



Comparison of Microstructure of White Winter Fur and Brown Summer Fur of Some Arctic Mammals

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Abstract

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Several species of Arctic mammals have brown hair in the summer and molt into a white pelage in the winter. It is unknown whether characteristics other than color of the hair also change during the color transition between seasons. We borrowed guard hair samples from museums to represent summer and winter pelages of five species: *Alopex lagopus* (Arctic fox), *Lepus americanus* (snowshoe hare), *Lepus Arcticus* (Arctic hare), *Mustela erminea* (ermine) and *Mustela nivalis* (least weasel). Micro-structural differences exist between the brown and white hairs. In general, white winter hairs had larger upper shaft medullas comprising more air-filled cells and smaller lower shafts. These structural changes may function in conservation of heat or in increasing light reflection to whiten the fur and aid as camouflage. © 1997 Published by Elsevier Science Ltd on behalf of The Royal Swedish Academy of Sciences.

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Introduction

Guard hairs are composed of three layers. The shingle-like cells of the outer layer, or cuticle, seal off the interior of the hair. Pigments responsible for coloration are contained in the middle layer, or cortex, which may protrude into the innermost layer, or medulla, and make it appear to be pigmented. The medulla consists of a series of discrete air-filled cells, and air trapped within these cells can provide insulation against heat loss (Clement *et al.* 1981).

The transition from brown to white hairs means that pigments are absent, thus the animal may be better concealed in the winter snow. However, absence of pigments from the cortex likely alters the physical structure of the cortex and medulla of the hair, and may allow further microstructural adaption to the colder winter environment. This could be effected by altering the size of the medulla or changing the number of cell spaces contained in it. Hammel (1955) noted that heat may be transferred through fur by conduction along the individual fibers, by conduction through the air and vapor entrapped in the fur, by natural and forced convection of the air pervading the fur, by evaporation of water and by radiation.

Air trapped between the skin and the surface of the fur reduces the amount of heat lost to the environment by retaining a layer of warmed air to serve as insulation (Korhonen & Harri 1986; Reynolds 1993; Stangl *et al.* 1986; Tregear 1965). Change in the diameters of the upper and lower shaft between seasons might allow alteration of how heat is dissi-

pated or retained by the pelage during warmer versus colder seasons. In this paper, we evaluate microstructure of guard hairs to determine whether seasonal variation in size or structure exists.

Materials and methods

Five species were selected for analysis: *Mustela erminea*, *Mustela nivalis*, *Lepus americanus*, *Lepus Arcticus* and *Alopex lagopus*. Hair samples were borrowed from museum specimens to represent the summer and winter phases of these species (appendix A). Microscope slides were prepared by embedding the hairs in a mounting medium, covering them with a coverslip and placing lead weights on the coverslips to insure that the hairs laid flat during the drying of the media. Hairs of many species of mammals are oval in cross-section and would be measured inaccurately if not induced to lay flat.

About 12 dorsal guard hairs were mounted from each available individual to account for variation within and between specimens. Sample size reflects the number of specimens available from lending institutions for each species and season. Basal portions of some guard hairs were broken during removal from skins; therefore not all mounted hairs could be used in the study. This problem was most common in the hares and fox.

An ocular micrometer was used to obtain measurements of the following variables to the nearest micrometer: shaft width at the widest point (in the upper shaft, also known as the shield region), medulla width at this widest point of the shaft, shaft width near the base (just above the root tip) and medulla width near the base (same position as previous measurement). The ocular micrometer also was used as a reference scale for a linear count of the number of air cells (in 125- μ m distance) in the medulla of both the upper and lower (basal) shaft. These counts were focused at reference points for the width measurements described previously. An analysis of variance was performed on each of these variables to determine if micro-structural differences exist between the white winter hair and the brown summer hair.

Results

In *Mustela erminea*, the linear count of the number of air cells in the upper medulla and the width of the upper medulla were significantly higher in the winter hair (Table 1). In contrast, the lower shaft width was more narrow in the winter hair, although the medulla in the lower shaft did not change in size.

In *Mustela nivalis*, linear cell counts of the upper and lower medullas were significantly higher in the winter hairs. Winter hairs also had wider medullas in both the upper and lower shafts. These factors should increase the number of pockets of air trapped inside the hair.

Lepus Arcticus differed in all aspects considered except the linear cell count of the lower shaft medulla. The upper shaft width and the upper shaft medulla width were both larger in the winter hair. The widths of the lower shaft and the lower shaft medulla were both smaller in the winter hair. The smaller medulla is a consequence of the greatly decreased shaft size. The linear cell count of the upper shaft medulla was lower in the winter hair.

Lepus americanus differed in all aspects considered except the cell count of the lower shaft medulla. The upper shaft width and the upper shaft medulla width both increased in the winter hair. The linear cell count of the upper medulla was higher in the winter hair. The lower shaft width and the lower shaft medulla width were both smaller in winter hair. The smaller medulla is an artifact of the smaller shaft.

Alopex lagopus differed only in the lower shaft width, which was smaller in the winter hair.

Discussion

It would be beneficial for the winter hair to be more insulative than the summer hair, particularly in mammals exposed to more extreme environmental temperatures to which they must adapt. Heat loss to the environment can be reduced by air trapped between the hair and the skin, and increased hair density (Korhonen & Harri 1986; Reynolds 1993; Stangl *et al.* 1986; Tregear 1965). Wider medullas would trap more air within a shaft, and more cells might increase the insulative capability of the hair in a manner analogous to double-paned windows. Also, more cells could increase light scatter and make hair appear whiter.

Increasing the diameter of the upper shaft and decreasing that of the lower shaft would make the fur more pliable, therefore wind more likely glances over the fur rather than pushing it around. This would enhance the ability of the fur to retain air next to the skin, and thus form a barrier against the loss of heat held by the insulating air. Also, decreased lower shaft size could allow for the production of a more dense coat, by providing room for more underfur hairs (Reynolds 1993; Stangl *et al.* 1986).

Microstructural evaluation suggests that the species examined display a variety of strategies for winter adaptation. All species, except *A. lagopus*, increase the amount of air trapped within the upper shaft of the white hairs. In all but *L. Arcticus*, this was accomplished by increased width of the medulla and greater number of cells that comprise the medulla. The increase in the amount of air trapped in the winter guard hairs could result in hairs that are better insulators. *Mustela nivalis* also increased the width of the medulla and

Table 1. Significance levels of variables measured on winter and summer dorsal guard hairs. Arithmetic means are provided for comparisons within each species, standard deviations appear in parentheses below each mean

Species	Upper shaft width	Upper medulla width	Upper cell count	Lower shaft width	Lower medulla width	Lower cell count
<i>Mustela erminea</i>	NS	0.0001	0.0110	0.0001	NS	NS
Summer (n=104)	85.86 (11.6)	64.23 (10.5)	15.45 (1.9)	24.79 (5.0)	14.10 (4.2)	19.47 (2.0)
Winter (n=153)	84.58 (9.8)	69.39 (8.9)	16.07 (1.9)	22.04 (4.1)	14.31 (3.6)	19.44 (2.6)
<i>Mustela nivalis</i>	NS	0.0001	0.0001	NS	0.0104	0.0001
Summer (n=233)	77.31 (8.8)	57.55 (7.7)	16.67 (1.8)	23.06 (5.6)	11.98 (3.5)	18.09 (1.8)
Winter (n=51)	78.93 (5.7)	64.05 (5.5)	17.86 (2.1)	22.50 (2.8)	13.34 (2.1)	19.56 (1.9)
<i>Lepus Arcticus</i>	0.0003	0.0001	0.0438	0.0001	0.0001	NS
Summer (n=29)	70.81 (16.4)	64.20 (17.9)	20.62 (2.3)	21.22 (6.6)	15.87 (6.3)	14.69 (2.5)
Winter (n=28)	86.04 (13.5)	82.61 (13.6)	19.39 (2.1)	14.30 (2.9)	9.21 (2.3)	15.14 (2.3)
<i>Lepus americanus</i>	0.0483	0.0001	0.0001	0.0001	0.0001	NS
Summer (n=71)	85.04 (14.2)	72.50 (17.5)	14.35 (2.1)	31.06 (11.4)	20.81 (9.1)	14.71 (3.2)
Winter (n=67)	89.56 (12.3)	85.91 (11.8)	16.22 (2.0)	16.22 (10.4)	12.42 (8.5)	14.27 (2.3)
<i>Alopex lagopus</i>	NS	NS	NS	0.0266	NS	NS
Summer (n=25)	84.66 (10.1)	64.85 (9.0)	13.95 (2.3)	40.84 (13.7)	23.07 (5.3)	15.92 (1.7)
Winter (n=43)	79.73 (15.1)	63.47 (14.8)	15.02 (2.0)	34.34 (9.7)	21.76 (6.2)	15.95 (1.7)

number of air cells within the lower shaft of the white winter hairs.

The width of the upper shaft of white hairs was increased in both Leporids, which should allow for more trapped air within the hair coat. Further, the increased width makes a more spatulate upper shaft, especially when combined with the much reduced lower shaft of winter hairs. For summer hairs of *L. Arcticus*, the lower shaft width is 30% that of the upper shaft width, but reduces to only 16.6% of the upper shaft width in winter. A similar shaft shape change occurs in *L. americanus*, with 36.5% in summer and only 18.1% in winter. This appreciable structural reorganization may allow hairs to function against wind or snow in a manner similar to the way otter hairs respond to aquatic environments. Otter guard hairs have a broad spatulate upper shaft and a narrow base. When an otter enters the water, only the upper shaft bends and the distal portion of the fur is matted down, trapping air next to the skin. This keeps the animal dry and provides significant insulation in the form of a warmed air layer (Ling 1970). A similar phenomenon based on relative size of the upper and lower shaft occurs in fossorial animals. By forming a barrier against soiling and wetting, the underfur remains undisturbed and the insulative properties of the fur are not compromised (Stangl *et al.* 1986).

By decreasing the size of their lower shaft, all species, except *M. nivalis*, provide room for greater hair density. Reynolds (1993) observed increased fur density in the winter pelage of the collared lemming (*Dicrostonyx groenlandicus*), another mammal that molts into a white pelage in the winter. Stangl *et al.* (1986) noted the increase in wool underfur hairs by the initiation of previously dormant hair follicles. Another consequence of decreased lower shaft size is more room for greater amounts of air trapped between the skin and the fur. This air layer is correlated to fur thickness (the distance from the skin to the outside of the fur) and contributes to increased insulation (Chappell 1980a; Hammel 1955; Davis & Birkebak 1975). Spotila & Gates (1975) noted that a change in fur thickness (and consequently air layer size) that occurs at a small energetic cost has the same effect on reducing heat loss as a large change in body size that occurs at a much higher energetic cost. Structural changes in guard hairs for winter likely accommodate these adaptive changes for thermoregulation.

The differences in strategies among species are probably due to differences in efficiencies, extremities of the climate to which they are exposed, habitats occupied, or bioenergetics of the species. *Lepus Arcticus* and *L. americanus* exhibit very similar strategies, with the only difference occurring in the cell counts of the upper medullas. Because the upper shaft medulla of *L. Arcticus* is larger in winter (28.7% increase), the decrease in cell count can be explained by increased size of cells. In *L. americanus*, the increase in cell count corresponds to an increase in shaft width, and results in an increased number of air cells in a larger area.

Mustela erminea and *M. nivalis*, although closely related, exhibit different lower shaft adaptations in their winter pelages. In *M. erminea*, the lower shaft size is reduced from summer to winter by 12.5%, resulting in a more pliable hair that should function to exclude wind and snow. Although width of the lower shaft of *M. nivalis* did not change, the width of the medulla of the lower shaft increased by 11.4% in winter hairs and the number of air cells that comprise the

medulla increased by 8.1% in winter. *Mustela nivalis* is unique among the species examined, being the only one to increase the size of the lower shaft medulla or to change the number of air cells that comprise the lower medulla.

Casey & Casey (1979) and Chappell (1980b) suggested that these Mustelids do not change the thermal conductance of their pelages in winter. To survive the winter either heat production must increase or heat loss must decrease. Hart (1956) suggested that an increase in metabolism may occur, but its role in thermoregulation is questionable (Casey & Casey 1979). The thickness of the coat does not change (Casey & Casey 1979), but structural differences found between the summer and winter hairs suggest that the winter hair might be more insulative.

An alternative to the thermoregulatory explanation for structural change is that of increased whiteness and therefore camouflage. Winter plumage is white in an Arctic bird, the Rock Ptarmigan (*Lagopus mutus*). Although the barbules of summer feathers are solid, the white winter feathers have air-filled barbules. Dyck (1979) found that the air spaces increase light reflection and add to the whiteness, aiding in camouflage in snow-covered habitats. The linear cell count near the base of guard hairs did not vary significantly in most species of mammals examined, yet upper shaft cell counts (and width of the upper medulla) tended to increase (Table 1). Because the upper shaft is more exposed to the environment, these observations are consistent with the hypothesis that increased numbers of air spaces could serve to whiten the winter fur for camouflage.

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Appendix I: Specimens Examined. Museum abbreviations follow Yates *et al.* (1987).

Mustela erminea Linnaeus, 1758—**CANADA: Manitoba:** Cedar Lake (ROM26904); Churchill (ROM27489); **Northwest Territories:** Eskimo Point (ROM10003); Mackenzie, Eskimo Lakes, 125 miles E of Aklavik (ROM25692); **Ontario:** Brant (ROM32184); Cochrane, Fort Albany (ROM15865); **USA: ALASKA:** Fairbanks area (UAM8069); (UAM uncat); **IOWA:** *Sioux Co.:* Ireton (UMMZ56608); **MICHIGAN:** *Antrim Co.:* Alden (MSU4654); *Delta Co.:* 1 mile S, 2 miles E Garden (MSU5907); *Iron Co.:* 7 miles S Crystal Falls (MSU5910); 5 1/4 miles N 7/8 mile W Amasa (MSU7886); *Kalamazoo Co.:* Kellogg Bird Sanctuary (MSU2159); *Schoolcraft Co.:* 9 miles ENE Hiawatha (MSU21032); **MINNESOTA:** *Beltrami Co.:* Grygla (UMMZ83611).

Mustela nivalis Linnaeus, 1766—**CANADA: Manitoba:** Gypsumville (ROM34.7.18.4); Oak Lake (ROM80117); **Ontario:** Kenora, Bearskin Lake (ROM26430); **DENMARK:** Glydensten (MSU2322); **UNITED KINGDOM:** *England:* Hunts, Selborne (ROM14417); Oxfordshire, Thame (ROM97330); **USA: ALASKA:** Cape Thompson (MSU13082); **INDIANA:** *Wabash Co.:* 8 km E Manchester (ROM77630); **MICHIGAN:** *Barry Co.:* Johnston Township (MSU5565); *Clinton Co.:* (MSU4462); *Eaton Co.:* Diamondale (MSU12389); *Gratiot Co.:* Ithaca (MSU2220); Ithaca (MSU9979); *Hillsdale Co.:* 5 miles N Hillsdale (MSU21193); *Ingham Co.:* Lansing (MSU5091); 1 mile SE Lansing (MSU6045); East Lansing: MSU Campus: (MSU22215), (MSU28942), (MSU16432), (MSU4688);

Wheatfield Township, Williamston 1/2 mile S Grand River on Barkley Road (MSU34814); *Jackson Co.:* Jackson (MSU12390); *Sanilac Co.:* 5 miles W Sandusky (MSU14888); *Washtenaw Co.:* 2 miles E Ann Arbor (MSU5413); **MINNESOTA:** *Winona Co.:* 2 miles S Winona (MSU6048).

Lepus arcticus Ross, 1819—**CANADA: Newfoundland:** 25 miles N LaPoile Bay (ROM63113); **Northwest Territories:** Bellot Strait (ROM19584); Casba River between Artillery Lake and Casba Lake (UMMZ57278); Numalla, between Churchill and Eskimo Point (ROM19628); Pangnirtung, Baffin Land (ROM28.7.12.4); **Ontario:** Kenora, Fort Severn (ROM40432); **GREENLAND:** Etah (MSU6144).

Lepus americanus Erxleben, 1777—**CANADA: Ontario:** York, Mount Albert (ROM10017); Victoria, Bobcaygeon (ROM10044); Thunder Bay: (ROM19858), (ROM36.2.27.4); **Quebec:** Lake Edward (ROM12053); Saguenay, Harrington Harbour (ROM26.5.4.6); **USA: ALASKA:** College, 1 1/2 miles from UAF on Ballaine Road (UAM6076); **MAINE:** *Franklin Co.:* Wilton (MSU1668); **MICHIGAN:** *Alcona Co.:* (MSU24332); *Alger Co.:* (MSU10630); 2 miles NE Shingleton (MSU5391, MSU5392); *Benzie Co.:* S Manitou Island, 1/2 mile N old lighthouse (MSU21907, MSU21908); *Charlevoix Co.:* Garden Island: (MSU7553), (MSU8436); Beaver Island, 5 miles S St. James (MSU7654); *Iosca Co.:* 2.5 miles W Oscoda (MSU8528), (MSU8688); *Iron Co.:* 12 miles S Crystal Falls (MSU5972); 7 miles S Crystal Falls (MSU7795); 1 3/8 miles E of Amasa (MSU7889); **NEVADA:** *Washoe Co.:* 350 yds NE junction of Nevada State Line and Lake Tahoe (MSU105); **WYOMING:** *Sublette Co.:* Clear Creek Canyon (MSU5544).

Alopex lagopus (Linnaeus, 1758)—**CANADA: Northwest Territories:** Keewatin District, NW section of Newltn Lake (MSU26281, ROM18904); Mackenzie: 100 miles NE of Aklavik (ROM25247); 175 miles NE of Alkavik (ROM25693); **Ontario:** Kenora, within 50 miles of Fort Severn (ROM25601); **USA: ALASKA:** Drift Station Bravo 40 (LACM57009); 48–50 miles E of Barrow (UAM4602); St. Matthew Island (UAM3499); **MICHIGAN:** Detroit Zoo (UMMZ165969).