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ORIGINAL ARTICLES

Thermal consequences of turning white in winter: a comparative study of red grouse *Lagopus lagopus scoticus* and Scandinavian willow grouse *L. l. lagopus*

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The red grouse *Lagopus lagopus scoticus* differs from the willow grouse *L. l. lagopus* of mainland Europe in not developing a white winter plumage. Previous studies have suggested that plumage colouration in birds can have important consequences for heat transfer through the feather layer. We examined the thermal consequences of plumage colouration in both subspecies of grouse. There were no differences in feather density, plumage depth or thermal resistance of the plumage between dark rufous Scottish and white Scandinavian grouse. In still air, heat gained from simulated solar radiation was greater through dark than through white plumage. However, in wind there was no difference in heat load between dark and white plumages. Our study suggests that there may be a trade-off between thermal and camouflage benefits of plumage colour for grouse in the wild.

Key words: grouse, Lagopus lagopus, plumage colouration, solar radiation, thermal properties

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The colour of a bird's plumage is generally considered to have evolved as an adaptation to its environment by providing camouflage from potential predators, or, conversely, maximum conspicuousness to make it more visible to others (Needham 1974, Baker & Parker 1979, Hill 1991, Fitzpatrick 1998, Cloudsley-Thompson 1999). Similarly, the colour patterns of plumage are usually explained as devices for both inter- and intra-specific signalling and social recognition (Krebs 1979, Walsberg 1982, Guilford & Stamp Dawkins 1991). There is little doubt that avian colouration does have important functions in crypsis and social signalling; however, this need not be the only fitness consequence of colouration, and several studies have indicated that there may be significant thermal implications of plumage colouration for a bird in a given environment (Hamilton & Heppner 1967, Lustick 1969, Cena & Monteith 1975, Walsberg et al. 1978, Walsberg 1983b, 1988, Louw 1993).

Colouration at the plumage surface influences the reflectivity to incoming short-wave solar radiation irrespective of the environment that the bird inhabits, as well as the proportion of long-wave radiative heat that penetrates into the feather layer (Hamilton & Heppner 1967, Lustick 1969, Cena & Monteith 1975, Walsberg et al. 1978, Lustick et al. 1980, Walsberg 1983b, 1988, 1992, Wolf & Walsberg 2000). The structure and optical properties of the plumage influence the amount of radiative heat that reaches skin level (Cena & Monteith 1975, Walsberg et al. 1978, Walsberg 1983b, 1992, Wolf & Walsberg 2000). This proportion of solar radiation has the capacity to influence thermal balance and metabolism (Lustick 1969, Ohmart & Lasiewski 1971, Wolf & Walsberg 1996), especially at ambient temperatures outwith the thermoneutral zone (Calder & King 1974, Walsberg 1983a, Wolf & Walsberg 1996, Wolf et al. 2000). In cold environments any radiative heat that increases heat load on a bird would reduce the energy cost of thermoregulation.

The willow grouse *Lagopus lagopus* provides a suitable system to study the thermal consequences of plumage colouration because in most of its range willow grouse have two contrasting plumage types: a white winter plumage that they moult into a dark cryptic plumage in summer. Willow grouse have a holarctic distribution with 19 subspecies currently recognised (del Hoyo et al. 1994). One of these subspecies, the red grouse *L. l. scoticus*, has plumage that remains dark reddish-brown throughout the winter (Wattel 1980, Hudson & Watson 1985). This is distinctive to this subspecies as only two other races retain some dark feathering throughout the winter (del Hoyo et al. 1994).

The aim of our study was to consider the thermal consequences of different colourations in willow grouse by comparing red grouse plumage with the Scandinavian willow grouse *L. l. lagopus* that moults into white plumage after the pre-winter seasonal moult. The European distributions of red grouse and willow grouse differ in longitude, as red grouse are found in Britain and Ireland, considerably further west and exposed to a milder, more maritime climate than the nominate *lagopus* subspecies. Willow grouse are generally found at more northerly latitudes, or in more continental areas such as in Scandinavia and northern Russia (Wattel 1980), regions that are often snow covered for longer periods of the year (Salomonsen 1972). Although the willow grouse inhabits more northern latitudes than the red grouse, both are found in open tundra or moorland areas (Wattel 1980, Hudson & Watson 1985, Korhonen 1989) and are subjected to low ambient temperatures and high wind speeds during the winter.

Material and methods

Plumage samples

Six red grouse (three male and three female) carcasses in winter plumage were obtained from Invercauld Estate near Braemar, Scotland (from an upland area of moorland, at 57°01'N, 3°24'W), in October 2000. Six willow grouse (sexes unknown) carcasses in white winter plumage were obtained from the province of Norrbotten in northern Sweden (from the mountains north of the Arctic Circle, at approximately 67°N, 18° E) in February 2001. The birds were stored at -20°C for analysis in 2002. Prior to removing plumage samples the total body mass (± 0.1 g) of each bird was measured. Rectangular sections of plumage with attached skin were obtained from the dorsal surface of each bird and deposits of subcutaneous fat and tissue were removed.

We performed three experiments. In the first experiment, we determined thermal resistance; in the second experiment, we determined heat gain from solar radiance; and in the third experiment, we measured the physical characteristics of plumage.

Determination of thermal resistance

In the first experiment, we determined the thermal resistance of plumage using a heated flat plate appa-

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ratus similar to the one used by Ward et al. (2001). It consisted of a flat copper plate (5.0 × 2.5 × 0.1 cm) electrically heated to body temperature (approximately 40°C). Each plumage sample was mounted on the heated plate with a thin layer of silicon heat transfer compound spread over the plate to ensure a good thermal contact. The feathers were gently fluffed up, and then laid in a natural position.

Heat transfer through the plumage was determined in still air and in moving air at a mean wind speed of 3.1 ms^{-1} (SE = 0.08) using a simple cylindrical wind tunnel (43 × 26 × 27 cm) controlled by a fan (Model No. 1061, Pico Ltd, Manchester, UK). This wind speed is representative of the wind speed experienced close to ground level in upland areas of Scotland (Page & Lebens 1986). A honeycomb of cylindrical baffles (with a diameter of 4-5 cm) close to the fan reduced turbulence. The heated plate with plumage was mounted at the mouth of the wind tunnel. Air speed was measured at the front of the plumage sample using a portable, hand-held anemometer (Kestrel 1000, Richard Paul Russell Ltd, Lymington, UK). A windshield (15 × 3 cm; 45° angle) was positioned at the front of the plumage sample to prevent flattening of the plumage at the leading edge of the sample.

Air temperature (± 0.1°C) and relative humidity (± 1%) were recorded in the centre of the wind tunnel with a thermo-hygrometer pen (RS Ltd, Corby, UK). Measurements were undertaken at an air temperature of 6.2°C (SE = 0.1) and a relative humidity of 83.3% (SE = 0.9). Thermocouples measured the temperature at the plate surface beneath the skin and air temperature adjacent to the plumage sample. Four thermocouples were positioned on the surface of the plumage using a light frame of wooden dowel rods that minimised disruption to air flow across the plumage surface. Thermocouple outputs were recorded with an eight-channel data logger (Model TC-08, PICO Technology, St Neots, UK), connected to a laptop computer.

Thermal resistance, r_c (s m^{-1}) of each plumage sample was determined by:

$$r_c = \frac{\rho C_p (T_s - T_c)}{G} \quad (1)$$

where G is sensible heat transfer through the plumage (W m^{-2}), ρC_p is the volumetric specific heat of air (1280 J m^{-3} K^{-1} at 5°C; Monteith & Unsworth 1990), T_s and T_c are the skin and plumage surface temperatures (°C), respectively.

All temperature measurements were made at steady state, therefore:

$$G = \frac{P}{A} = \frac{IV}{A} \quad (2)$$

where P is the power of the heater (W), A is surface area of the plate (0.00125 m^2), I is the current (amps), and V is the voltage (volts). The current was calculated from the measured value for voltage divided by the electrical resistance of the system (108.6 ohms).

Determination of heat gain from simulated solar radiation

In the second experiment, we mounted each plumage sample on top of an unheated flat copper plate (5 × 2.5 × 0.1 cm) embedded in a block of expanded polystyrene. A thin layer of silicon heat transfer compound ensured good thermal contact, and plumage was laid in a natural position as described above. A 500 W tungsten halogen lamp (wavelength = 400-750 nm; Type No: DFL 500, IQ (Europe) Ltd, Wetherby, UK) was mounted 50 cm above the plumage sample to simulate solar radiative heating of the plumage surface. Infrared heat produced by the lamp was removed using a filter consisting of a clear glass chamber containing 2 cm of water. Water was maintained at a temperature of 14.2°C (SE = 0.05) by circulating water from a temperature controlled water bath. This apparatus was positioned at the entrance to the wind tunnel (as described above) and measurements were carried out at an air temperature of 21.0°C (SE = 0.1) and a relative humidity of 35.1% (SE = 0.5) in still air and at a wind speed of 3.1 ms^{-1} (SE = 0.08).

The radiation balance above the plumage surface was determined at steady state on one red and one willow grouse sample using a net radiometer (Model Q7-1, Radiation & Energy Systems, Seattle, Washington, USA). At steady state the net radiation was 172.5 Wm^{-2} for red grouse and 165.6 Wm^{-2} for willow grouse plumage. The downward flux of short wave radiation was estimated to be 239 and 243 Wm^{-2} for red and willow grouse, respectively (see Methods, Appendix I and Table 1). These irradiances were comparable with short wave fluxes for Scotland in winter (Page & Lebens 1986).

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Table 1. Radiation fluxes (Wm^{-2}) for red and willow grouse plumage. $R_{net\ 1}$ is net radiation above the plumage surface, $R_{net\ 2}$ is total radiation measured with the lower hemisphere of the net radiometer covered in black cloth. L is the long-wave flux and S is the short-wave flux where u is the flux upwards from the surface, and d is the downward flux. $L_{u\ 1}$ and $L_{u\ 2}$ represent long-wave radiation fluxes, without and with black cloth covering the lower hemisphere of the net radiometer, respectively.

	$R_{net\ 1}$	$R_{net\ 2}$	$L_{u\ 1}$	$L_{u\ 2}$	L_d	S_u	S_d
Red grouse	172.5	186.3	476.4	422.5	369.5	-40.1	239.3
Willow grouse	165.6	186.3	447.7	424.3	367.5	-2.7	243.1

Temperature gradients through the plumage were measured with five thermocouples positioned on a 2 mm diameter wooden dowel rod at approximately equal intervals through the plumage. The temperatures at each thermocouple were measured at 1-minute intervals for 30 minutes, starting the moment the lamp was switched on. The heat that penetrated to skin level, H (Wm^{-2}), was calculated according to:

$$H = \frac{d\rho c\Delta T}{t} \quad (3)$$

where d is the depth in centimetres of the copper plate (in this case 0.1 cm), ρ is the density of copper (8.02 g cm^{-3}; Lide 1999), c is the specific heat of copper (0.385 J g^{-1} $°C^{-1}$; Lide 1999), ΔT is the change in plate temperature and t is the length of time (in seconds) over which the temperatures were recorded (in this case 30 minutes).

Physical characteristics of plumage

In the third experiment, we measured the depth of plumage (± 0.01 cm) by gently pushing a blunt needle vertically through the plumage until it rested on the skin surface. The mass of feathers per unit area of plumage was measured by cutting two circular samples of plumage from each specimen using a 1-cm diameter stainless steel borer. These samples were removed from the region where thermal resistance and solar heat gain measurements had been taken. The skin was removed from each sample, and the remaining feathers were placed inside filter paper and dried in an oven at 30°C for 18 hours. The total mass (± 0.01 mg) of each feather sample was recorded and an estimate of the mean number of feather layers overlying the skin of each bird was made by taking the total feather mass and dividing this by the mass of a single feather layer.

Statistical analysis was performed using the SPSS 8.0 statistical package for Windows (SPSS Inc., Illinois, USA). Where required, non-parametric tests were used to examine differences between species due to small sample sizes and lack of normality in distributions.

Results

Physical and thermal characteristics of plumage

Mean body mass of red grouse and willow grouse was 616.5 g (SE = 24.0) and 610.9 g (SE = 21.4), respectively, and there was no significant difference between the two subspecies (t test: t = 0.17 P = 0.86). The median feather mass per unit area of skin did not differ significantly between red grouse and willow grouse (Mann-Whitney U test: U = 17 P = 0.94; Table 2), nor did the mean mass of a single feather layer (U = 7 P = 0.09). The median number of feather layers was not significantly different when red grouse and willow grouse plumages were compared (U = 17 P = 0.94). Median plumage depth did not differ significantly between red grouse and willow grouse plumages (U = 15 P = 0.70).

Thermal resistance of red grouse and willow grouse plumage did not differ significantly, neither in still (U = 13, P = 0.48) nor in moving air (U = 8.0, P = 0.13)). However, the thermal resistance of both plumages showed a small increase in wind (Wilcoxon Rank test: Z = -2.2, P = 0.028 both cases; Table 3).

Heat gain from simulated solar radiation

In still air the temperature profiles through red and willow grouse plumages were similar with relatively high temperatures recorded within the plumage and with a decrease close to the skin (Fig. 1). Tempera-

Table 2. Physical characteristics expressed as median and range of red and willow grouse plumage (N = 6 in all cases).

	Depth (cm)		Number of feather layers		Feather mass/unit area ($g\ cm^{-2}$)	
	Median	Range	Median	Range	Median	Range
Red grouse	2.05	1.7-2.3	43.3	29.3-71.3	0.042	0.015-0.058
Willow grouse	2.10	2.0-2.6	42.3	32.4-49.6	0.039	0.035-0.054

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Table 3. Median and range of thermal resistances (sm^{-1}) recorded in red and willow grouse plumages in still air and in wind (3.1 ms^{-1}; N = 6 in all cases).

		Thermal resistance (sm^{-1})	Range
Red grouse	Still air	83.2	67.2 - 90.9
Willow grouse	Still air	84.2	79.4 - 97.2
Red grouse	Wind	89.8	82.9 - 103.4
Willow grouse	Wind	96.7	89.7 - 107.1

tures within red grouse plumage were greater than within willow grouse in still air, but in wind the temperatures recorded were similar. In still air, after 30 minutes there was a greater increase in plate temperature under red grouse than under white willow grouse plumage (U = 0 P = 0.04; Fig. 2). In wind, there was no significant difference in the temperature change after 30 minutes between the two plumage types (U = 8 P = 0.11; see Fig. 2).

In still air the median heat load beneath the plumage of red grouse (11.2 Wm^{-2}) was greater than the heat load below the white willow grouse plumage (6.4 Wm^{-2}; U = 0 P = 0.04; Fig. 3). However, in wind, there was no significant difference between median heat loads of red grouse (3.6 Wm^{-2}) and willow grouse (2.7 Wm^{-2}; U = 8 P = 0.11).

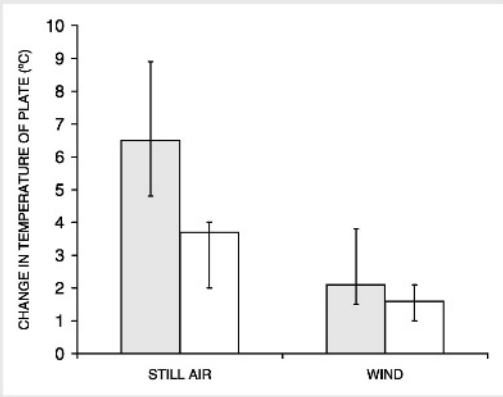


Figure 2. Median change in temperature beneath red (■) and willow (□) grouse plumages (N = 6 in both cases) following 30 minutes of simulated solar radiation in still air and in wind. The error bars show minimum and maximum values recorded.

Discussion

The aim of our study was to examine how differences in the colouration of *Lagopus lagopus* influenced their thermal balance. This species of grouse was chosen, as it was possible to compare two subspecies that had different plumage colours in winter. No differences in the depth, number of feather layers and feather mass/area or thermal resistance of their plumage were found. Being based on such a small sample size, our results lacked the statistical power to be able to make conclusions about differences in plumage between subspecies, given that different subspecies may also moult at different times of the year. However, for the purpose of our

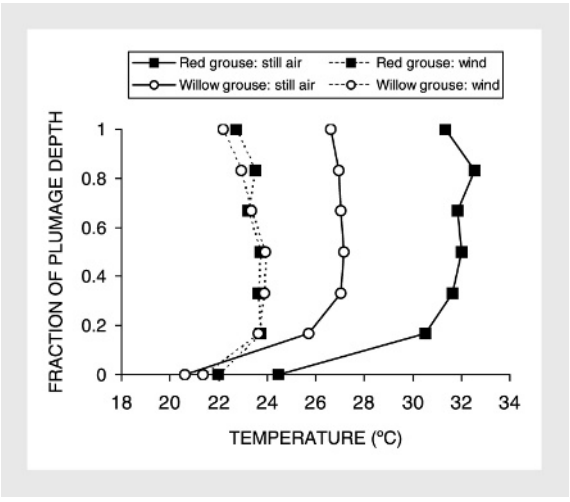


Figure 1. Temperature (in °C) profiles measured through red (■) and willow grouse (○) plumages (N = 6 in both cases) following 30 minutes of simulated solar radiation in still air (——) and in wind (----).

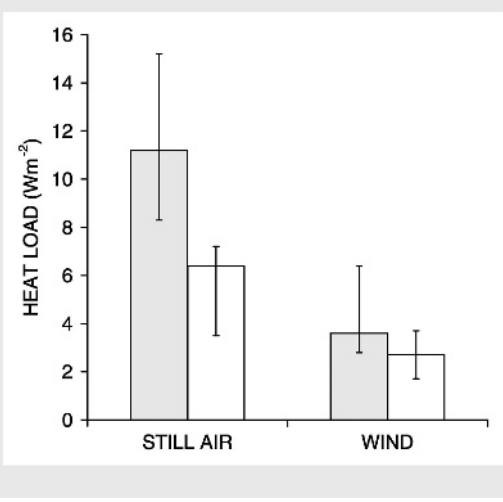


Figure 3. Median heat load (in Wm^{-2}) beneath red (■) and willow (□) grouse plumages (N = 6 in both cases) following 30 minutes of simulated solar radiation in still air and in wind. The error bars show minimum and maximum values recorded.

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study it was demonstrated that samples differed principally in colour and were similar in other physical properties that influence heat exchange. Although willow grouse inhabit a more northerly climate than red grouse (Wattel 1980), they frequently burrow into snow to keep warm (Korhonen 1989). Willow grouse may be exposed to colder ambient conditions, but behavioural adaptations such as selection of more favourable microclimates may negate the need for a more resistant plumage. Beasley & Ankney (1992) undertook a similar study of light-coloured (snow) and dark-coloured (blue) lesser snow geese *Chen caerulescens caerulescens* goslings. They also found no differences in the physical characteristics of plumage, but found a small difference in insulation (white insulated slightly better). Although the light coloured forms had slightly higher body temperatures, there was no overall difference in rate of thermogenesis. The lack of difference in heat loss reiterates that plumage colour has little impact upon long-wave emission or conductive and convective heat losses to the environment. Thus, it appears that differences in pigmentation of the feather elements do not influence heat transfer from the bird's body to the environment.

The lack of differences in feather density, plumage depth and resistance to heat loss from the body to the environment between red and willow grouse suggested that heat gained by short-wave radiation resulted from plumage colouration. In still air, red grouse plumage samples gained significantly greater heat loads as was predicted by Walsberg et al. (1978) for dark-coloured plumages. Under windless conditions and high levels of insolation, many dark-coloured avian species have been found to gain radiative heat (Howell & Bartholomew 1962, Hamilton & Heppner 1967, Ohmart & Lasiewski 1971, Marder 1973, Howell et al. 1974, Walsberg et al. 1978, Ellis 1980, Maloney & Dawson 1995). This increased heat load can allow a reduction in metabolic heat production (Lustick 1969, Ohmart & Lasiewski 1971, Calder & King 1974). Such dark-coloured species are likely to actively select more shaded microhabitats (see Howell & Bartholomew 1962, Walsberg 1977, Ellis 1980), except in habitats that lack shade, or where adults are incubating eggs, in which case behaviour such as panting and gular fluttering prevents hyperthermia (Howell & Bartholomew 1962, Howell et al. 1974, Ellis 1980, Ellis et al. 1995, Hochscheid et al. 2002). The energy expenditure of two colour morphs of the lesser snow goose was not different when birds were exposed to weak sunlight. It is possible that the two plumage colour morphs in this goose species did not differ to the same extent as the two colour morphs that were examined in our study, and the authors stated that conditions were 'rarely sunny' (Beasley & Ankney 1992). However, Ellis (1980) compared the responses to solar radiation of dark and white heron and egret species (Ardeidae) in Florida, where the birds must contend with high levels of insolation whilst incubating eggs and rearing young. These dark coloured birds gained more solar heat, were more likely to seek shade and had higher body temperatures than white birds, even under windy conditions (Ellis 1980). Hochscheid et al. (2002) also found that the dark plumage colouration of juvenile Cape gannets *Morus capensis* exposed to solar heat in South Africa resulted in greater heat loads than the white plumage of adults.

Using the relationship between resting metabolic rate of non-passerines (Aschoff & Pohl in Schmidt-Nielsen 1984) and the relationship between skin surface area and body size in birds (Walsberg & King 1978), the estimated resting metabolic rate of a 610 g grouse was calculated to be equivalent to a heat flux of 42 Wm^{-2} (214 kJ day^{-1}). In still air conditions, the heat load of 6-11.0 Wm^{-2} (15-26%) measured in our study therefore represents an important energy saving for a bird in an energetically demanding environment with difficult access to food.

In wind there was no significant difference in heat load at skin level between red and willow grouse plumages, and the heat gained at high wind speed was less than in still air. Solar heat gain was also found to decrease with increasing wind speed in the verdin *Auriparus flaviceps* (Wolf & Walsberg 1996) and the emu *Dromaius novaehollandiae* (Maloney & Dawson 1995). This suggests that neither subspecies gains a considerable thermal benefit in moderate winds. Both black and reddish-brown plumage colours result from melanin-based (see Burkhardt 1989), heavily pigmented feather elements that are likely to affect penetration and absorption of radiative heat similarly; certainly the contrast between these coloured feathers and the unpigmented white feathers in terms of transmissivity of heat is likely to be substantial (Finger 1995). Temperatures were higher in red grouse plumage in still air due to absorption of radiative heat at the plumage surface (Marder 1973, Walsberg et al. 1978), whereas the white plumage of willow grouse tended to reflect short-wave solar radiation at the surface in still

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air (Walsberg et al. 1978). The temperature profiles through grouse plumages were almost identical to those shown for pigeon plumages by Walsberg et al. (1978), and this finding may constitute a universal rule of heat transfer through plumages. Dark plumages absorb heat better than light ones in still air, but at higher wind speeds, the radiative heat reaching dark plumages is generally held at the surface and dissipated by forced convection from wind (Walsberg et al. 1978). This mechanism of prevention of excessive heat gain by dark plumages was also suggested for the desert inhabiting brown-necked raven *Corvus corax ruficollis* (Marder 1973) and grey gull *Larus modestus* (Howell et al. 1974). In species such as emus (Maloney & Dawson 1995) and the brown-necked raven (Marder 1973), potentially high heat loads from solar radiation are avoided as the majority of heat is absorbed close to the plumage surface where convective heat loss is facilitated (Marder 1973, Maloney & Dawson 1995). A further advantage of dark plumage is that melanin may be associated with minimising effects of parasites. Kose & Møller (1999) have shown that white parts of tail feathers lacking melanin were more often found to be the site of feather breakage due to feather lice than similar-sized melanised feathers in barn swallows *Hirundo rustica*.

Ecological implications

The rock ptarmigan *Lagopus mutus*, a closely related species found in both Scotland and northern Scandinavia, also moults into a predominantly white winter plumage (Snow & Perrins 1998). This species has been subjected to more detailed investigation of its plumage structure. The translucent white feathers contain small air spaces that are thought to increase insulation (Salomonsen 1972, Horsfall 1984, but see Dyck 1979). An additional function of the ptarmigan's white feathers is to facilitate the transfer of solar radiative heat through the plumage layer to heat the skin beneath (Dyck 1979). This has not been experimentally verified, but may be an additional benefit of white winter plumage colouration in some high-latitude and high-altitude species, including the willow grouse in our study.

It is usually thought that camouflage in a snowy environment is the main selective force operating on white winter colouration, despite the fact that red grouse are also frequently exposed to prolonged snow cover during the winter in their upland habitat (Hudson & Watson 1985). *Lagopus lagopus* is an important prey species in the diet of many raptors and mammalian predators (e.g. Smith & Willebrand 1999, Tornberg 2001, Thirgood et al. 2002), and white plumage in a snowy habitat reduces conspicuousness (Needham 1974, Walsberg et al. 1978, Grojean et al. 1980). This is particularly true for the willow grouse, which inhabits a snowy environment for much of the time when its plumage is white (Salomonsen 1972). Female willow grouse in white winter plumage forage predominantly upon buds growing above snow (Steen et al. 1992). As their plumage becomes darker they mainly forage on the snow margin with bare ground, and subsequently only on bare ground once they have moulted into the darkly pigmented summer plumage (Steen et al. 1992). The closely related male rock ptarmigan that maintains white plumage after the snow has melted deliberately soil their plumage, apparently to make it less conspicuous to potential predators (Montgomerie et al. 2001). The finding that differences in plumage colouration result in differences in heat gained from solar radiation suggests that there may be a trade-off between thermal and camouflage benefits of plumage colour for grouse in the wild.

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Appendix I

Determination of radiation fluxes

Net radiation balance of a surface is represented as:

$$R_{net\ 1} = (L_d + S_d) - (L_{u\ 1} + S_u) \qquad (4)$$

where $R_{net\ 1}$ is the net radiation (Wm^{-2}), L_d is the downward long-wave flux, S_d is the downward short-wave flux, $L_{u\ 1}$ is the upward long-wave flux, and S_u is the short-wave flux reflected upwards. L_d is calculated as follows:

$$L_d = e_d \sigma T_d^{\ 4} \qquad (5)$$

where e_d is the emissivity of the upper surface above the plumage and net radiometer (in this case, the surface of the glass filter plate), σ is the Stefan-Boltzmann constant, and T_d is the temperature (K) of the upper surface (in this case, the circulating water over the filter plate). In the current situation, e_d is the emissivity of glass (0.95), T_d for red grouse = 287.8 K, and T_d for willow grouse = 287.4 K. L_{u1} is calculated as follows:

$$L_{u1} = e_u \sigma T_u^{\ 4} \qquad (6)$$

where e_u is the emissivity of the lower surface beneath the net radiometer (in this case, the plumage surface), and T_u is the temperature (K) of the lower surface (in this case, the plumage surface). In the current situation, e_u is the emissivity of plumage, which is 0.98 (Hammel 1956), T_u for red grouse = 304.3 K, and T_u for willow grouse = 299.6 K.

To calculate S_u the lower hemisphere of the net radiometer was covered with black cloth so that it became a black body with an emissivity of 1, with short-wave radiation reflected from the lower surface eliminated. Measurements of net radiation, with this short-wave radiation eliminated, were taken for a further 30 minutes for each plumage, and calibrated in the same way as before. Net radiation levels under these conditions consist of:

$$R_{net\ 2} = (L_d + S_d) - L_{u2} \qquad (7)$$

where $R_{net\ 2}$ (Wm^{-2}) is the net radiation after elimination of short-wave radiation from the lower surface, and $L_{u\ 2}$ is calculated as for $L_{u\ 1}$, except that in this case T_u is the temperature of the black cloth surrounding the lower hemisphere of the net radiometer (this temperature corresponds to room temperature). In this equation, T_u for red grouse = 295.3 K, and T_u for willow grouse = 295.6 K. The short-wave radiation from the lower (plumage) surface, S_u, is then calculated as the difference between $R_{net\ 1}$ and $R_{net\ 2}$.

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List of symbols used in equations 1-7

r_c	thermal resistance of plumage	s m^{-1}
G	sensible heat transfer through plumage	W m^{-2}
ρC_p	volumetric specific heat of air	J m^{-3} K^{-1}
T_s	skin temperature	°C
T_c	surface temperature of plumage	°C
P	power of heater	W
A	surface area	m^2
I	current	amps
V	voltage	volts
H	heat flux at skin level	W m^{-2}
d	depth	m
ρ	density of copper	8.02 g cm^{-3}
c	specific heat capacity of copper	0.385 J g^{-1} °C-1
ΔT	change in plate temperature	°C
t	time	seconds

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