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Comment

No evidence for warming climate theory of coat colour change in Soay sheep: a comment on Maloney *et al.*

Maloney *et al.* (2009) propose that the decline in frequency of dark Soay sheep on St Kilda, first reported by Gratten *et al.* (2008), is due to climate change. As supporting evidence, they report that the proportion of dark sheep is negatively correlated with average minimum winter temperature in the previous year. Although we accept that climate change is likely to have important effects on natural populations, we have serious doubts about Maloney *et al.*'s hypothesis, because it is inconsistent with key results from recent studies on Soay sheep, and because their statistical evidence appears to be overstated.

Maloney *et al.*'s main hypothesis is that dark coats absorb more solar radiation than light coats, and that this can offset the metabolic costs of thermoregulation in cold conditions. They argue that warming climate has reduced the selective advantage enjoyed by dark sheep in harsh winters, such that more light-coloured sheep are surviving to reproduce. The essential difficulty with this hypothesis is that it requires dark and light sheep to differ in lifetime fitness, but Gratten *et al.* (2008) showed that there was no evidence for this. In fact, the fitness difference we identified was between homozygous (genotype GG) and heterozygous (GT) dark sheep, which are phenotypically indistinguishable (because the dark G allele at *TYRP1*—the coat colour gene—is dominant). Therefore, explanations that invoke differential absorption of solar radiation are incompatible with the data. This finding, clearly stated in our paper, was the main reason why we did not consider direct selection on coat colour to be a plausible explanation for the decline in dark coats. Maloney *et al.* have overlooked this fact.

Maloney *et al.*'s alternative (or parallel) hypothesis is that the coat colour trend is explained by climate-related effects on body size, either because of a 'Bergmann's rule effect', whereby warming climate is attenuating the fitness advantage conferred by larger size, or because resource limitation associated with the expanding Soay population favours smaller sheep. These ideas are based on the observation that, dark sheep are larger, on average, than light-coloured sheep, and selection for larger size has weakened as the population has grown and the climate has warmed (Coulson *et al.* 2006). On first appearances, this is a more beguiling idea because there is evidence for a size decline in Soays, which appears to be driven by ecological processes associated with warming climate (Ozgul *et al.* 2009). However, this hypothesis is also poorly conceived for the following reasons. Coulson *et al.* (2006) showed that although selection for larger size has weakened, it is nonetheless consistently positive. Ozgul *et al.* (2009) also demonstrated that the contribution of selection to the body size trend is positive. Therefore, as large body size is genetically associated with dark coat colour (Gratten *et al.* 2008), there is no expectation that the frequency of light coats should have increased. In our view, selection on body size cannot explain the temporal trend in allele frequency at *TYRP1*.

Maloney *et al.*'s strongest statistical evidence for a role of climate change is a correlation between average winter minimum temperature and the frequency of dark coats. We have two misgivings with this analysis. First, the correlation is based on minimum temperatures from two winters (i.e. 18 months) prior to the August coat-colour frequency estimates. It is well established that it is the weather in the winter immediately preceding the period of peak mortality (February–April) that best explains the dynamics of this population (Coulson *et al.* 2001; Hallett *et al.* 2004). Using the same weather data as Maloney *et al.*, we found no evidence for a correlation between the proportion of dark coats in August and mean minimum temperature in the preceding (i.e. six months earlier) winter ($r^2 = 0.08$, $F_{1,18} = 1.66$, $p = 0.214$). Second, it could be argued that because coat-colour frequency is not independent from one year to the next (owing to overlapping generations and sampling of gametes), it would be more appropriate to examine the correlation between the annual *change* in frequency of dark coats and average minimum temperature in the intervening winter; again though, this relationship is not significant ($r^2 = 0.019$, $F_{1,16} = 0.307$, $p = 0.587$). The other correlation presented by Maloney *et al.*, involving annual average minimum temperature, has also been overstated: it is claimed that r^2, the coefficient of determination, equals 0.53, but in fact it is the product–moment correlation coefficient, r which equals -0.53 and therefore r^2 is only equal to 0.28.

Finally, not all temporal trends, of which there are many examples in natural populations, and which will often be correlated with ambient temperature, are necessarily driven by warming climate. For example, the Stornoway weather data used by Maloney *et al.* is more strongly correlated with UK human population size ($r^2 = 0.45$, $p < 0.001$) than it is with Soay sheep coat colour ($r^2 = 0.28$, $p = 0.049$); yet, nobody would suggest that temperature on the Outer Hebrides is responsible for UK population growth. Given the scrutiny that climate change science is currently under, attributing biological changes to global warming should surely require the highest standards of proof. In this case, there is

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no evidence that warming climate is responsible for the decline in frequency of dark Soay sheep on St Kilda.

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