contexts has rarely been considered. Finally, the study of compromise camouflage may have important links to other camouflage strategies and aspects of visual ecology that are only just beginning to be explored.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

Funding. The work was supported by a BBSRC grant (BB/P018319/1) to M.S. and A.H. This grant was part-funded by QinetiQ, a UK-based company primarily working in the defence, security and aerospace markets.

References

- Cuthill IC *et al.* 2017 The biology of color. *Science* **357**, 221. (doi:10.1126/science.aan0221)
- Stuart-Fox D, Moussalli A, Whiting MJ. 2007 Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *Am. Nat.* **170**, 916–930. (doi:10.1086/522835)
- Walton OC, Stevens M. 2018 Avian vision models and field experiments determine the survival value of peppered moth camouflage. *Commun. Biol.* **1**, 118. (doi:10.1038/s42003-018-0126-3)
- 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)
- Troszianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode CN. 2016 Camouflage predicts survival in ground-nesting birds. *Sci. Rep.* **6**, 19966. (doi:10.1038/srep19966)
- Robledo-Ospina LE, Escobar-Sarria F, Troszianko J, Rao D. 2017 Two ways to hide: predator and prey perspectives of disruptive coloration and background matching in jumping spiders. *Biol. J. Linn. Soc.* **122**, 752–764. (doi:10.1093/biolinnean/blx108)
- Wilson-Aggarwal JK, Troszianko JT, Stevens M, Spottiswoode CN. 2016 Escape distance in ground-nesting birds differs with individual level of camouflage. *Am. Nat.* **188**, 231–239. (doi:10.1086/687254)
- Caro T, Sherratt TN, Stevens M. 2016 The ecology of multiple colour defences. *Evol. Ecol.* **30**, 797–809. (doi:10.1007/s10682-016-9854-3)
- Norris KS, Lowe CH. 1964 An analysis of background color-matching in amphibians and reptiles. *Ecology* **45**, 565–580. (doi:10.2307/1936109)
- Endler JA. 1984 Progressive background in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22**, 187–231. (doi:10.1111/j.1095-8312.1984.tb01677.x)

11. Harris AC, Weatherall IL. 1991 Geographic variation for colour in the sandburrowing beetle *Chaerodes trachyscelides* White (Coleoptera: Tenebrionidae) on New Zealand beaches analysed using CIELAB L* values. *Biol. J. Linn. Soc.* **44**, 93–104. (doi:10.1111/j.1095-8312.1991.tb00609.x)
12. Duarte RC, Flores AAV, Stevens M. 2017 Camouflage through colour change: mechanisms, adaptive value and ecological significance. *Phil. Trans. R. Soc. B* **372**, 20160342. (doi:10.1098/rstb.2016.0342)
13. Stevens M. 2016 Color change, phenotypic plasticity, and camouflage. *Front. Ecol. Evol.* **4**, 51. (doi:10.3389/fevo.2016.00051)
14. Stevens M, Ruxton GD. 2018 The key role of behaviour in animal camouflage. *Biol. Rev. Camb. Philos. Soc.* **94**, 116–134. (doi:10.1111/brv.12438)
15. Merilaita S, Tuomi J, Jormalainen V. 1999 Optimization of cryptic coloration in heterogeneous habitats. *Biol. J. Linn. Soc.* **67**, 151–161. (doi:10.1111/j.1095-8312.1999.tb01858.x)
16. Sherratt TN, Pollitt D, Wilkinson DM. 2007 The evolution of crypsis in replicating populations of web-based prey. *Oikos* **116**, 449–460. (doi:10.1111/j.0030-1299.2007.15521.x)
17. Houston AI, Stevens M, Cuthill IC. 2007 Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behav. Ecol.* **18**, 769–775. (doi:10.1093/beheco/arm039)
18. Nilsson J, Ripa J. 2010 The origin of polymorphic crypsis in a heterogeneous environment. *Evolution* **64**, 1386–1394. (doi:10.1111/j.1558-5646.2009.00918.x)
19. Ruxton GD, Sherratt TN, Speed MP. 2004 *Background matching*. Oxford, UK: Oxford University Press.
20. Abbott KR. 2010 Background evolution in camouflage systems: a predator–prey/pollinator–flower game. *J. Theor. Biol.* **262**, 662–678. (doi:10.1016/j.jtbi.2009.09.001)
21. Kelber A, Vorobyev M, Osorio D. 2003 Animal colour vision—behavioural tests and physiological concepts. *Biol. Rev. Camb. Philos. Soc.* **78**, 81–118. (doi:10.1017/S1464793102005985)
22. Troscianko J, Wilson-Aggarwal J, Griffiths D, Spottiswoode CN, Stevens M. 2017 Relative advantages of dichromatic and trichromatic color vision in camouflage breaking. *Behav. Ecol.* **28**, 556–564. (doi:10.1093/beheco/arw185)
23. Merilaita S, Lyytinen A, Mappes J. 2001 Selection for cryptic coloration in a visually heterogeneous habitat. *Proc. Biol. Sci.* **268**, 1925–1929. (doi:10.1098/rspb.2001.1747)
24. Toh KB, Todd P. 2017 Camouflage that is spot on! Optimization of spot size in prey-background matching. *Evol. Ecol.* **31**, 447–461. (doi:10.1007/s10682-017-9886-3)
25. Bond AB, Kamil AC. 2006 Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *PNAS* **103**, 3214–3219. (doi:10.1073/pnas.0509963103)
26. Troscianko J, Lown AE, Hughes AE, Stevens M. 2013 Defeating crypsis: detection and learning of camouflage strategies. *PLoS ONE* **8**, e73733. (doi:10.1371/journal.pone.0073733)
27. Troscianko J, Skelhorn J, Stevens M. 2018 Camouflage strategies interfere differently with observer search images. *Proc. R. Soc. B* **285**, 20181386. (doi:10.1098/rspb.2018.1386)
28. Merilaita S, Dimitrova M. 2014 Accuracy of background matching and prey detection: predation by blue tits indicates intense selection for highly matching prey colour pattern. *Funct. Ecol.* **28**, 1208–1215. (doi:10.1111/1365-2435.12248)
29. Marshall KLA, Philpot KE, Damas-Moreira I, Stevens M. 2015 Intraspecific colour variation among lizards in distinct island environments enhances local camouflage. *PLoS ONE* **10**, e0135241. (doi:10.1371/journal.pone.0135241)
30. Stevens M, Lown AE, Wood LE. 2014 Camouflage and individual variation in shore crabs (*Carcinus maenas*) from different habitats. *PLoS ONE* **9**, e115586. (doi:10.1371/journal.pone.0115586)
31. Nokelainen O, Maynes R, Mynott S, Price N, Stevens M. 2019 Improved camouflage through ontogenetic colour change confers reduced detection risk in shore crabs. *Funct. Ecol.* **33**, 13280. (doi:10.1111/1365-2435.13280)
32. Hocking B. 1964 Fire melanism in some African grasshoppers. *Evolution* **18**, 332–335. (doi:10.1111/j.1558-5646.1964.tb01606.x)
33. Forsman A. 2018 On the role of sex differences for evolution in heterogeneous and changing fitness landscapes: insights from pygmy grasshoppers. *Phil. Trans. R. Soc. B* **373**, 20170429. (doi:10.1098/rstb.2017.0429)
34. Karpestam E, Merilaita S, Forsman A. 2013 Detection experiments with humans implicate visual predation as a driver of colour polymorphism dynamics in pygmy grasshoppers. *BMC Ecol.* **13**, 17. (doi:10.1186/1472-6785-13-17)
35. Eacock A, Rowland HM, Edmonds N, Saccheri IJ. 2017 Colour change of twig-mimicking peppered moth larvae is a continuous reaction norm that increases camouflage against avian predators. *PeerJ* **5**, e3999. (doi:10.7717/peerj.3999)
36. Kang C, Kim YE, Jang Y. 2016 Colour and pattern change against visually heterogeneous backgrounds in the tree frog *Hyla japonica*. *Sci. Rep.* **6**, 22601. (doi:10.1038/srep22601)
37. 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.
38. Merilaita S, Lind J. 2005 Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. Lond. B* **272**, 665–670. (doi:10.1098/rspb.2004.3000)
39. Michalis C, Scott-Samuel NE, Gibson DP, Cuthill IC. 2017 Optimal background matching camouflage. *Proc. R. Soc. B* **284**, 20170709. (doi:10.1098/rspb.2017.0709)
40. Troscianko J, Stevens M. 2015 Image calibration and analysis toolbox: a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol. Evol.* **6**, 1320–1331. (doi:10.1111/2041-210X.12439)
41. Dimitrova M, Merilaita S. 2010 Prey concealment: visual background complexity and prey contrast distribution. *Behav. Ecol.* **21**, 176–181. (doi:10.1093/beheco/arp174)
42. Dimitrova M, Merilaita S. 2012 Prey pattern regularity and background complexity affect detectability of background-matching prey. *Behav. Ecol.* **23**, 384–390. (doi:10.1093/beheco/arr201)
43. Kjernsmo K, Merilaita S. 2012 Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. *Proc. Biol. Sci.* **279**, 4192–4198. (doi:10.1098/rspb.2012.1547)
44. Dimitrova M, Merilaita S. 2014 Hide and seek: properties of prey and background patterns affect prey detection by blue tits. *Behav. Ecol.* **25**, 402–408. (doi:10.1093/beheco/art130)
45. Merilaita S. 2003 Visual background complexity facilitates the evolution of camouflage. *Evolution* **57**, 1248–1254. (doi:10.1554/03-011)
46. Xiao F, Cuthill I. 2016 Background complexity and the detectability of camouflaged targets by birds and humans. *Proc. R. Soc. B* **283**, 20161527. (doi:10.1098/rspb.2016.1527)
47. Tedore C, Nilsson D-E. 2019 Avian UV vision enhances leaf surface contrasts in forest environments. *Nat. Commun.* **10**, 238. (doi:10.1038/s41467-018-08142-5)
48. Merilaita S, Lind J. 2006 Great tits (*Parus major*) searching for artificial prey: implications for cryptic coloration and symmetry. *Behav. Ecol.* **17**, 84–87. (doi:10.1093/beheco/arj007)
49. Cuthill IC, Hiby E, Lloyd E. 2006 The predation costs of symmetrical cryptic coloration. *Proc. R. Soc. B* **273**, 1267–1271. (doi:10.1098/rspb.2005.3438)
50. Talas L, Fennell JG, Kjernsmo K, Cuthill IC, Scott-Samuel NE, Baddeley RJ. 2018 Evolving optimum camouflage with generative adversarial networks. *bioRxiv* 429092. (doi:10.1101/429092)
51. Stevens M, Merilaita S. 2009 Defining disruptive coloration and distinguishing its functions. *Phil. Trans. R. Soc. B* **364**, 481–488. (doi:10.1098/rstb.2008.0216)
52. Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga CA, Troscianko TS. 2005 Disruptive coloration and background pattern matching. *Nature* **434**, 72–74. (doi:10.1038/nature03312)
53. Schaefer HM, Stobbe N. 2006 Disruptive coloration provides camouflage independent of background matching. *Proc. R. Soc. B* **273**, 2427–2432. (doi:10.1098/rspb.2006.3615)
54. Fraser S, Callahan A, Klassen D, Sherratt TN. 2007 Empirical tests of the role of disruptive coloration in reducing detectability. *Proc. R. Soc. B* **274**, 1325–1331. (doi:10.1098/rspb.2007.0153)
55. Stevens M, Cuthill IC, Windsor AM., Walker HJ. 2006 Disruptive contrast in animal camouflage. *Proc. Biol. Sci.* **273**, 2433–2438. (doi:10.1098/rspb.2006.3614)
56. Skelhorn J, Ruxton G. 2010 Predators are less likely to misclassify masquerading prey when their

- models are present. *Biol. Lett.* **6**, 597–599. (doi:10.1098/rsbl.2010.0226)
57. Dimitrova M, Stobbe N, Schaefer H, Merilaita S. 2009 Concealed by conspicuousness: distractive prey markings and backgrounds. *Proc. R. Soc. B* **276**, 1905–1910. (doi:10.1098/rspb.2009.0052)
58. Stevens M, Graham J, Winney IS, Cantor A. 2008 Testing Thayer's hypothesis: can camouflage work by distraction? *Biol. Lett.* **4**, 648–650. (doi:10.1098/rsbl.2008.0486)
59. Stevens M, Marshall KLA, Troscianko J, Finlay S, Burnand D, Chadwick SL. 2013 Revealed by conspicuousness: distractive markings reduce camouflage. *Behav. Ecol.* **24**, 213–222. (doi:10.1093/beheco/ars156)
60. Olofsson M, Dimitrova M, Wiklund C. 2013 The white 'comma' as a distractive mark on the wings of comma butterflies. *Anim. Behav.* **86**, 1325–1331. (doi:10.1016/j.anbehav.2013.10.003)
61. Cuthill IC, Sanghera NS, Penacchio O, Lovell PG, Ruxton GD, Harris JM. 2016 Optimizing countershading camouflage. *Proc. Natl Acad. Sci. USA* **113**, 13 093–13 097. (doi:10.1073/pnas.1611589113)
62. Penacchio O, Lovell P, Harris J. In press. Is countershading camouflage robust to lighting change due to weather? *R. Soc. open sci.* **5**, 170801. (doi:10.1098/rsos.170801)
63. Merilaita S, Tullberg BS. 2005 Constrained camouflage facilitates the evolution of conspicuous warning coloration. *Evolution* **59**, 38–45. (doi:10.1554/04-410)
64. Barnett JB, Cuthill IC. 2014 Distance-dependent defensive coloration. *Curr. Biol.* **24**, R1157–R1158. (doi:10.1016/j.cub.2014.11.015)
65. Bond AB. 2007 The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Ann. Rev. Ecol. Evol. Syst.* **38**, 489–514. (doi:10.1146/annurev.ecolsys.38.091206.095728)
66. Edmunds M. 2000 Why are there good and poor mimics? *Biol. J. Linn. Soc.* **70**, 459–466. (doi:10.1006/bjil.1999.0425)
67. Sherratt TN. 2002 The evolution of imperfect mimicry. *Behav. Ecol.* **13**, 821–826. (doi:10.1093/beheco/13.6.821)
68. Feeney WE, Stoddard MC, Kilner RM, Langmore NE. 2014 'Jack-of-all-trades' egg mimicry in the brood parasitic Horsfield's bronze-cuckoo?. *Behav. Ecol.* **25**, 1365–1373. (doi:10.1093/beheco/aru133)
69. Penney HD, Hassall C, Skevington JH, Abbott KR, Sherratt TN. 2012 A comparative analysis of the evolution of imperfect mimicry. *Nature* **483**, 461–464. (doi:10.1038/nature10961)
70. Kazemi B, Gamberale-Stille G, Tullberg BS, Leimar O. 2014 Stimulus salience as an explanation for imperfect mimicry. *Curr. Biol.* **24**, 965–969. (doi:10.1016/j.cub.2014.02.061)
71. Baling M, Stuart-Fox D, Brunton DH, Dale J. 2016 Habitat suitability for conservation translocation: the importance of considering camouflage in cryptic species. *Biol. Conserv.* **203**, 298–305. (doi:10.1016/j.biocon.2016.10.002)
72. Wilson EC, Shipley AA, Zuckerberg B, Peery MZ, Pauli JN. 2019 An experimental translocation identifies habitat features that buffer camouflage mismatch in snowshoe hares. *Cons. Letters* **12**, e12614. (doi:10.1111/conl.12614)