

Fur color diversity in marmots

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Fur color that differs from the typical shades of brown and gray occurs in eight species of marmots. Albinism generally is rare whereas melanism is more common. Melanism may persist in some populations at low frequencies averaging 16.1% in *M. monax* and in *M. flaviventris* for as long as 80 years. White (not albino) and “bluish” marmots generally are rare, but a population of white *M. marmota* persisted for at least 10 years. Four species are characterized as having pelages of “extreme colors”; *M. caudata*, red; *M. vancouverensis*, dark brown; *M. caligata*, white; *M. baibacina*, gray. Fur is involved in heat transfer between the marmot and its environment. Heat transfer depends on fur structure (fur depth, hair length, density, and diameter), on fur spectral properties (absorptivity, reflectivity), and on the thermal environment (temperature, wind speed, radiation). Heat transfer is highly sensitive to solar radiation. Metabolic rates calculated from the fur model corresponded closely with measured values at ambient temperatures ≤ 20 °C. Solar radiation can either provide heat that could reduce metabolism or thermally stress a marmot. *M. flaviventris* orients towards the sun when solar radiation is low and reduces exposure when it is high. Light fur reduces and dark fur color increases absorptivity. I hypothesize that fur color functions primarily in heat transfer. This hypothesis is supported by the occurrence of light-colored *M. flaviventris*, *M. caudata aurea*, and *M. himalayana* in warmer environments. Experiments to test this hypothesis are suggested.

KEY WORDS: marmots, fur color, albinism, melanism, heat transfer, fur model, solar radiation.

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INTRODUCTION

The color of marmot species varies, but shades of brown and gray, often with streaks or splotches of white, black, reddish brown or yellow, predominate on the dorsal surface (Fig. 1a-c) (ARMITAGE 2003a). This diversity of color is produced by two pigments, yellow pheomelanin and black eumelanin (CANDILLE et al. 2007). Among marmot species, marmot fur color varies from white (*Marmota caligata*, the hoary marmot) to dark brown (*M. vancouverensis*, the Vancouver Island marmot). Switching between the synthesis of eumelanin and pheomelanin, mutations in their genes, and the possible role of other genes probably accounts for the ranges in marmot fur color among species of marmots and for unusual or extreme colors, such as albinism and melanism.

Fur plays a critical role in heat transfer between an animal and its environment (COSSINS & BOWLER 1987). Marmots may gain or lose heat through their pelage, especially through the dorsal surface that is more exposed to solar radiation and wind. Fur color affects reflectance and absorption of short range radiation, mostly in the visible range (LOUW 1993). In general, light color increases reflection and dark color increases absorption.

This role of fur color raises questions about the diversity of fur color in marmots. All marmots are diurnal and the daily activity is bimodal during the hot summer months (ARMITAGE 1962, BRONSON 1962, TURK & ARNOLD 1988). The decrease in midday activity is less in some high elevation species where air temperatures are cooler (BIBIKOW 1996). Marmot physiology is highly adaptive for coping with a low temperature environment and characterized by mechanisms for conserving energy (ARMITAGE 1998, 2008). Thus, one might predict that the fur color of marmots would be related to thermoregulation. If so, why is there such a diversity of fur color among marmot species? This paper explores both intraspecific and interspecific color variation in marmots and its possible adaptive significance.

COLOR EXTREMES

I identified four fur colors as extreme variants: albino, white, "blue", and melanistic. One or more of these were reported for eight species (Table 1). I observed bluish *M. bobak* near Veiliky Borouk in 1990; this color phase and black and dark brown marmots average 7 to 11% of the population in the Kharkov region (MASHKIN 1997) and often occur in homogenous populations. Melanistic bobacs are rarely observed in the Lugansk and Voronezh regions (MASHKIN 1997).

Melanism and albinism were reported in more species than the other color morphs (Table 1). The only known albino *M. flaviventris* (Fig. 1d) was observed by Frank F. Drumm Jr near Jewell Lake adjacent to the Glacier Creek Trail at 10,231 ft in Rocky Mountain National park on June 25, 2006 (F. DRUMM pers. com.). The adult of unknown sex was completely white with pink eyes and appeared to be partially blind (Fig. 1d). The many abrasions, scabs

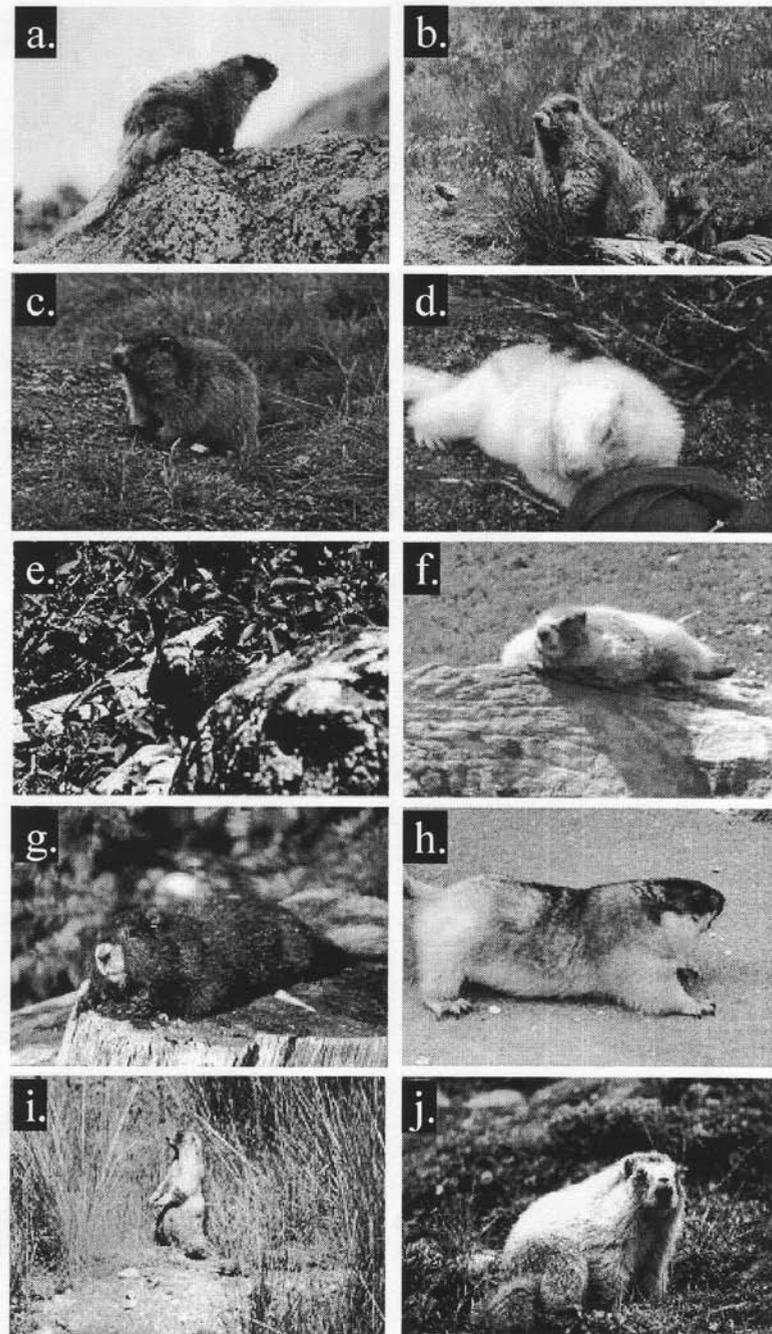


Fig. 1. — Fur color of marmots. All photographs by the author (except d. from Frank Drumm): a. Typical yellow-bellied marmot, *M. flaviventris*; b. Typical Olympic marmot, *M. olympus*; c. Typical alpine marmot, *M. marmota*; d. Albino yellow-bellied marmot; e. Melanistic yellow-bellied marmot; f. Light-colored yellow-bellied marmot; g. Vancouver Island Marmot, *M. vancouverensis*; h. The red or long-tailed marmot, *M. caudata*; i. The gray marmot, *M. baibacina*; j. The hoary marmot, *M. caligata*.

Table 1.
Color extremes in marmots (*Marmota*).

Species	Albinism	White	Blue	Melanism	References
<i>flaviventris</i>	X			X	1, 2
<i>caligata</i>				X	3
<i>monax</i>	X	X		X	4, 5, 6, 7, 8, 9, 10, 11, 12, 13
<i>marmota</i>	X	X		X	14, 15, 16
<i>caudata</i>	X				17
<i>baibacina</i>	X	X		X	14, 18
<i>bobak</i>	X	X	X	X	14, 19, 20, 21
<i>camtschatica</i>				X	14

References: ¹ F. DRUMM pers. com., ² ARMITAGE 1961, ³ HOWELL 1915, ⁴ C. MAHER pers. com., ⁵ HOFFMEISTER 1989, ⁶ SETON 1929, ⁷ HAMILTON & WHITAKER 1979, ⁸ GROSVENOR 1960, ⁹ BANFIELD 1974, ¹⁰ MUMFORD & WHITAKER 1982, ¹¹ HAZARD 1982, ¹² JACKSON 1961, ¹³ ANDERSON 1934, ¹⁴ BIBIKOW 1996, ¹⁵ VEVEY et al. 1992, ¹⁶ GOURREAU 2000, ¹⁷ ISAKOV 1987, ¹⁸ BRANDLER 2003, ¹⁹ ARMITAGE pers. obs., ²⁰ MASHKIN 1997, ²¹ TOKARSKII 1997.

and scars around the nose suggest the marmot had been involved in an agnostic conflict, but it appeared healthy otherwise.

Albinism likely is rare in other species of marmots, but its frequency may vary locally. Reports of albinism were frequent in the Kosh-Agach population of *M. baibacina* (BRANDLER 2003), but no albino was found among 12,000 marmots in eastern Tien Shan (BIBIKOW 1996). Albinism occurred in *M. marmota* in Valle D'Aosta, Italy. First observations dated back to 1950-1955 and a maximum number of 6 or 7 occurred in two different families; 4 were present in the area in 1991 (VEVEY et al. 1992).

Reports on the frequency of albinism in the woodchuck, *M. monax*, are contradictory. Albinos were reported as common (SETON 1929), as not uncommon in Canada (BANFIELD 1974), as "by no means rare" in the eastern United States (HAMILTON & WHITAKER 1979), as not uncommon in Illinois (HOFFMEISTER 1989), and as rarely occurring in Wisconsin (JACKSON 1961). One obvious albino was recorded from Indiana (MUMFORD & WHITAKER 1982). This variation in the frequency of albinism may reflect geographic variation in the frequency of mutations producing albinism or may be a reflection of what various authors mean by rare or common. Because albinism is associated with various physiological defects, such as impaired vision, it would not be expected to persist in a population and occur only as a consequence of the pairing of individuals each of whom carries a recessive gene for that trait.

By contrast, melanism may be so common that it is considered a normal coat color variant in *M. monax* (e.g. GROSVENOR 1960) and frequently is reported as common (SETON 1929, HAMILTON & WHITAKER 1979). Woodchucks at a research site in Maine have a mixture of color phases categorized as a light brown, dark not melanistic, and melanistic (C. MAHER pers. com.). In the past 10 years, the proportion of melanistic individuals varied from 6 to 29% and averaged 16.1%. *Marmota caligata vigilis* on the west shore of Glacier Bay, Alaska, is characterized by a tendency toward melanism (HOWELL 1915).

A melanistic population of yellow-bellied marmots (Fig. 1e), *M. flaviventris*, has persisted for at least 80 years since the report of its presence (FRYXELL 1928). A survey of this population in the Teton Mountains, Wyoming, reported that 23% of the 111 marmots of all ages were melanistic (ARMITAGE 1961). Surveys of the population in 1994 and 1995 reported 15.5 and 16.7% melanistic individuals, respectively (MONTOPOLI et al. 1996). Although these percentages are significantly lower than reported in 1961, it does not mean that melanistic individuals are in a long-term decline but does suggest that, similar to woodchucks in Maine, there can be considerable variation among years in the frequency of melanism.

The relatively high frequency of melanism in some populations raises the question of whether melanism has a fitness advantage over normal coloration. In the Teton yellow-bellied marmots, differential survival rates occurred among age groups for marmots categorized as melanistic, normal, or other (fur coloration that was neither melanistic or the normal brown). In both 1994 and 1995, there was a greater proportion of melanistic juveniles than of adults and a greater proportion of adults with normal fur color. The proportion of the "other" category did not differ among age classes (MONTOPOLI et al. 1996). In 1995, the proportion of adults that was melanistic was significantly lower than that of subadults and juveniles and in 1994, the proportion of melanistic subadults exceeded that of adults and juveniles. Overall, there appeared to be a survival advantage for melanistic individuals in younger age classes which apparently was reversed in adults. There were small but significant differences in pelage and age groupings between the 2 years. This study and that of Maher suggest that there are both costs and benefits to melanism in woodchucks and yellow-bellied marmots and that the function of these color morphs should be further investigated.

OTHER COLOR VARIATIONS

White (not albino) marmots were reported to occur in four species (Table 1). Of particular interest are two populations of white alpine marmots, *M. marmota*; one population near Courmayeur in Aosta Valley in Italy and the other in the National Park of the Ecrins in France. The Courmayeur population was discovered in about 1990 and the colony in Ecrins, in 1999 (GOURREAU 2000). The Courmayeur population apparently is decreasing in number, but the reason is unknown. The gene W/KIT was the probable cause of the color; this gene can allow for some dark color to appear, such as on the head and tail.

Although the Olympic marmot, *M. olympus*, is described as being brownish drab (HOWELL 1915), some individuals are light, tan, or almost white (S. GRIFFIN pers. com.). Early in the active season, Olympic marmots may be bi-colored with very dark, even melanistic fur anteriorly and lighter, reddish-brown fur posteriorly. By late summer these marmots may be uniformly light brown. This pattern could be a consequence of differential gene expression, the process of molting, or bleaching by sunlight.

Considerable color variation occurs in yellow-bellied marmots in the Upper East River Valley in Colorado. Fur color varies from very dark, almost

black individuals, to light, yellowish-appearing marmots (Fig. 1f). These variations have not been systematically recorded, but the dark and yellowish forms probably occur in a frequency no greater than the 11.6% reported for the "other" category of the Teton yellow-bellied marmots (MONTOPOLI et al. 1996).

The diversity and frequency of fur color morphs in marmots suggest that there is considerable genetic diversity on which natural selection could act to produce adaptive fur color in marmots. In the next section, I will consider several species of marmots whose typical fur color would be considered extreme variants in other marmot species.

SPECIES CHARACTERIZED BY EXTREME FUR COLOR

The Vancouver Island marmot, *M. vancouverensis* (Fig. 1g), is uniformly dark brown (HOWELL 1915, ARMITAGE 2003a). No color variations have been reported for this species, apparently the dark brown color became fixed in this small, island population (NAGORSEN 1987).

M. caudata, the long-tailed marmot, is also known, for good reason, as the red marmot (Fig. 1h). Some populations of this species are considerably lighter and the large subspecies, *M. c. aurea*, is known as the golden marmot. This species is adapted to general aridity and those that live in the drier climate are paler in coloration (DAVYDOV 1991). Interestingly, *M. f. avara*, that lives in semi-arid, lower elevations in eastern Washington and Oregon (COUCH 1930) is known as the pallid yellow-bellied marmot whose colors are paler and the upperparts are overlaid with buff (HOWELL 1915). Similarly, light-colored *M. himalayana* occurred in a semi-desert environment (KHOLODNA 2008).

Both *M. baibacina* (Fig. 1i) and *M. caligata* (Fig. 1j) are light-colored, which is expressed in their common names, the gray marmot and the hoary marmot. The degree of whiteness varies among subspecies of the hoary marmot (HOWELL 1915). *M. c. caligata* and *M. c. canadensis* are characterized as having the general tone of the upperparts as white. *M. c. nivaria* is the whitest of the group whereas *M. c. oxytona* and *M. c. okanagana* are somewhat darker.

Among populations of *M. baibacina*, those living in xerophytic areas are more lightly-colored whereas those in subalpine meadows within or adjacent to the spruce belt are much darker (OGNEV 1947).

FUNCTIONS OF FUR COLOR

The presence of intraspecific and interspecific variations in fur color raises the question of what is the function or functions of fur color in marmots. In general, color in animals functions in crypsis, mate attraction, and thermoregulation (LOUW 1993).

The importance of fur color in crypsis is difficult to evaluate without extensive experimentation with different color morphs. Marmots are not an animal of choice for such experiments. However, some insight into the impor-

tance of crypsis can be gained from considering marmot activity and habitat. To my eyes, a hoary marmot lying on a rock is more conspicuous than a yellow-bellied marmot doing likewise. But there is no evidence that a hoary marmot is more vulnerable to predation. Marmots are inconspicuous when foraging in high vegetation but are easily seen when the vegetation is sparse or low. The brown tones of marmot fur seem to provide some crypsis in rocky areas, but cannot account for the fur color in *M. caudata*, *M. caligata*, and *M. baibacina*. It is likely that marmots rely more on detecting predators than hiding from them, except when in their burrows.

There is no indication that fur color functions in mate attraction in marmots. During mating by yellow-bellied marmots, only one male may be present, thus restricting any female choice (ARMITAGE 1965). In the alpine marmot, the frequency of extrapair paternity is influenced by genetic similarity and females prefer as extrapair mates transient males in search of a territory (COHAS et al. 2008). The mechanism of choice is unknown, but it seems that familiarity could be important as females prefer males with whom they are least likely to be familiar. It seems improbable that general fur color would be important in female choice, although streaks or patches of different colors or shades could be important.

The rejection of crypsis and mate attraction as major factors accounting for fur color diversity leaves thermoregulation as the presumed important factor. As I will discuss in the following sections, fur color may be critical in heat transfer through fur and thus, in thermoregulation. Whatever roles, if any, crypsis and mate choice have in the diversity of fur color, those roles must be integrated with the unavoidable function of heat transfer.

HEAT TRANSFER THROUGH FUR

The discussion that follows is almost entirely based on the work of MELCHER (1987). Heat transfer through fur depends on fur structure (fur depth, hair length, hair diameter, hair density), on the fur spectral properties (absorptivity and reflectivity), and on the thermal environment. Important environment conditions are temperature, wind speed, and the radiant environment. Sensitivity analyses of the fur model used to quantify heat transfer through marmot fur revealed that heat loss was most sensitive to changes in solar radiation. Heat transfer was far less sensitive to changes in ambient temperature or wind velocity.

Metabolic rates calculated from fur model predictions of heat loss corresponded closely to values measured for adult and juvenile marmots at ambient temperature of 20 °C or less. The predictability of the model improved when values for evaporative water loss were included, but model predictions did not correspond with metabolic rates at higher ambient temperatures. The fur model did not account for short term physiological adjustments such as changes in piloerection or peripheral circulation. The key points are that the pelage plays a prominent role in heat transfer between the marmot and its environment, that this heat transfer affects metabolic rate, and that heat loss is most sensitive to changes in solar radiation.

Under intense solar radiation, net heat transfer can be toward the skin. Absorbed solar radiation can reduce heat needed for thermoregulation or thermally stress an animal. At mid day, clear with little wind, heat gain on the portion of a marmot's surface receiving direct solar radiation can be up to 10 times basal heat production (MELCHER 1987).

Under environmental conditions marmots are likely to encounter, changes in solar radiation have the greatest influence on heat energy transfer. Marmots can affect heat transfer over short time periods by altering fur depth and skin temperature. However, hair density and diameter can be altered only over long time periods, primarily by molt. The primary role of fur color in this heat transfer system is to affect absorption of solar energy; dark fur should increase absorption and light-colored or white fur should decrease absorption by increasing reflection, especially in the visible range. Do we have evidence that marmots respond to solar radiation in ways that could affect metabolism?

MARMOT RESPONSE TO SOLAR RADIATION

We investigated the behavior of yellow-bellied marmots with respect to solar radiation. High ambient temperatures and high solar radiation exceed the ability of marmots to thermoregulate by physiological or physical means (MELCHER 1987). Yellow-bellied marmots allow the body temperature to increase to about 40 °C at which time they seek shelter, typically by entering a burrow (MELCHER et al. 1990). However, early in the active season and early in the morning throughout the summer, ambient conditions (low temperature, wind) were stressful and would be expected to increase metabolism. Under these conditions, marmots should use solar radiation to decrease heat loss (and thus reduce metabolism). But when ambient conditions become thermally stressful, marmots should avoid solar radiation in order to reduce heat stress.

We tested the above predictions by recording the cumulative number of marmots sitting or lying in the sun during the morning at Picnic Colony. Because animals can adjust body posture to maximize or minimize heat gain (MCNAB 2002), we recorded whether the marmot had its body angled toward the sun, which would expose the maximum amount of body surface to solar radiation. Both the number of marmots in the sun and the proportion whose body was angled significantly decreased with time (number, $P = 0.026$; proportion, $P < 0.001$) after increasing early (Fig. 2). Proportion of marmots with body angled was not a function of the number of marmots in the sun ($P = 0.082$). Marmots reduce the amount of solar radiation they receive when in sunlight by sitting or lying on the back; i.e. shady, side of a rock. This pattern is prevalent after about 10:00 hr.

This pattern of exposure to sunlight is correlated with the thermal environment at Picnic Colony. Radiation increases markedly after 08:00 hr and radiation in watts per m² reaches 50% of maximum about 09:00 hr; the air temperature curve is similar to the radiation curve and temperature may reach 20 °C about 10:00 hr (MELCHER 1987). Thus, when radiation and temperature are low early in the morning, more marmots sit or lie in the sun with bodies angled toward the sun. As air temperature and radiation increase, sitting in the sun with body angled toward the sun decreases.

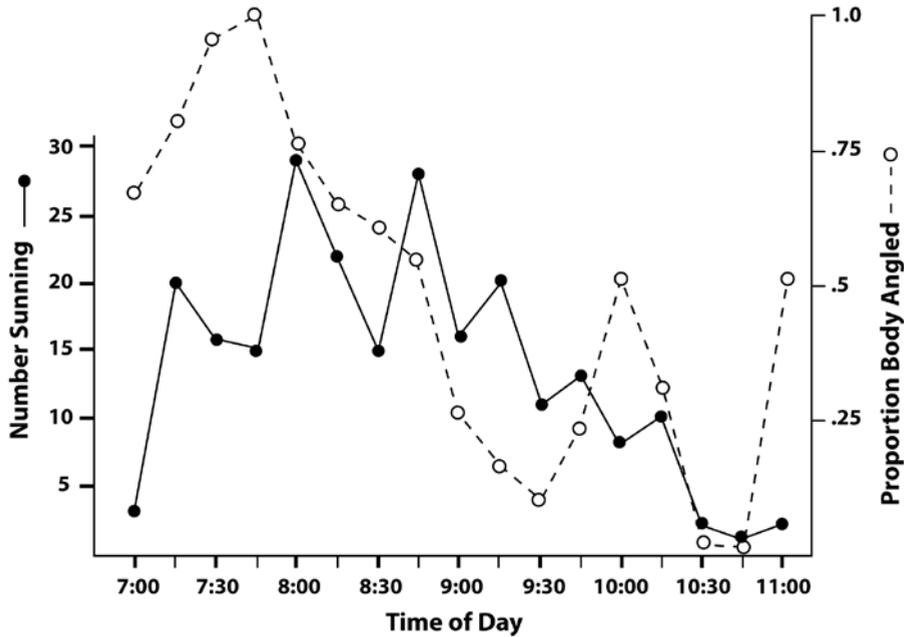


Fig. 2. — The number of marmots sitting in the sun and the proportion with body angled toward the sun.

DISCUSSION

It is well established that marmot diurnal activity during the active season is bimodal with reduced activity during the period of high ambient temperature and thermal radiation and that sitting or lying in the sun, especially early in the morning, is common (TRAVIS & ARMITAGE 1972, TURK & ARNOLD 1988, BARASH 1989, ARMITAGE & CHIESURA CORONA 1994, ARMITAGE et al. 1996, LENTI BOERO 2003). Marmots generally live in open landscapes and are exposed to solar radiation. Clearly, intense solar radiation is stressful (MELCHER et al. 1989); thus, the question is do marmots utilize solar radiation to reduce the cost of heat production in thermoregulation?

Indirect evidence suggests that marmots do so. First, marmots have metabolic rates lower than expected for their body size (ARMITAGE & SALSBURY 1992). Second, tissue growth efficiency of marmots is about five times greater than that of typical homeotherms (KILGORE & ARMITAGE 1978). Third, marmots spend only 1 to 6% of their daily energy expenditure on thermoregulation (MELCHER et al. 1989). Fourth, the lowest heart rates of free-ranging yellow-bellied marmots were recorded when marmots were lying in the sun (ARMITAGE 2003b).

If marmots use solar energy to reduce the costs of maintenance and are stressed by intense solar radiation, the costs and benefits of fur color will differ depending on the amount of solar energy the marmot receives. During cool conditions; e.g., early in the morning or early in the active season, dark fur would be advantageous as more solar energy would be absorbed. However, during

warm conditions; e.g., during mid day and summer, dark fur would be disadvantageous and light-colored fur would be advantageous because more solar energy would be reflected. Perhaps the shades of brown that characterize fur color in most species of marmots represents a compromise between these two functions; some thermal gain during cool periods, but not too much heat absorption during warm periods. Heat absorption may be the more critical factor as marmots can reduce heat stress by sitting in the wind or entering a burrow.

This leads us to back to the question of why there are white, grey, red, and dark brown marmot species and why melanism persists in some populations. Phylogenetic relationships seem unimportant as a factor producing fur color diversity; e.g., *M. vancouverensis*, dark brown, and *M. caligata*, white, are in the same clade (STEPAN et al. 1999). I hypothesize that these fur colors are adaptive to the thermal regimes in which these species live. This hypothesis is supported by marmot subspecies living in drier, warmer environments having lighter-colored pelage (COUCH 1930, DAVYDOV 1991).

Two sets of studies are required to determine the function of fur color in marmots and to test the hypothesis that fur color is important in heat transfer between the marmot and its environment. One set of studies should determine if solar radiation can reduce metabolic rate. These studies can be done in the laboratory where metabolic rate can be measured with and without a source of thermal radiation.

The second set of studies should determine heat transfer through the fur of marmot species with different fur colors. The role of color is not simply one of absorptivity or reflectivity. The effects of wind and of penetrance and emissivity need to be considered (WILLMER et al. 2000).

Although I have argued that the major factor selecting for fur color in marmots is heat transfer through the fur, fur color can be associated with other functions. The melanocortico system that controls the synthesis of melanin has also been implicated in cortisol production, body weight regulation, and immunity (CANDILLE et al. 2007). Thus, marmot fur color may be a complex compromise between heat transfer and one or more other physiological factors. I predict that many fruitful years of research into the function of fur color of marmots could be quite profitable and teach us much about how marmots are adapted to live in harsh environments (ARMITAGE & BLUMSTEIN 2002).

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