Invited reply

A warming climate remains a plausible hypothesis for the decrease in dark Soay sheep

The decrease in the frequency of dark-coloured Soay sheep on the island of St Kilda between 1985 and 2005 is something of a conundrum because dark sheep tend to be larger than light-coloured sheep, and larger sheep have been reported to have a fitness advantage. In spite of the large size being a historic advantage, being large and dark coloured has been a disadvantage, between 1985 and 2005 at least. Colour in Soay sheep is conferred by a single quantitative trait locus (QTL) termed TYRP1, with the dark allele (G) being dominant to the light allele (T). The explanation for the conundrum offered by Gratten *et al.* (2008) is that, close to G allele of TYRP1, there is a QTL of unknown function that confers a negative fitness effect. Genes conferring large body size must also tend to be assorted with these loci. We can see how such a QTL would constrain an increase in the frequency of the G allele, but cannot see how it would explain the observed decrease in the frequency of the G allele; the decrease requires that the relative benefits/costs of at least one of the alleles of the genes for body size, colour or the unknown QTL have been altered between 1985 and 2005. As pointed out by Gratten *et al.* in their reply, the body size advantage has waned, but remained positive during this period.

Sheep that are both large and dark apparently either have lost a selective advantage, or have been placed at a selective disadvantage, over the period analysed. That shift may be related to an associated gene of unknown function, as hypothesized by Gratten *et al.* (2008), or it may be related to the biophysical effects of being both large and dark coloured on an island that is warming and has limited resources, as hypothesized by us, or to neither of our hypotheses. Our alternative hypothesis was based on the known energetic effects of colour and body size. If colour itself is not a factor, and the proposed linked QTL is a factor, then since 1985 the negative fitness effects of the linked QTL have become quantitatively more important than the fitness benefit ascribed to the large body size. What has changed since 1985? Temperature has done so, and statistically, the effects of the linked QTL, if that is the factor, must be correlated with the increasing temperature. We agree with the comment of Gratten *et al.*, of course, that correlation never proves causality,

fortunately for the future of the exploding UK population facing climate change.

To analyse the effect of environmental conditions on a trait requires knowing the probable timing of the environmental effects on the relative success of that trait. We considered two possibilities: (i) conditions during the winter before the August census affected coat colour proportion via the differential survival of pregnant ewes and their offspring, and (ii) conditions the year before affected the condition of the ewes and the likelihood of successful ovulation and conception, which occurs in November and therefore before the bulk of the winter immediately before the census. An important determinant of whether a ewe ovulates and conceives is her body condition and fat stores (Robinson 1996).

We tested both scenarios and found a stronger association with events earlier than those prevailing in the winter immediately before the census, as confirmed by Gratten *et al.* in their comment. We thank Gratten *et al.* for repeating our calculations, and discovering our error in reporting r rather than r^2 for one equation; the correlation remains significant and the principle of our argument unchanged. That the earlier events are a stronger predictor of the morphology changes accords with the hypothesis put forward by Ozgul *et al.* (2009). They found that the average size of the sheep has decreased over the same time period, mainly because smaller ewes are breeding more than previously and smaller ewes have smaller offspring, suggesting that it is the constraint of ewe's body condition and ability to breed that is driving the process. More of the smaller, light-coloured ewes breeding and contributing to the population would decrease the relative success of larger, darker sheep. If the condition to breed is in fact driving the process, then analysing the change in frequency of dark coats from August to August against conditions during the intervening winter will not be helpful, because the ewe's condition would have its effect at the November rut, before the intervening winter. The change in frequency of dark coats tends to be related to the winter conditions the year before ($r^2 = 0.23$, $F_{1,15} = 4.4$, $p = 0.05$).

If the association of coat colour with body size and environmental temperature turns out to be causative, and environmental temperature continues on the same upward trend, then a prediction is that the proportion of dark sheep will decrease to 50 per cent by 2054 (extrapolation of fig. 1 in Maloney *et al.* 2009). Of course, if the effect of the unknown QTL is causatively associated with environmental temperature, then testing that prediction will not help to determine which hypothesis is correct. Distinguishing the hypotheses, and proving causality, will require experimentation.

We agree that proof requires high standards. Before proof comes the hypothesis. The field of climate change science being under close scrutiny should not hinder the free exchange of ideas. We have presented a plausible hypothesis alternative to that of Gratten *et al.*, and their recent comments do not persuade us to retract that hypothesis. What we have presented is not a proof. It is an idea, just as a co-assorted QTL of unknown function is an idea.

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