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Response to Delhey *et al*.

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Predicting how organisms will respond to future climate change is a challenging task for biologists. In general, there are three ways to make such biotic predictions. First, by manipulating climatic conditions, such as temperature, humidity, etc. in laboratory experiments, it is possible to observe how adaptation or extinction occurs. Second, historical data can be synthesised using a meta-analysis to test for any relationship between biotic changes and climatic warming since the industrial revolution. Lastly, theoretical trends in biotic change can be associated with observed spatial variation (where, for example, climatic gradients result in spatial variations equivalent to climate changes).

Recently, Tian and Benton [1] proposed that biologists could use seven classic ecogeographic rules to predict potential biotic responses to future climatic warming. These ecogeographic rules are actually 'general trends' that have been determined based on empirical observations by many pioneering biologists since the middle of the 19th century, rather than 'rules' or 'laws' in a strict sense. We also presented some related studies with historical records to confirm the validity of the rules in certain animal groups and to determine their generality, especially with regard to the kinds of changes that rising temperatures might cause. One of these predictions was that the colours of birds, mammals and insects could become darker under future climatic warming, according to Gloger's rule.

However, in this issue of *Current Biology*, Delhey and colleagues [2] make the opposite prediction; they propose that species will generally become lighter, rather than darker, and that colour changes might vary geographically. Indeed, we agree that there is unlikely to be a universal trend in colour changes, which could vary geographically, intraspecifically, and interspecifically.

Indeed, close study of Gloger's rule shows that humidity plays a more important role than temperature in animal colouration: most darker morphs occur in wet environments rather than cold [3]. Based on climate modelling results, most parts of the southern hemisphere, middle America and the Mediterranean area will become hotter but drier, whilst other areas, especially at high latitudes, will experience significant increases in precipitation associated with profound temperature rises [4]. Thus, it would be best to predict that the colour of animals will be lighter in these hot, dry areas while darker colours can be expected in other areas. But we have to be aware that many of these hot, dry areas might become uninhabitable as temperatures rise too high, resulting perhaps in some colour adaptation at the assemblage level, as darker species go locally extinct and are replaced by lighter species [5,6], and if temperatures go too high then animals could well migrate or become extinct.

Gloger's rule was established from observations on birds and mammals [7], and it also works in certain ectothermic animals [3]. However, it is difficult to identify a simple trend in the colour changes of ectotherms like insects and reptiles with climate changes [8]. As Delhey *et al.* [2] mention, the thermal melanism hypothesis was originally proposed for insects. However, in synthetic datasets, darker morphs of insects occurred in very varied habitats: 3 out of 15 species showed a preference for darker colours in cold conditions [3]. As Delhey and colleagues show [2], we agree that the interaction of Gloger's rule and the thermal melanism hypothesis is complex.

As noted earlier [3,7], an intriguing aspect of Gloger's rule and the thermal melanism hypothesis is that melanin in the integument is involved in nearly all cases of tetrapod and insect colouration. Dark-coloured eumelanin increases with humidity, whereas brownish-ginger phaeomelanin increases with aridity, but both decrease at very low temperatures, phaeomelanin first, then eumelanin [3,7]. In tetrapods, the melanin may reside in scales and skin, or be encapsulated in melanosomes in feathers or hair of birds and mammals, and so it would be intriguing to determine differences between endotherms and ectotherms in their colour reactions to environmental change.

Delhey *et al.* [2] present several studies on colour changes where historical records show a trend towards colour lightening associated with recent global warming. Tian and Benton [1] also cited a few studies with historical observations on birds to support the opposite, darkening model. The debate probably cannot be resolved with the available data, and decisive evidence may be required from laboratory experiments on numerous animals, with temperature and humidity controlled.

In addition, as Delhey and colleagues demonstrated [2], the colour of organisms is often needed for camouflage. At colder latitudes and higher elevations, snow decreases with warming. Therefore, white and light-coloured morphs may reduce in these settings and darker morphs may increase to match soil or rock exposure, which are generally darker than snow.

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