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Melanin-based coloration and host–parasite interactions under global change

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The role of parasites in shaping melanin-based colour polymorphism, and the consequences of colour polymorphism for disease resistance, remain debated. Here we review recent evidence of the links between melanin-based coloration and the behavioural and immunological defences of vertebrates against their parasites. First we propose that (1) differences between colour morphs can result in variable exposure to parasites, either directly (certain colours might be more or less attractive to parasites) or indirectly (variations in behaviour and encounter probability). Once infected, we propose that (2) immune variation between differently coloured individuals might result in different abilities to cope with parasite infection. We then discuss (3) how these different abilities could translate into variable sexual and natural selection in environments varying in parasite pressure. Finally, we address (4) the potential role of parasites in the maintenance of melanin-based colour polymorphism, especially in the context of global change and multiple stressors in human-altered environments. Because global change will probably affect both coloration and the spread of parasitic diseases in the decades to come, future studies should take into account melanin-based coloration to better predict the evolutionary responses of animals to changing disease risk in human-altered environments.

1. Melanin-based coloration and changing disease risk

Global change is modifying host–parasite interactions and the occurrence of diseases at an unprecedented rate, and the outcomes will depend on the level of host intraspecific variability in parasite resistance and tolerance [1–3]. Global change is also rapidly modifying the levels of intraspecific variability [4], which could potentially amplify or dampen emerging effects of changing host–parasite encounters and interactions. As a phenotypic marker of intraspecific genetic variation in many vertebrates (figure 1), melanin-based colour polymorphism is also altered by environmental changes (e.g. [7]). Moreover, melanin-based coloration is associated with many critical biological functions, including metabolism, reproduction, stress response and immunity [8], which can have consequences for the ability of differently coloured morphs to respond to natural and human-driven environmental changes [9–11]. However, the relationship between melanin-based coloration and host–parasite interactions has been understudied for a long time, thereby hindering our ability to predict the response of wild populations to changing environments and disease risk. Here, we review evidence that variation in melanin-based coloration has implications for parasite exposure and resistance, and argue that melanin-based coloration should be taken into account to better predict the consequences of global change on disease emergence in wild populations.

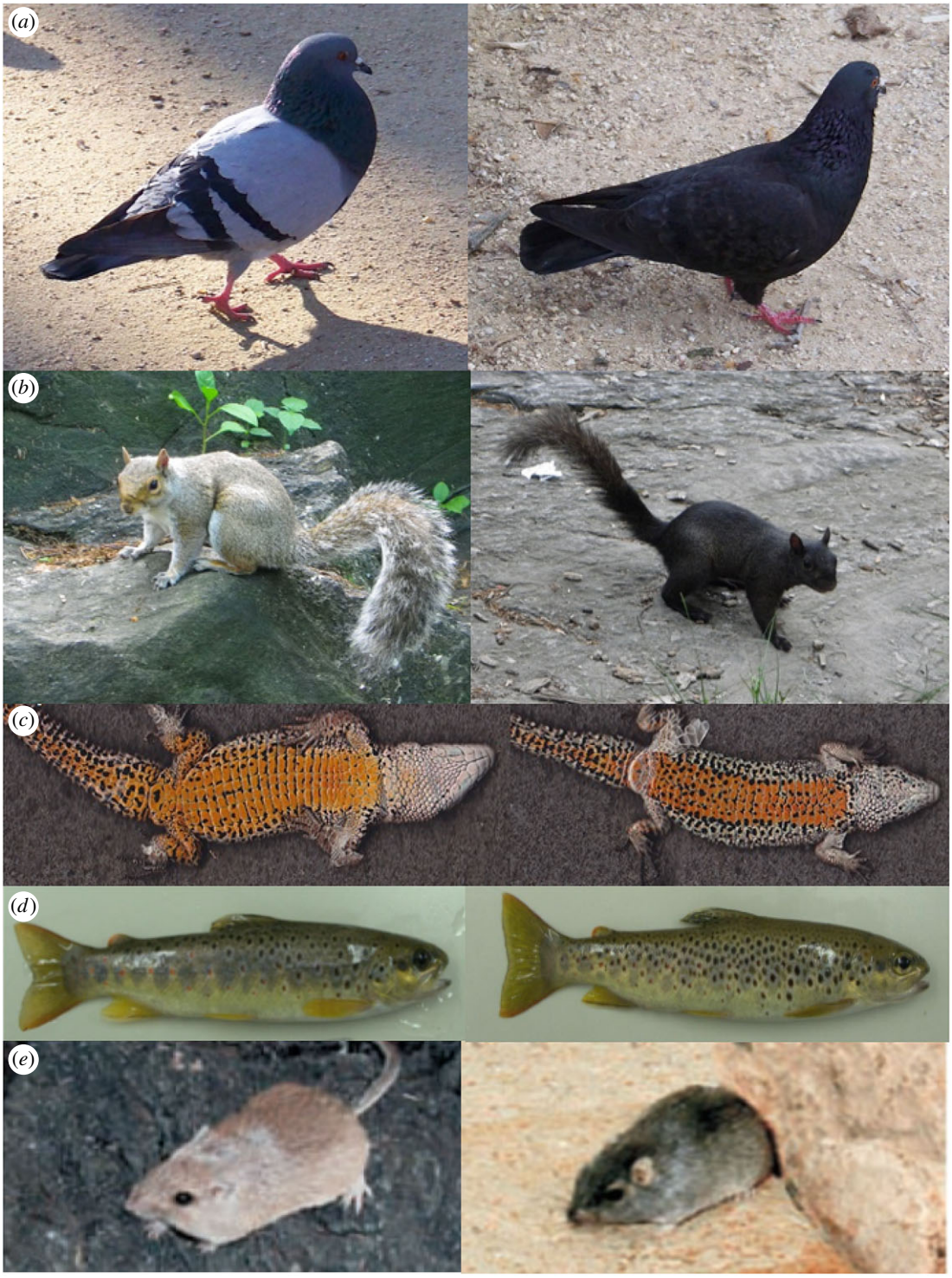

Figure 1. Light (left) and dark (right) melanin-based colour variations in (*a*) feral pigeon *Columba livia* (credit: L. Jacquin), (*b*) grey squirrel *Sciurus carolinensis* (credit: L. Jacquin), (*c*) viviparous lizards *Zootoca vivipara* (credit: Martin M), (*d*) brown trout *Salmo trutta* (from Jacquin *et al*. [5]) and (*e*) pocket mice *Chaetodipus intermedius* (from Nachman *et al*. [6]). (Online version in colour.)

2. The biological significance of melanin-based coloration

Melanin-based coloration is mainly due to two pigments: eumelanin (responsible for black and grey coloration) and pheomelanin (responsible for brown and reddish coloration) [12,13]. These melanin pigments have a direct role on some biological functions, such as UV protection, thermoregulation and camouflage [13]. Consequently, predation and climate play an important role in the evolution of melanin-based colour polymorphism (e.g. [14]). By contrast, the link between parasites and melanin-based coloration has been neglected so far.

Instead of melanin, most studies on colour–parasite interactions have focused on carotenoid-based colour [13]. Carotenoid pigments are obtained through the diet and have a direct role in the immune system [15]: individuals with more carotenoid pigments are often more resistant to parasites than are their duller counterparts (e.g. [16]). In contrast, the links between melanin-based coloration and parasitism are still unclear. Melanin pigments are synthesized by the animal, mostly genetically determined, and the link

between melanin-based coloration and individual condition is complex [17–20]. Interestingly, recent pharmacological and molecular studies have argued for evidence of genetic and physiological links between melanin-based colours and various aspects of individual quality, behaviour and physiology, opening new avenues of research [8,20,21].

In particular, knowledge of the underpinning molecular and genetic mechanisms of melanin-based coloration has rapidly expanded, and now enables us to make more accurate predictions (e.g. [8,22,23]). For instance, pharmacological studies have shown that the production and expression of melanin pigments are mostly regulated by melanocortins (such as the melanocyte-stimulating hormone α-MSH, and the melanin-concentrating hormone) that can bind to various melanocortin receptors MCR across tissues, and are highly conserved among vertebrates [12,24]. Melanocortins have pleiotropic effects on several behavioural and physiological traits, including activity, aggressiveness, reproduction, stress response and immunity in various vertebrates [8]. This raises expectations that melanin-based coloration might be related to some aspects of parasite resistance.

Several recent studies of various vertebrate species directly inform this possibility (studies electronic supplementary material, table S1). For instance, darker grey morphs of the tawny owl (*Strix aluco*) had fewer blood parasites than did rufous morphs [25], and similar patterns were seen for darker feral pigeons (*Columba livia*) [26]. In contrast, no link between melanin-based coloration and infection by intestinal coccidians (*Isospora* sp.) was found in American goldfinches (*Carduelis tristis*) [27]. Considered across studies, melanin-based colour is associated with higher (three studies) or lower (seven studies) parasite loads, with no difference seen in a few other cases (four studies) (electronic supplementary material, table S1). One study suggests that results could depend on the type of parasites considered (endoparasite or ectoparasite), which might be differently linked to coloration. For instance, darker buzzards (*Buteo buteo*) had more ectoparasites but fewer blood parasites, maybe because darker morphs are more attractive to ectoparasites and more resistant to endoparasites [28], but few studies measured different types of parasites in the same host species. In addition, behavioural differences between morphs might expose them to different types of parasites, which might complicate the relationships between melanin-based coloration and parasite load. We argue that, because parasite load is determined by both behavioural and physiological defences, it is necessary to consider multiple traits and to discriminate between different types of parasites to inform direct, indirect and correlated effects of individual variation in melanin-based coloration on parasite load [29].

3. Objectives

We here review recent evidence that melanin-based coloration can be tightly linked to individual behavioural and physiological ability to defend against parasites. We discuss the links between melanin-based coloration and parasitism, separately considering parasite exposure (i.e. probability of encountering parasites) and parasite resistance (i.e. ability to limit parasite infection once exposed). We do not to discuss the links between melanin and parasite tolerance (i.e. ability to reduce effects on fitness for a given parasite load) because too few studies are available on this last topic. We focus on vertebrates because the physiological mechanisms accounting for melanin-based coloration are better known and better conserved in vertebrates than in invertebrates.

We propose that (1) differences between colour morphs can result in variable exposure to parasites, either through direct effects of colour (i.e. more or less visible or attractive to parasites) or indirectly through variation in behaviour, depending on the transmission mode of the parasites. Once infected, we propose that (2) immune variation between differently coloured individuals might result in different abilities to cope with parasite infections. We then discuss (3) how these different abilities could translate into variable sexual and natural selection in environments varying in parasite pressure. Finally, we address (4) the potential role of parasites in the maintenance of melanin-based coloration polymorphism, especially in the context of global change and multiple stressors in human-altered environments.

4. Melanin, behaviour and exposure risk

The probability of encountering parasites can be influenced in two primary ways: (i) hosts can be more or less visible or attractive to parasites or vectors, or (ii) hosts can display particular behaviours influencing their exposure risk. For instance, the alternation of black and white stripes of zebras (*Equus quagga*) is believed to decrease their attractiveness to Tabanidae fly vectors [30]. The role of more homogeneous coloration with respect to parasite attractiveness is still unclear. Darker individuals are sometimes asserted to be more attractive to ectoparasites than their paler counterparts, for instance, in common buzzards *Buteo buteo* and horses *Equus caballus* [28,31], but further studies will be needed to test the generality of this hypothesis on other species.

Behavioural differences between differently coloured individuals can also strongly influence their probability of encountering parasites [32]. Parasites can be transmitted through two main routes: through social contacts and through the environment. Socially contagious parasites rely on direct host-to-host contact, such as viruses causing respiratory infections and transmitted through coughing, or *Gyrodactylus* sp. parasites that can jump from one fish to another (e.g. [33]). In such cases, social interactions and the propensity to form groups could influence the probability of encountering parasites (e.g. [34,35]). In addition, more socially dominant or bolder individuals (proactive behavioural type) could be exposed to more socially and sexually contagious parasites (reviewed in [36–38]). Darker individuals are generally more dominant and sexually more active, and could have a higher propensity to live in groups (electronic supplementary material, table S1), probably because of pleiotropic effects of the melanocortin system [7]. These behavioural differences between morphs might have consequences for parasite exposure, although few studies have directly tested this supposition (electronic supplementary material, table S1; figure 2).

In contrast, environmentally transmitted parasites, such as plathelminthia larvae or *Guardia* sp., spread through environmental substrates (soil and water), while other pathogens, such as *Plasmodium* sp., are principally transmitted through vectors [32]. In such cases, behavioural differences in habitat and space use are keys to exposure probability [32]. For instance, more

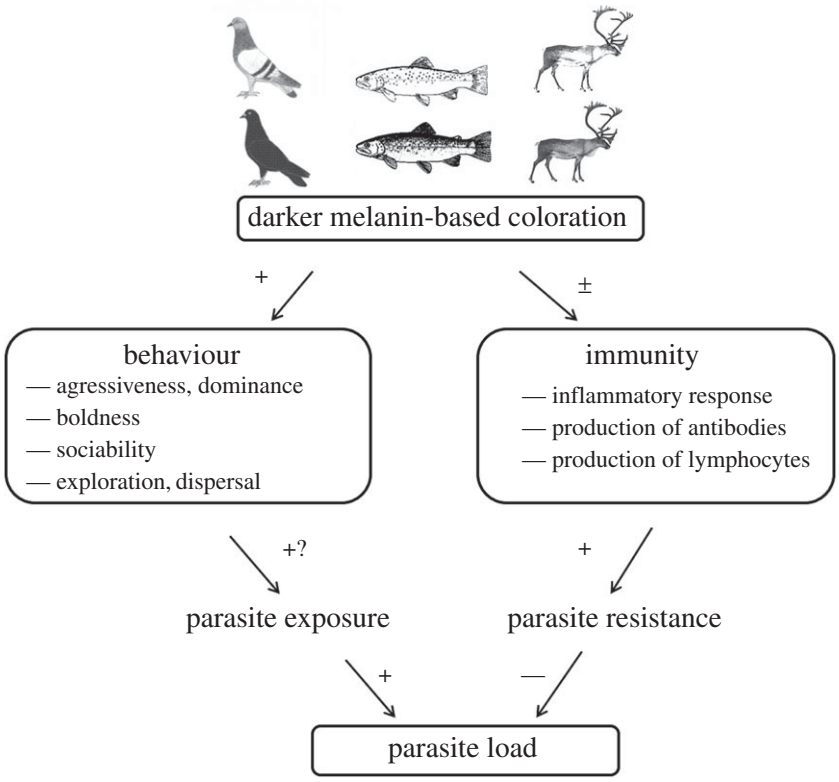

Figure 2. Proposed links between melanin-based coloration and parasite load and their underlying mechanisms in vertebrates.

exploratory and active chipmunks *Tamias sibericus* could be more exposed to environmentally transmitted ticks [39]. Also, inter-individual differences in dispersal propensity could generate important differences in parasite exposure. Darker individuals could have a higher exploration and/or dispersal propensity compared with their paler counterparts, but few studies are available (electronic supplementary material, table S1). In addition, darker individuals are known to have higher activity levels and metabolic rates, and might forage more actively to sustain their higher metabolic needs, again due to the pleiotropic effects of melanocortin hormones [8]. Darker versus paler morphs are also often found in different microhabitats and might exploit alternative trophic niches (e.g. [25,40–42]), which might expose them to different levels or types of environmentally transmitted parasites. However, few experimental studies are available and this hypothesis remains to be formally tested.

In summary, darker individuals often display particular combinations of morphological (e.g. differential parasite attraction) and behavioural traits (e.g. sociability, dominance, space use). Such behavioural differences could potentially influence their exposure to socially and environmentally transmitted parasites (electronic supplementary material, table S1; figure 2), but for now, only indirect evidence exists. Future work should now formally test these hypotheses, for instance, by experimentally exposing differently coloured individuals to parasites in different environments or social group structures.

5. Melanin and physiological defences against parasites

Once exposed to parasites, individuals often vary in their physiological ability to resist the infection either by killing or removing parasites. Melanin-based coloration could have several influences here. First, skin melanization could directly prevent the proliferation of parasites on (or in) the body through the toxicity of melanin molecules [43]. Dark feathers are also more resistant to bacterial degradation in birds [44]. Second, melanocortins such as ACTH appear to stimulate grooming activity (e.g. reviewed in [8,24]), which could favour parasite removal in darker vertebrates compared to their paler counterparts. Third, melanin is tightly linked to the immune system, for instance, through pleiotropic effects of melanocortins that can bind to various receptors in the skin and in the immune cells [8,45]. This could enable differently coloured individuals to mount different immune responses and limit parasite proliferation [26,45,46].

Evidence of a link between melanin and immunity mostly comes from experimental studies comparing immunocompetence between differently coloured morphs based on immune challenges with artificial or natural antigens (reviewed in electronic supplementary material, table S1). Such approaches are useful to investigate immunology in wild populations because they enable testing the ability of animals to mount an immune response while controlling for their past exposure to parasites and avoiding any pathogenic effects of parasites. Interestingly, results are mixed across studies: that is, associations between melanin-based coloration and immunocompetence are sometimes positive, negative or absent (summarized in electronic supplementary material, table S1). For instance, immune response after the injection of phytohaemagglutinin (PHA) is associated with melanism in various species, although in a positive or negative direction depending on the study (electronic supplementary material, table S1). Indeed, darker pigeons *Columba livia* also have a higher cellular immune response against PHA than their paler counterparts; but the opposite relationship was found in falcons *Falco eleonorae* [26,45]. A number of empirical studies also support a link between melanin-based coloration and antibody production

(electronic supplementary material, table S1). Darker reddish owls (*Strix aluco*) produced more antibodies for a longer period of time in response to antigen injection than did paler owls [47], but other studies found negative relationships or no relationship (electronic supplementary material, table S1).

Variable results across studies might depend on the type of pigment (eumelanin or pheomelanin) or might arise because melanin is differently linked to different components of the immune system that have different costs and pay-offs (e.g. [48]). However, the immune system is complex and it remains difficult to disentangle the different components of immunity (for instance, the PHA test reflects both inflammation and lymphocyte proliferation [49]). Future studies using genomic and transcriptomic tools will be a powerful way to refine our view of the immune pathways associated with coloration. In addition, differently coloured individuals might have different strategies to cope with the costs of immunity [47], including oxidative costs [50–52]. By comparing how differently coloured individuals trade off their immune investment against other crucial life-history traits, future studies will help us understanding the evolution of immune strategies to cope with parasites in phenotypically diverse populations.

6. Underlying mechanisms

The genetic underpinnings of variations in melanin-based coloration are now better known [22,53]. Genetic variations in MC1R melanocortin receptor can affect the type and/or quantity of melanin (eumelanin or phaeomelanin) deposited in the skin, feather and hair (e.g. [6,53,54]). Genetic variations in numerous other genes (e.g. POMC, ASIP, TYRP1 and others) have been highlighted depending on the species (e.g. [55,56]), with different implications for correlated traits depending on the level of pleiotropy expected [23,53].

Genetic variations in melanocortin ligands (POMC and its products MSH, ACTH) can have particularly important pleiotropic effects because they can bind to five different melanocortin receptors (MCR1–5) that are expressed in various tissues (for instance, MC1R in the skin and immune cells; MC3R in central nervous system, immune cells and adrenal glands; MC5R in skin and immune cells) [8]. Overall, a growing number of studies outline the potential role of melanocortin ligands and receptors in the covariations between pigmentation, behaviour and immunity. For instance, variations in MSH and ACTH blood levels are correlated with skin darkening and behavioural response to social stress in artic charr *Salvelinus alpinus* [57]. Variations in the coding sequence of Melanocortin 1 receptor are also associated with different pigmentation and immunity in Eleanora's falcon *Falco eleanorae* [45]. Experimental manipulations of melanocortin ligands (α-MSH and ACTH) can affect the expression of the major histocompatibility complex class I, inflammation and leucocyte activity when bound to MC1R in lymphocytes [8,58,59]. By binding to MC3R and MC5R, melanocortins also have anti-inflammatory and antipyretic activities, thereby reducing acute and allergic inflammation [8], which could partially explain the covariations between pigmentation and parasite resistance in wild animals.

Besides melanocortins, steroid hormones such corticosteroids and/or testosterone could also affect the covariation between colour, behaviour and immunity, because both hormones can jointly affect the synthesis of melanin, influence behavioural responses and have immunosuppressive effects [60–64]. Further studies are now needed to determine whether the levels of expression of melanocortin receptors, ligands and hormones are correlated across tissues and how covariations with behaviour and immunity are regulated and shaped by natural and sexual selection.

7. Implications for sexual selection in variable environments

Taken together, the above studies illustrate the links between melanin-based coloration and parasite exposure and resistance. As a result, melanin-based coloration should be under strong sexual and natural selection in environments subject to high risk of parasitism. The signalling role of melanin ornaments as a reliable and honest cue of individual quality, and its role in sexual selection, have been discussed in previous work [13,20], and so they are only quickly summarized here. Melanin-based coloration is used as a mate choice criterion in several species and the benefits derived might be directly or indirectly related to aspects observed in association with melanin-based coloration such as offspring quality, parasite resistance and parental investment [5,65–68]. In short, individuals might benefit from choosing darker mates, because they would have a lower risk of being infected by parasites during mating, and/or obtain juveniles of better quality.

However, choosing darker mates might not always be advantageous, depending on the context (e.g. [5]). Because immunity is costly and trades off against other life-history traits, it could be advantageous to choose darker mates only in heavily parasitized environments and/or rich environments. Coloration thus might be under fluctuating sexual selection depending on parasitism risk, parasite type and other environmental conditions, which could result in spatiotemporal and/or frequency-dependent variability in mate choice [18,20]. However, only indirect correlative evidence exists so far. For instance, different conspecific populations differ substantially in their preferences for melanin-based coloration, especially in spatiotemporally variable environments (e.g. [69]), yet the role of variable parasitism risk in heterogeneous environments on the evolution of melanin-based coloration remains poorly known. We thus encourage future studies to test how sexual selection differs among environments varying in parasitism risk.

8. Melanin in a changing world: implications for responses to global change

By exposing animals to multiple stressors, global change is expected to strongly influence the outcome of selection on colour morphs interacting with their parasites and other factors. Indeed, recent empirical studies have shown that different colour morphs within species respond differently to alternative environmental conditions such as temperature [70], food availability [71,72] and pollutants [73,74]. More generally, differently coloured individuals have different physiological abilities to respond to stressors [75,76]. Such alternative genotype–environment interactions can have strong implications for the ability to respond to global change [9]. For instance, darker individuals could have a selective advantage over paler ones in warmer and human-altered environments due to better radiation protection and

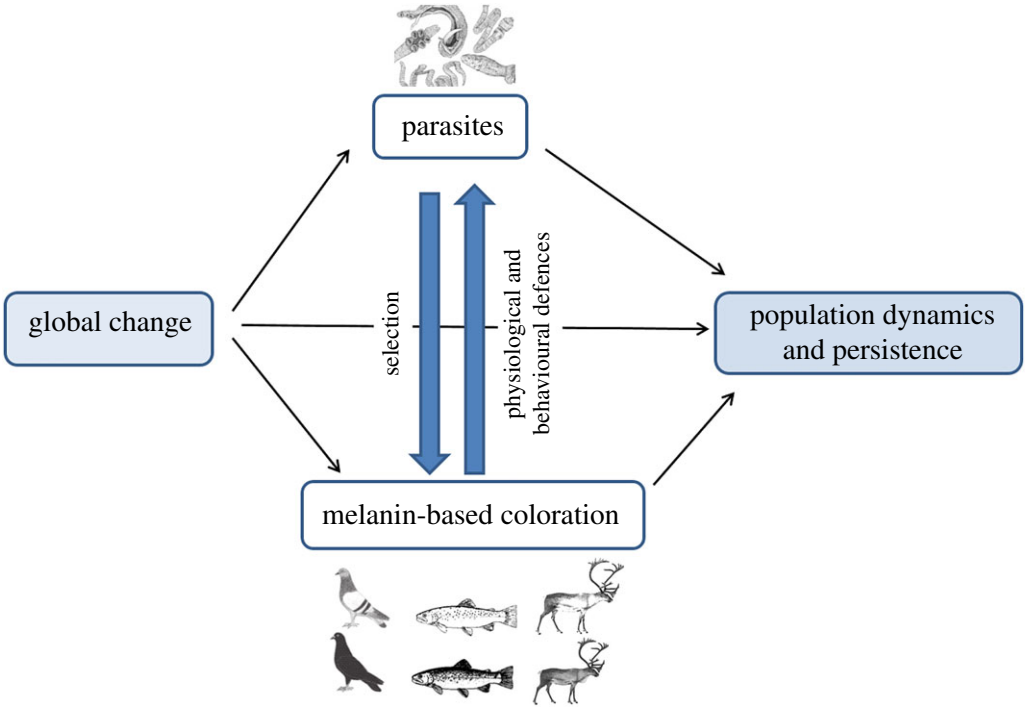

Figure 3. Proposed links between colour polymorphism and parasitism under global change. (Online version in colour.)

thermoregulation, better ability to detoxify pollutants and/or higher competitive abilities (reviewed in [9]). As a result, colour polymorphic species might be able to respond to a wider range of environmental conditions, and colour polymorphism within a species might act as a buffer against extinction [10]. In this context, the effects of parasites on differently coloured individuals should be considered in depth.

Disease risk and exposure to pathogens are expected to be dramatically altered in the future [1,77]. For instance, invasive species bring new pathogens, and pollution has immunosuppressive effects that have strong impacts on host susceptibility to diseases [77,78]. As a result, environmental stressors can drastically modify host–parasite interactions through direct effects on parasites and through indirect effects on host immunity [1,77,78]. For such cases, we propose that pathogens could select for particular colours of morphs during epidemics, owing to different investment in immunity and/or ability to cope with the costs of immunity between differently coloured individuals. Fitting this idea, an emerging disease has been shown to favour darker birds in greenfinches *Carduelis chloris* [79].

However, the relationship between coloration and parasite load probably depends on other environmental stressors that vary along disturbance gradients, which might explain the different outcomes from different studies (electronic supplementary material, table S1). Indeed, immunity and behaviour are highly sensitive to biotic and abiotic stressors [80], and differently coloured individuals often differ in their ability to deal with such stressors. For instance, darker pigeons are less infected by blood parasites than paler ones (as noted earlier), but only in heavily urbanized conditions [40]. Although the underpinning environmental factors remain difficult to identify, the reason could be higher resistance of darker birds to pollutants [74] or to stressful conditions [75,76]. For instance, darker individuals are more resistant to pollution by heavy metals, because melanin pigments have detoxifying properties and the relationship between plumage colour and immunity thus depends on trace metal contamination [73]. In addition, melanin-based coloration and resistance to oxidative stress are tightly linked [51,52,81]. More generally, recent studies outline the increasing role of pollutants and oxidative stress in the signalling role of animal coloration [82]. Alternatively, darker morphs could be at a disadvantage compared with paler ones when food is scarce, because the former have a higher metabolic rate and higher energetic requirements [8]. As a consequence, darker individuals might be able to achieve higher immunity and resistance to parasites only in environments where food resources are abundant and predictable, thereby enabling them to sustain the associated energetic costs. Additional studies are now needed to understand how new stressors can interact with parasites in shaping immunity, which will help to elucidate the role of melanin as a context-dependent indicator of multistress resistance.

9. Promising avenues for future research

Differently coloured individuals could differ in their exposure and resistance to parasites through particular combinations of morphological (e.g. differential parasite attraction), behavioural (e.g. different sociability, exploration and activity) and physiological (e.g. innate and acquired immunity) traits (electronic supplementary material, table S1; figure 2). We thus encourage future studies to take into account parasites as a potent evolutionary pressure shaping melanin-based coloration diversity in vertebrates, especially at the intraspecific level. We believe that such studies will both enhance our understanding of parasitism as a selective force shaping diversity, and improve our knowledge of the high variability in disease susceptibility and extinction risk observed in wild populations (figure 3). We identify several productive avenues for research (table 1). First, future studies should encompass both behavioural and physiological traits involved in anti-parasite defences in phenotypically diverse species. Studies of this nature will inform why different phenotypes differ in their response to parasitism, and the respective role of different types of defences in the dynamics

Table 1. Promising avenues for future research.

Question 1. How do differently coloured individuals differ in their behavioural and physiological defences against parasites? Which kind of parasite favours which kind of morph?
Current limitations and future prospects. Experimental approaches linking realistic parasite exposure and behavioural and immune assessments of host responses are still rare (electronic supplementary material, table S1). Different kind of transmission modes might affect the outcome of host–parasite interactions, so future studies should discriminate between differently transmitted parasites.
Question 2. What are the underlying mechanisms explaining the covariations between coloration and host traits?
Current limitations and future prospects. Few existing studies have explicitly considered the genetic and physiological mechanisms underlying the covariations between traits. Variations in the melanocortin system and steroid hormones are good candidates but different mutations and levels of coordination across tissues could have different implications for pleiotropic effects and selective processes.
Question 3. What are the effects of alternative behavioural and physiological strategies for parasite load?
Current limitations and future prospects. More formal field or experimental tests are now needed to compare alternative traits and parasite load at the same time between coloured morphs and their effects on host fitness traits. This will expand our knowledge on the evolutionary consequences of intraspecific variability and parasites on differently coloured hosts.
Question 4. What are the immune strategies of differently coloured individuals and how do they cope with immune energetical and oxidative costs?
Current limitations and future prospects. Future studies consider explicitly the different components of the immune system and decipher the costs and benefits of alternative immune responses. Recent advances in genomics and transcriptomics will help understanding why alternative morphs differ in their susceptibility to disease once infected.
Question 5. What are the consequences for sexual selection?
Current limitations and future prospects. Future studies should test mate choice between environments varying in parasitism risk. This will expand our knowledge on the signalling value of melanin in variable environment.
Question 6. What are the consequences of melanin-based polymorphism for responses to global change in a multistress context? Can colour polymorphism act as a buffer against extinction?
Current limitations and future prospects. Global change will probably affect multiple environmental factors at the same time. Experimental approaches manipulating multiple stressors will help understanding how global change affect the ability of different morphs to resist parasite attacks and multiple stressors. Conjointly, comparative meta-analyses approaches testing the response of polymorphic versus non polymorphic species to global change and pathogens will help predicting the responses of biodiversity to current and future stressors.

of host–parasite interactions in polymorphic species. In this process, we advocate separately considering parasites depending on their transmission mode and pathogenic effect on hosts because doing so will influence the key traits involved in parasite resistance. Second, we think that future research would benefit from an explicit consideration of the underlying genetic and physiological mechanisms explaining the covariations between coloration and host traits, especially with regard to the melanocortin system and its pleiotropic effects. Third, because immunity is associated with different costs and benefits, we encourage future studies to target different immune traits linked to melanism and their associated costs in determining disease risk. This approach will considerably increase our ability to predict the susceptibility of colour polymorphic species to pathogens. Fourth, because immunity and behaviour are highly sensitive to environmental perturbations, we encourage future studies to consider parasites in the context of multiple stressors. Only then can we predict how differently coloured individuals will cope with increasing parasitism risk in the context of global change, and how global change will affect the epidemiology of diseases in the future.

Data accessibility. The manuscript is a review of published work and the data used can therefore be accessed from the referred publications and in the supplementary material.

Authors' contributions. All authors participated in writing the first and revised version of this review.

Competing interests. The authors declare no competing interests.

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