

REVIEW

Melanin-based colour polymorphism responding to climate change

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Climate warming leads to a decrease in biodiversity. Organisms can deal with the new prevailing environmental conditions by one of two main routes, namely evolving new genetic adaptations or through phenotypic plasticity to modify behaviour and physiology. Melanin-based colouration has important functions in animals including a role in camouflage and thermoregulation, protection against UV-radiation and pathogens and, furthermore, genes involved in melanogenesis can pleiotropically regulate behaviour and physiology. In this article, I review the current evidence that differently coloured individuals are differentially sensitive to climate change. Predicting which of dark or pale colour variants (or morphs) will be more penalized by climate change will depend on the adaptive function of melanism in each species as well as how the degree of colouration covaries with behaviour and physiology. For instance, because climate change leads to a rise in temperature and UV-radiation and dark colouration plays a role in UV-protection, dark individuals may be less affected from global warming, if this phenomenon implies more solar radiation particularly in habitats of pale individuals. In contrast, as desertification increases, pale colouration may expand in those regions, whereas dark colourations may expand in regions where humidity is predicted to increase. Dark colouration may be also indirectly selected by climate warming because genes involved in the production of melanin pigments confer resistance to a number of stressful factors including those associated with climate warming. Furthermore, darker melanic individuals are commonly more aggressive than paler conspecifics, and hence they may better cope with competitive interactions due to invading species that expand their range in northern latitudes and at higher altitudes. To conclude, melanin may be a major component involved in adaptation to climate warming, and hence in animal populations melanin-based colouration is likely to change as an evolutionary or plastic response to climate warming.

Keywords: climate change, colour polymorphism, melanin, melanocortin, phenoloxidase, pleiotropy

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Introduction

Climate change is predicted to accelerate evolutionary processes. Rapid modifications in climate can be detrimental to natural populations because their habitats are disappearing and most organisms have little time to evolve new adaptations or pre-existing adaptations did not have the time to spread in populations (Quintero & Wiens, 2013). Lack of genetic variation may increase the risk of extinction, since the probability that at least one genotype is adapted to the new prevailing environmental conditions is lower in species with lower genetic diversity (Thompson *et al.*, 2012). This phenomenon should be pronounced when climate change modifies environmental conditions to which species are specifically adapted and when these species are not phenotypically plastic enough to modify their physiology and

behaviour accordingly. Furthermore, organisms often face new competitive species that expand their range in regions where the climate is becoming warmer (Thomas & Lennon, 1999; Levy, 2004) at northern latitudes and higher altitudes (IPPC, 2007). As a result, many species already disappeared or are threatened leading to a decline in biodiversity (Parmesan, 2006). If studying how climate will change in the mid- to long term is the focus of huge research efforts, predicting which species or individuals are particularly vulnerable is another challenge.

Climate change is predicted to influence the pace of evolutionary processes. Although the assumption that climate warming exerts strong directional selection on organisms is well accepted, evidence for the evolution of novel genetic adaptations has received fewer empirical supports (Jump & Peñuelas, 2005; Gienapp *et al.*, 2008). However, the effects of climate change on evolutionary processes may not be straightforward to predict. If climate change sets unfavourable conditions, the

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expression of the genetic potential for any given trait may be constrained (Hoffmann & Merilä, 1999). Under such conditions, the relative contribution of environmental components to total phenotypic variance may increase, hindering evolutionary change. For instance, climate change may heavily interfere with sexual selection processes (Spottiswoode & Saino, 2010). This is the case because it may influence the cost of the expression of sexual signals relevant to mate choice and therefore disrupt the reliability of the expression of epigamic signals as signals of the underlying genetic quality. Finally, because climate warming modifies the environment to which animals are adapted, it may affect the equilibrium frequency at which colour-specific reproductive strategies achieve equal fitness (e.g. Sinervo & Lively, 1996; Tuttle, 2003).

Environmental changes due to climate warming are so rapid that to persist organisms have to quickly evolve new phenotypes that are adapted to the new environmental conditions, an outcome that is more likely to happen if these organisms are sufficiently variable at genes implicated in response to stressful factors induced by climate change (Franks & Hoffmann, 2012). Here, I discuss the possibility that the degree of genetic variation is positively associated with resilience to climate change (e.g. Pearman *et al.*, 2010). I consider the specific case of melanin-based colour polymorphism, a phenotypic marker of genetic adaptations (Roulin, 2004; McKinnon & Pierotti, 2010) with the specific prediction that colour polymorphic species may be more resistant to global warming than colour monomorphic species. In polymorphic species, some morphs may be more resistant to climate change and a key issue is whether the same morph (e.g. dark rather than pale coloured morph) is more resilient to stress across organisms. This may be the case since most colour polymorphisms are due to differential deposition of melanin pigments on the integument, pigments that have very similar effects on thermoregulation, protection against pathogens and resistance to abrasion of the integument across animals. Furthermore, the genetics of melanogenesis is very well conserved and the few genes that have pleiotropic effects on a number of other phenotypes have very similar effects across vertebrates (Sugumaran, 2002; Ducrest *et al.*, 2008).

In this review, I first discuss scenarios about how global warming could differentially affect dark and pale melanistic morphs. I then review the current scientific evidence that global change indeed differentially affects dark and pale melanistic individuals. The main message of this review is that melanin-based colouration is associated with evolutionary and plastic responses to global warming. Even if dark colourations may often have a selective advantage over pale colourations under global

warming, there are situations where the opposite pattern is predicted.

How global warming can differentially affect dark and pale melanistic morphs

I discuss scenarios about how climate warming may generate fitness differences between colour morphs. This discussion shows that climate warming acts as a new selective agent that favours dark over pale individuals in many situations.

UV-radiation

Climate warming induces an increase in ultraviolet (UV) radiation in regions where the stratospheric ozone is depleted (Manney *et al.*, 2011) and where cloudiness has not increased (Min *et al.*, 2011). Ectotherms (and to a lower extent endotherms) rely on solar radiation to warm up with black colouration absorbing more solar energy, thereby reducing the metabolic cost of homeothermy (Heppner, 1970; Walsberg *et al.*, 1978; Clusella-Trullas *et al.*, 2008). Differently coloured individuals often exploit alternative ecological niches (Galeotti & Rubolini, 2004; Roulin, 2004; Stoletzki & Schiererwater, 2005; Castilla *et al.*, 2013) such as in reptiles in which dark melanistic individuals often reside in shady habitats with less UV-radiation (Tanaka, 2007; Kearney *et al.*, 2009; Karpeštam *et al.*, 2012). In this case, paler ectotherms may be more affected by global warming because of the increase in UV-radiations. However, if pale and dark individuals exploit the same habitat, it is unclear which of them will suffer more from the increase in UV-radiations. On the one hand, dark individuals may suffer from overheating and on the other hand melanin pigments can confer a protection against UV-radiations (Andersen, 2011). This protective role of melanin explains why humans are darker in regions where UV-radiation levels are higher (Jablonski & Chaplin, 2000). Animals for which melanin plays such a protective function may therefore become darker coloured in regions, where UV-radiations are increasing due to climate warming (Häkkinen *et al.*, 2002; Rautio & Korhola, 2002; Garcia *et al.*, 2004; Gao *et al.*, 2010; Manney *et al.*, 2011), as an outcome of selection favouring genes encoding a darker colouration and from tanning induced by UV-radiations. This change would be adaptive because in human skin cancer is predicted to rise due to the higher exposure to UV-radiations (Diffey, 2004).

Humidity and thermoregulation

Climate warming leads to a change in humidity and temperature in a number of regions (Min *et al.*, 2011;

D'Odorico *et al.*, 2013). According to the Gloger's rule, animals are usually darker coloured in more humid environments and paler in drier habitats (Zink & Remsen, 1986; Kamilar & Bradley, 2011; Singaravelan *et al.*, 2013). The frequency of light coloured individuals may therefore increase in regions where deserts are expanding and darker coloured in regions where humidity is predicted to increase (Min *et al.*, 2011). The Gloger's rule is based on the assumption that melanin pigments or colouration itself confers fitness benefits (Burt & Ichida, 2004). The situation is more complex if we consider that genes implicated in the production of melanin pigments have numerous pleiotropic effects on the resistance to various stressful factors as observed in vertebrates (Ducrest *et al.*, 2008; Roulin & Ducrest, 2011; Emaresi *et al.*, 2013). Indeed, ambient temperature profoundly affects physiological processes (Walters *et al.*, 2012) and hence climate warming may be experienced as physiologically stressful. Resistance conferred by pleiotropic genes involved in melanogenesis may therefore give a selective advantage to dark over pale coloured individuals.

Pathogens

Invertebrates lack adaptive immunity and use nonspecific immune defence mechanisms to resist pathogen invasions. This includes, among other molecules, melanin to encapsulate parasites (which does not appear to be the case in vertebrates) and enzymes of the phenoloxidase cascade involved in the melanin-producing cascade and immunity (Armitage & Siva-Jothy, 2005). This explains why in insects darker melanic individuals are usually more resistant to pathogens (Fedorka *et al.*, 2013a,b). As climate warming is associated with an increase in infectious diseases in many ecosystems (e.g. Harvell *et al.*, 2009; Altizer *et al.*, 2013), melanic individuals may have a selective advantage. For instance, in a cricket heat induces an increased activity of phenoloxidase probably to enhance immunocompetence (Adamo & Lovett, 2011 but see Seppala & Jokela, 2011 and Karl *et al.*, 2011), and phenoloxidase activity is higher in dark than pale individuals (Bailey, 2011). Therefore, melanic individuals may have a selective advantage under the threat of climate warming due to an increase in pathogens.

Increased interspecific competition

Climate warming offers new areas to be colonized by competitive species. For instance, many species could expand their range at northern latitudes and higher altitudes where climate is becoming warmer (Thomas & Lennon, 1999; Levy, 2004; IPCC, 2007). Therefore,

species that evolved adaptations to live at northern and alpine climates are faced with new competitors. The ability to compete against new invading species is related to colouration (Brazill-Boast *et al.*, 2013) and because darker melanic individuals are commonly more aggressive and competitive than paler conspecifics (Senar & Domenach, 2011), probably as a consequence of the pleiotropic effects of melanogenic genes (Ducrest *et al.*, 2008), darker coloured individuals may better cope with the new competitive environment than their paler conspecifics. Furthermore, in a comparative study, it has been shown that darker species show more circulating testosterone (Bókony *et al.*, 2008) and hence darker melanic species may also better cope with the threat of invading species that expand their distributional range due to climate warming.

Evidence for melanic-specific responses to global warming

I review here the current evidence about the colour-specific responses to climate warming (Anderson *et al.*, 2012).

Genetic adaptations

Climate change acts as a selective factor that can promote the evolution of new adaptations or the spread of pre-existing adaptations initially found at low frequencies, although evidences for such a mechanism are still limited (e.g. Gienapp *et al.*, 2008; Karell *et al.*, 2011). Because melanin-based colouration plays a role in diverse functions as diverse as camouflage, thermoregulation or integument protection against biophysical agents but also because genes implicated in melanogenesis pleiotropically regulate many other physiological and behavioural functions (Ducrest *et al.*, 2008; Fedorka *et al.*, 2013a,b), the frequency of melanin-based colour morphs may change as a consequence of direct selection exerted by climate warming on colouration itself or indirect selection exerted on phenotypic traits that are genetically correlated with colouration.

I surveyed the literature about temporal changes in the frequency of colour morphs accounted to climate warming. A first study performed in Italian scops owls (*Otus scops*) reported a strong increase in the frequency of darker reddish melanic individuals between 1870 and 2007 among skin specimens preserved in natural history museums (Galeotti *et al.*, 2009). This increase in frequency was maximal, when three years before specimen collection the climate was warmer and wetter. This observation suggests that dark reddish birds born in warmer/wetter years have higher fecundity and/or survival than pale individuals, a finding that is

consistent with studies in other owls. In the screech owl (*Otus asio*), dark reddish individuals have a selective advantage in warm years and pale reddish birds in cold years (Mosher & Henny, 1976); additionally, in Italy dark and pale reddish tawny owls were found dead more often in cool-dry and warm-wet years, respectively (Galeotti & Cesaris, 1996). These temperature- and morph-specific advantages have a physiological basis as shown by measuring oxygen consumption under controlled ambient temperatures (Mosher & Henny, 1976 and see also Roulin *et al.*, 2005).

These patterns of colour-specific adaptations to climate may apply to many species because on the northern hemisphere, owl species are on average darker reddish near the equator than polewards where they are paler (Roulin *et al.*, 2011). Because climate changes to a larger extent at high than low latitudes (IPPC, 2007), dark reddish owls may expand their range northwards more than pale reddish owls may expand their range southwards. Thus, in colour polymorphic owls the frequency of the dark reddish morph may currently increase in frequency at the expense of pale reddish morph. Accordingly, using data collected in northern Europe (Finland) between 1981 and 2009 dark reddish tawny owls increased drastically in frequency because winters became warmer and in turn the survival of dark reddish owls increased disproportionately compared to pale reddish conspecifics (Karell *et al.*, 2011).

Altogether, these studies indicate that darker melanic owls have currently a selective advantage over paler melanic owls. However, because dark reddish colouration is due to a higher deposition of both pheomelanin and eumelanin pigments (Gasparini *et al.*, 2009), it remains unclear which of the two pigments are favoured under climate warming. This is an important issue because the hormones that trigger the production of pheomelanin (ASIP and possibly AGRP) and eumelanin (α -MSH) by binding melanocortin-1-receptors (MC1R) have different physiological effects when binding the four other melanocortin receptors (MC2-5Rs) (Ducrest *et al.*, 2008). Thus, the key question is whether climate warming favours eumelanic individuals, and thus potentially those that produce more α -MSH, or pheomelanic individuals producing more ASIP and/or AGRP. Suitable organisms to discriminate between these two alternative scenarios should display a colour trait that varies from dark eumelanic (black) to dark pheomelanic (brown). A recent study tackled this question in pied flycatchers (*Ficedula hypoleuca*) (Sirkiä *et al.*, 2013) in which plumage colouration varies continuously from black to brown. These authors found that the proportion of brown males strongly decreased in Finland from 1954 to 2008. The probable causes are a decline of brown immigrants coming from Central

Europe where flycatcher populations strongly declined due to climate change and also colour- and temperature-specific metabolic rates (Sirkiä *et al.*, 2010).

Colour-specific dispersal

If dispersal itself can be affected by climate warming (Massot *et al.*, 2008), it is instrumental to individuals for tracking their shifting habitat explaining why many species extended their range polewards and to higher altitudes (Wilson *et al.*, 2005). The first reaction animals can adopt in a hostile environment is to flee or look for refuges to buffer the new extreme conditions (Garcia *et al.*, 2004), a property that can be colour-specific (Mateos-Gonzalez & Senar, 2012; Van den Brink *et al.*, 2012; Roulin, 2013; Saino *et al.*, 2014). Immigration from a source population where the conditions are beyond the individual tolerance limits may explain a change in the genetic constitution of a sink population. In species showing geographic colour variation, differential immigration between populations should generate in sink populations an increase in the frequency of the colour variants usually found in source populations. Furthermore, if the conditions met in the sink population are particularly favourable to immigrants, their colour morph may thrive. If climate warming causes a decrease in the size of the source or sink populations, this will affect the colour composition of the sink population because the proportion of immigrants to residents will be modified, as found in Finnish pied flycatchers (*Ficedula hypoleuca*) (Sirkiä *et al.*, 2013) and the common lizard (*Lacerta vivipara*) (Lepetz *et al.*, 2009).

Evolutionary implications of global warming on melanin-based colouration

In a number of animals, evidences are accumulating that darker coloured individuals have a selective advantage over paler conspecifics under the new prevailing environmental conditions caused by climate warming (Fig. 1). However, there are situations under which pale individuals are favoured. Variation in the degree of colour variation may therefore decrease in animal populations and in turn genes encoding for a specific colouration may become fixed, a phenomenon that is not restricted to colouration (Rubidge *et al.*, 2012). Because episodes of strong directional selection due to changes in climate occurred many times in history (e.g. D'Andrea *et al.*, 2011), the equilibrium frequency at which colour variants achieve the same fitness may only rarely persist during very long periods of time. For instance, when climate becomes warmer or colder, nonadapted colour variants may become

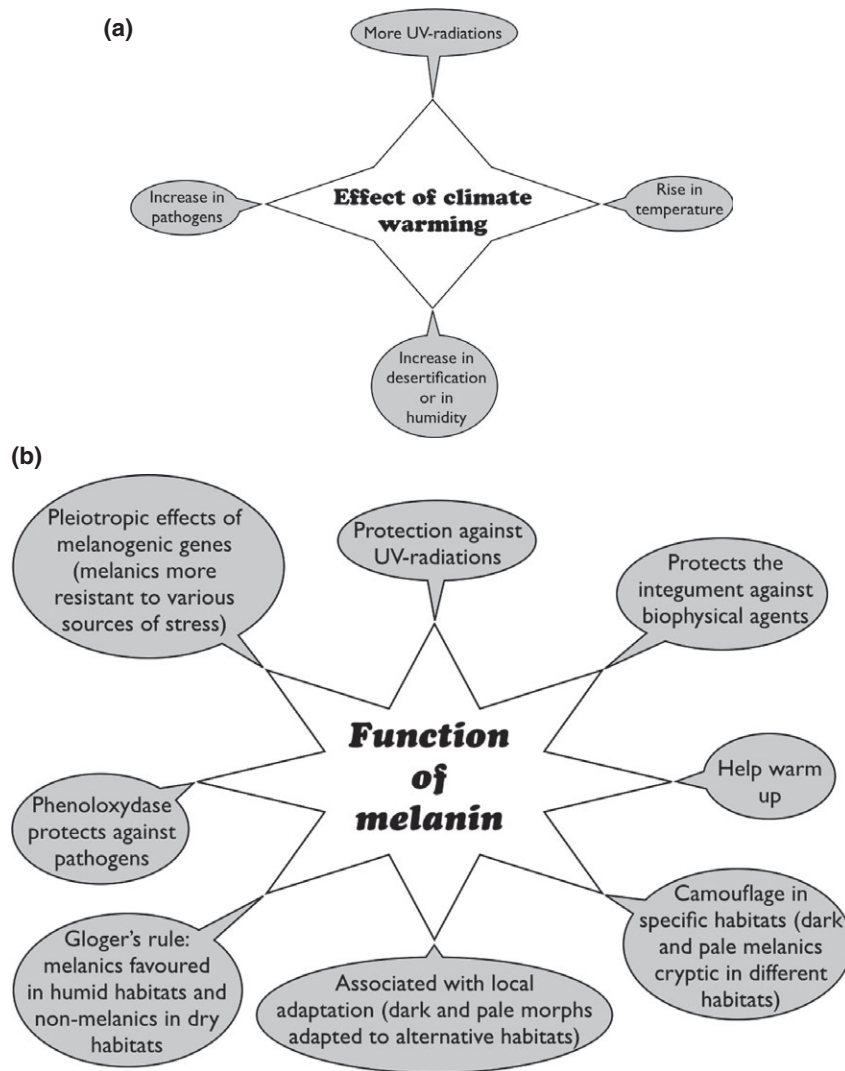


Fig. 1 Summary of the effects of climate warming on ecological factors (a) and adaptive function of melanin-based colouration that could participate in the resilience to climate warming (b).

extinct. This may explain, at least in part, why colour polymorphic species are so rare in nature (e.g. 3% in birds, Galeotti *et al.*, 2003) perhaps because the most adapted morph persists implying that polymorphic species rapidly evolve towards monomorphism. Indeed, colour morphs are often adapted to alternative environmental conditions, implying that polymorphic species can exploit a larger diversity of habitats (Galeotti & Rubolini, 2004; Forsman & Aberg, 2008) and expand their distributional range over larger areas than monomorphic species (Forsman & Aberg, 2008). Since climate warming is more pronounced in some areas than in others (IPPC, 2007), alternative morphs may become more abundant in different parts of the species range potentially promoting intraspecific geographic variation and possibly allopatric speciation (Hugall & Stuart-Fox, 2012). However, because climate warming

is particularly pronounced in regions that are usually cold (such as those at high latitude and altitude), global change should lead to an increase in environmental homogeneity at very large geographic scales. For this reason, we can predict that the degree of colour variation will decrease not only within populations but also among populations because morphs adapted to warm climates should be selected over larger geographic areas.

Conclusion

This review emphasizes the fact that climate warming can differentially affect different species but also that individuals from a given population are not all similarly affected. Climate warming can therefore be viewed as a new selective factor that can select some

specific variants or morphs that are more resilient to this new source of stress. A number of research programmes can be proposed (Box 1) as the study of melanin-based colouration can be viewed as one example among many other traits that may confer resistance to climate change.

Box 1

A number of studies can be proposed about the potential effect of climate change on melanin-based colouration:

- Assess whether the frequency of melanin-based colour morphs changes as a result of climate warming. This can be done using data from long-term monitoring of free-living populations or by measuring specimens preserved in natural history museums and collected over more than 1.5 century (e.g. Galeotti *et al.*, 2009).
- Assess whether the temporal change in the frequency of genes underlying variation in melanin-based colouration is associated with climate change.
- Measure the effect of climate change on the heritable and environmental components of melanin-based colouration. Mean colouration in a population can indeed change as a result of microevolution (change in the frequency of the genes underlying colouration) and/or because colouration is phenotypically plastic (e.g. skin colour in human is sensitive to UV radiation).
- Measure gene expression levels/phenoloxdase activity in relation to temperature or UV-radiation to estimate the potential effect of climate warming on melanogenesis.
- Determine whether species that declined in abundance or even disappeared due to climate change are differently coloured compared to species for which population sizes are stable or even increased.

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