

Climate change: is the dark Soay sheep endangered?

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It was recently reported that the proportion of dark-coloured Soay sheep (*Ovis aries*) in the Hebrides has decreased, despite the fact that dark sheep tend to be larger than lighter sheep, and there exists a selective advantage to large body size. It was concluded that an apparent genetic linkage between loci for the coat colour polymorphism and loci with antagonistic effects on body size explained the decrease. Those results explain why the proportion of dark animals is not increasing, but not why it is decreasing. Between 1985 and 2005 there was a significant increase in mean ambient temperature near the islands. We suggest that, while in the past a dark coat has offset the metabolic costs of thermoregulation by absorbing solar radiation, the selective advantage of a dark coat may be waning as the climate warms in the North Atlantic. In parallel, Bergman's rule may be operating, reducing the selective advantage of large body size in the cold. Either or both of these mechanisms can explain the decrease in the proportion of dark-coloured larger sheep in this population in which smaller (and light-coloured) sheep should be favoured by their lower gross energy demand. If environmental effects are the cause of the decline, then we can expect the proportion of dark-coloured Soay sheep to decrease further.

Keywords: thermoregulation; colour; selection

1. INTRODUCTION

When environmental change occurs such that a species' habitat becomes incompatible with its niche requirements, the species or a population within that species, may become locally extinct, may emigrate to a new suitable environment, may employ phenotypic plasticity or may adapt genotypically (Hughes 2000). The Soay sheep (*Ovis aries*) is a rare breed of domesticated sheep restricted to the islands of Soay and Hirta in the St. Kilda archipelago about 70 km west of the outer Hebrides, rendering migration impossible. They probably arrived there 4000 years ago with early human settlers, and have been monitored intensively since the 1950s (Pemberton *et al.* 1996).

One potential adaptive mechanism in mammals and birds responding to climate change is selection on coat colour (Dawson & Maloney 2008). While the fate of solar radiation impinging on an animal coat depends on more than colour (Cena & Monteith 1975), the

general finding is that dark-coloured animals absorb more solar radiation than do light-coloured animals (Walsberg *et al.* 1978). The heat from radiation absorption can offset the metabolic cost of thermoregulation in the cold, providing a potential selective advantage to dark-coloured individuals. Changes in climate therefore might alter the selective pressures on populations exhibiting variation in colour morphology. Coat colour in the Soay sheep is either dark brown or light tawny, with variation being controlled at a single autosomal locus for the tyrosine-related protein 1 (*TYRP1*; Gratten *et al.* 2008).

Food availability limits the population of St. Kilda sheep, resulting in regular population crashes on a 3- to 5-year cycle, when up to 60 per cent of the population can perish, with deaths predominantly in winter (Pemberton *et al.* 1996). Eighty per cent of ewes born in years of low sheep density, but less than 10 per cent of ewes born in years of high sheep density survive up to 5 years (Clutton-Brock & Pemberton 2004). One might expect animals that have reduced energy expenditure in colder winters, as might occur with a dark coat, to have a survival advantage during these winter die-offs. Indeed, in years of high density, when large winter die-off occurs, selection for the dark phenotype has been strongest (Moorcroft *et al.* 1996). That selection may have been strong enough to counteract another selection pressure, namely that favouring the survival of smaller sheep (which also tend to be light-coloured) that will have lower gross energy demand, and therefore should be favoured in a food-limited environment.

Gratten *et al.* (2008) recently presented data showing that the proportion of dark Soay sheep in the St. Kilda population decreased between 1985 and 2005 (figure 1a). They dismissed environmental effects on the frequency of the *TYRP1* gene that controls coat colour because 'it is difficult to envisage how *TYRP1* could directly influence size or fitness' (p. 320). However, because a dark coat may offset energy costs in the cold, we investigated if it is possible that the selective advantage of a dark coat is being attenuated as climate warms in the Northern Atlantic.

2. MATERIAL AND METHODS

We obtained climate data from the UK Meteorological Office. The nearest station to St. Kilda with historical records is at Stornaway airport (58°12'56" N, 6°19'52" W) on the Outer Hebrides isle of Lewis, approximately 80 km to the east of St. Kilda. The data consisted of the monthly means of daily minimum and maximum ambient temperatures. We averaged the 12 monthly values per year to arrive at the annual means of daily minimum and maximum ambient temperatures and used those values for analysis. Data on the proportion of dark sheep in the St. Kilda population were obtained from fig. 2a in Gratten *et al.* (2008). We then used correlation analysis to test if the decrease in proportion of dark sheep was associated with average temperature. Since surveys quantifying coat colour are conducted in August each year, with births occurring in April following mating in November, we also correlated the proportion of dark sheep in the population with the summer (July–August) and winter (January–February) mean temperatures of the previous year.

3. RESULTS

Linear regression analyses revealed a significant increase in both the minimum and maximum daily annual air temperatures at Stornaway during the 20 years between 1985 and 2005 (figure 1a; daily

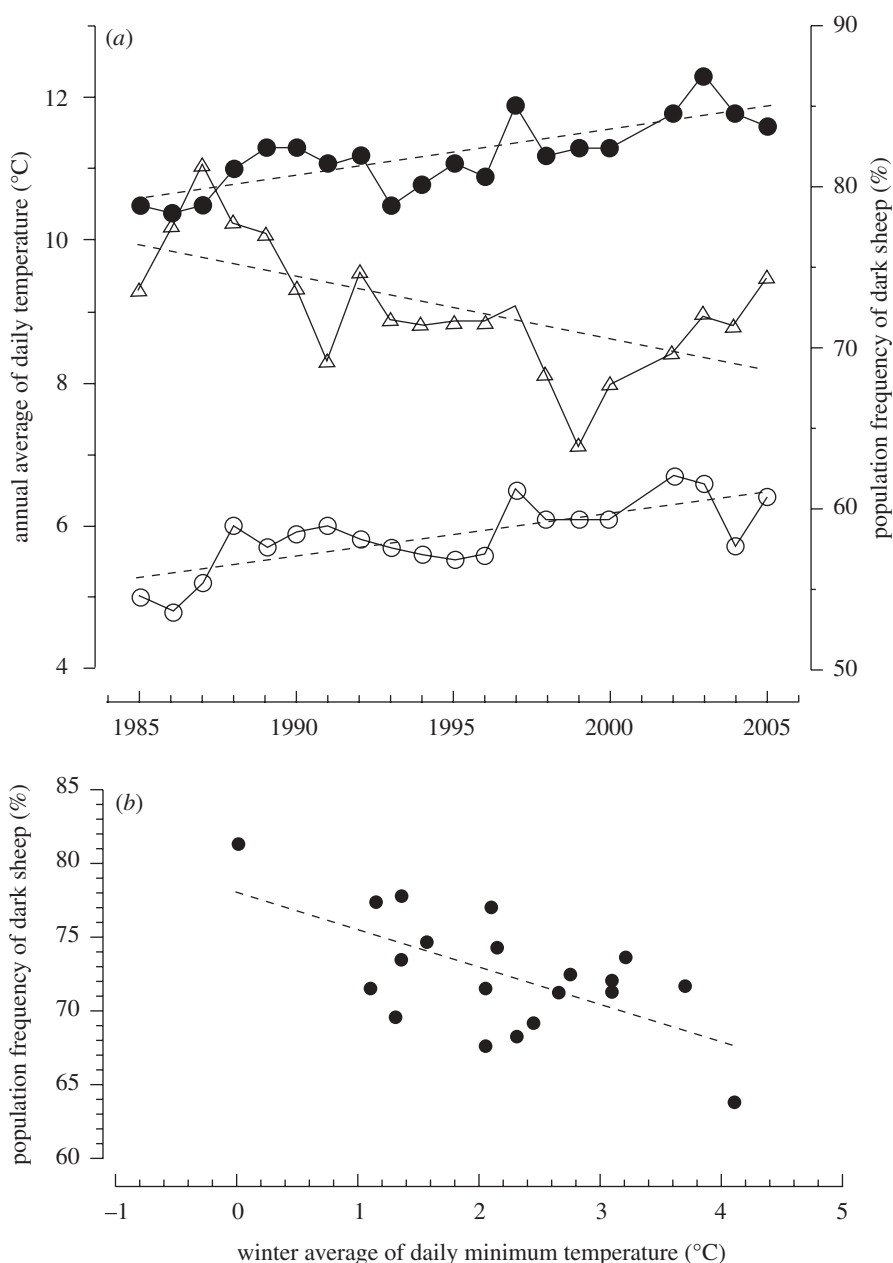


Figure 1. (a) Annual average of daily maximum (closed circles) and minimum (open circles) ambient temperature at Stornaway and the proportion of dark sheep in the St. Kilda population (open triangles, data read from fig. 2a in Gratten *et al.* 2008) for the years 1985 to 2005. (b) The proportion of dark sheep on St. Kilda in each year from 1985 to 2005 plotted against the average minimum ambient temperature during winter in the previous year.

maximum $R^2 = 0.55$, $F_{1,21} = 25.5$, $p < 10^{-4}$; daily minimum $R^2 = 0.53$, $F_{1,21} = 23.8$, $p < 10^{-4}$).

Between 1985 and 2005 there was a significant decrease in the frequency of dark-coloured sheep in the St. Kilda population, as reported by Gratten *et al.* (2008) (figure 1a, open triangles; $R^2 = 0.37$, $F_{1,18} = 9.5$, $p = 0.006$).

The correlation between annual mean of daily minimum temperature and the proportion of dark individuals in the population is significant ($R^2 = 0.53$, $F_{1,18} = 4.4$, $p = 0.049$). Dissecting the analysis to seasons, the proportion of dark sheep in the population was not related to conditions during the previous summer ($R^2 = 0.11$, $F_{1,18} = 2.3$, $p = 0.15$), but was significantly related to winter conditions during the previous year (figure 1b; $R^2 = 0.39$, $F_{1,18} = 11.7$, $p = 0.003$).

4. DISCUSSION

Our finding that the proportion of dark-coloured Soay sheep decreased over the past 20 years as ambient temperature increased over the past 20 years could be interpreted in several ways, the most parsimonious being that dark coloration has provided an energetic advantage in winter that is being attenuated in a warming climate. Our finding that coloration is associated with winter temperature the previous year suggests that it is the differential survival through winter to the subsequent breeding season and the breeding success the subsequent year that provides the mechanism for colour selection. With warming winters, more of the lighter phenotype is apparently surviving to reproduce.

While the fate of solar radiation incident onto a fur coat is complex (Cena & Monteith 1975; Walsberg

et al. 1978), a reduced energetic cost of homeothermy in dark-coloured animals, via their better access to solar heat, has often been reported (Hamilton & Heppner 1967; Heppner 1970; Dmi'el *et al.* 1980; Finch *et al.* 1980; Lustick *et al.* 1980). It was recently shown that the body temperature of black morphs of the African springbok (*Antidorcas marsupialis*) increased faster in the morning than those of the wild-type (brown) or white morphs. Further, the black morphs spent less time foraging in winter (Hetem *et al.* 2009), suggesting that augmented solar heat load due to the dark coloration contributed to energy balance. If the situation is similar in Soay sheep, there would be a selective advantage for the dark morph, over the light morph, in cold winters, and that is what has been found (Moorcroft *et al.* 1996). With the climate becoming warmer that advantage looks to be waning.

In this sheep population, dark-coloured sheep tend to be larger than the light-coloured sheep. The study performed by Gratten *et al.* (2008) was designed to explain why the proportion of dark Soay sheep was not increasing, despite an apparent selective advantage of large body size. They concluded that genes conferring reduced fitness occur close to the *TYRP1* gene for coat colour and constrain the expression of the body size advantage. However, the selection pressure for large body size decreased gradually from 1986 to 2003 (Coulson *et al.* 2006), paralleling the decrease in frequency of dark coloration.

The confounding of coat colour with body size provides an interesting conundrum. The general biological principle known as Bergmann's rule states that larger phenotypes have a selective advantage at higher latitude (Bergmann 1847) and in cooler climates (Meiri & Dayan 2003). The rule is formulated on the physical principle that surface area increases as only the two-third power of body mass. Thus, larger homeotherms have a smaller body surface area per unit mass, and are more resistant to heat loss, than are smaller homeotherms. A warming climate would attenuate the advantage that exists in the cold for larger homeotherms.

The body size of wood rats (*Neotoma* spp.) has fluctuated predictably with temperature over the past 40 000 years (Smith & Betancourt 2006), decreasing when the climate warmed. There has been a linear decrease in body mass in several species of passerine birds in England over the past 25 years that has been attributed to a warming climate (Yom-Tov *et al.* 2006). Recently, Teplitsky *et al.* (2008) concluded that red-billed gulls (*Larus novaehollandiae*) were getting smaller as the climate warms in New Zealand, not because of an effect of Bergmann's rule, but because resources were becoming more limited. The number of female Soay sheep on the island of Hirta fluctuates with the winter die off, but showed a significant increase from 1985 to 2002 (analysis of data from fig. 3.1b in Clutton-Brock *et al.* 2003). The warming climate at St. Kilda could have attenuated a selection pressure favouring larger Soay sheep, historically advantaged in the cold, via a Bergmann's rule effect, or perhaps augmented selection for smaller variants as resources have become more limited with the expanding population.

We have presented data supporting a parsimonious climatic mechanism for the recent decline in

proportion of dark-coloured Soay sheep of St. Kilda. The trend could be due to reduced selection for either darker colour or larger body size, or both, allowing an increase in the proportion of smaller and lighter-coloured variants.

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