Seasonal pelage color change of two sympatric arboreal squirrel species in the subarctic region

W. MITSUZUKA\textsuperscript{1}, M. KATO\textsuperscript{2}, & T. OSHIDA\textsuperscript{1}\textsuperscript{*}

\textsuperscript{1}Laboratory of Wildlife Biology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan, and \textsuperscript{2}Botanic Garden & Museum, Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan

(Received 16 July 2019; accepted 15 October 2019)

Abstract

Some mammal species exhibit pelage color change with seasonal molt. Seasonal molt and pelage color change are beneficial to thermoregulation and concealment, associated with seasonal environmental change. The Eurasian red squirrel \textit{Sciurus vulgaris} Linnaeus, 1758 and the Siberian flying squirrel \textit{Pteromys volans} (Linnaeus, 1758) are arboreal and sympatrically distributed in the subarctic northern Eurasian Continent and Sakhalin and Hokkaido islands. We expect that diurnal \textit{S. vulgaris} may demonstrate more conspicuous difference between summer and winter pelages than nocturnal \textit{P. volans}, because of its protective coloration in each season. To test this conjecture, we investigated their seasonal pelage color change. To diminish the effect of geographic variation in pelage color, we chose \textit{S. vulgaris orientis} Thomas, 1906 and \textit{P. volans orii} (Kuroda, 1921), which are endemic subspecies of Hokkaido Island, Japan. We used skin and stuffed specimens and frozen materials and categorized them into two pelage groups (summer and winter pelages) based on collection date. Pelage color characteristics were measured with a spectrophotometer for lightness, redness and yellowness. Countershading was examined by comparing dorsal and ventral lightness. Both subspecies showed lighter winter pelage than summer pelage, suggesting their greyish-white winter pelage was beneficial to concealment from predators during winter. As we expected, seasonal changes of redness and yellowness were more clearly recognized in \textit{S. vulgaris} than in \textit{P. volans}. As \textit{S. vulgaris} is diurnal and vulnerable to attack by diurnal avian predators, reddish and yellowish pelage patterns may be important for concealment. Because it is nocturnal, \textit{P. volans} may not need this reddish and yellowish pelage. \textit{Sciurus vulgaris} also had a remarkably counter-shaded body, indicating that its body may reduce predation risk from daytime visual predators. Differences in seasonal pelage color change of these two arboreal squirrels may be caused by their different circadian rhythms.

Keywords: Countershading, Hokkaido, \textit{Sciurus vulgaris orientis}, \textit{Pteromys volans orii}

Introduction

Some mammal species exhibit seasonal pelage color change due to seasonal molts (Cott 1940; Mills et al. 2013). Of these, several mammal species such as hares (Severaid 1945; Mills et al. 2013) and weasels (Bissonnette & Bailey 1944; Rust & Meyer 1969; Atmeh et al. 2018) in temperate, boreal and arctic zones alternate between a white winter pelage and a brown summer pelage. Their molt and color change are helpful for crypsis by matching the snow cover and for thermoregulation by changes in pelage composition (Underwood & Reynolds 1980), microstructure (Russell & Tumlison 1996) and spectral properties (Zimova et al. 2018). In high latitudes, ambient conditions and food availability of habitat are seasonally changeable, providing strong selection pressures compared to tropical habitats (Barta et al. 2008; Beltran et al. 2018). Unlike weasels and hares, the small vesper mouse \textit{Calomys laucha} (Fisher, 1814) in South America alternates between a dark grey winter pelage and a deep orange summer pelage (Camargo et al. 2006): its seasonal pelage color change may be beneficial to crypsis because this mouse feeds in the sand dunes in summer, but in winter it moves to the dark soils and brown log
cabins of human populated areas (Camargo et al. 2006). Although little is known of how mammals without winter fur seasonally change pelage coloration, it may be explained by environmental conditions.

It is likely that seasonal molts are regulated by photoperiod (Funakoshi et al. 2017; Zimova et al. 2018). Therefore, seasonal pelage color change with each molt may be associated with seasonal environmental change. Mammals adapted to a similar environment may exhibit a similar pattern of pelage color change; we may find the similarity particularly in mammal species occupying a similar niche. In the northern part of the Palearctic region, there are just two arboreal squirrel species: the Eurasian red squirrel *Sciurus vulgaris* (Linnaeus, 1758) and the Siberian flying squirrel *Pteromys volans* (Linnaeus, 1758), which are sympathetically distributed in the subarctic northern Eurasian Continent, Sakhalin of Russia and Hokkaido of Japan (Gurnell 1987; Hanski et al. 2000; Lurz et al. 2005). They have a greyish-white dorsal pelage in winter, but a brown dorsal pelage in summer (Ognev 1966). They do not hibernate (Timm & Kirstaja 2002; Lurz et al. 2005; Dausmann et al. 2013), so their pelage color may be an adaptation for seasonal environmental change. They are the two widest ranging arboreal squirrels in the world (Gurnell 1987; Koprowski & Nandini 2008). Both *S. vulgaris* and *P. volans* are well adapted to boreal coniferous and mixed forests (Gurnell 1987; Hanski et al. 2000; Timm & Kirstaja 2002; Lurz et al. 2005). Although the two species similarly occupy an arboreal niche, they differ in circadian rhythm: *S. vulgaris* is diurnal and *P. volans* is nocturnal (e.g., Thorington et al. 2012). Therefore, we expect that the two species have a different pattern of seasonal pelage color change. *Sciurus vulgaris* may demonstrate a more conspicuous difference between summer and winter pelages than *P. volans* (*Sciurus vulgaris* may need more protective coloration in each season, because of its diurnal niche). Most mammal species, however, show geographical variation in pelage color (Lai et al. 2008) in relation to genetic and environmental effects (Caro 2005). Because of their wide range, subspecies of *S. vulgaris* and *P. volans* also show pelage color variations (Ognev 1966; Lurz et al. 2005; Zaida 2018). Thus, we focused on *S. vulgaris orientis* Thomas, 1906 and *P. volans orii* (Kuroda, 1921) which are endemic subspecies of Hokkaido Island, Japan. Both subspecies are considered geographically isolated from the Eurasian Continent (Oshida & Masuda 2000; Oshida et al. 2005). Therefore, by using these two subspecies, we expect to reduce effects of geographical variation in pelage color.

Both *S. vulgaris* and *P. volans* have a countershaded body: a darker dorsal surface and a lighter ventral surface. Countershading is widespread in mammals (Caro 2005) and common among arboreal squirrel species (Ancillotto & Mori 2017). The function of countershading is considered to be crypsis by self-shadow concealment. Self-shadow concealment reduces visual recognition by predators by reducing intra-body visual contrasts or by obliterating shadowing, thus making three-dimensional bodies appear optically flat when viewed from the side (Thayer 1896; Rowland 2009; Kelley et al. 2017). In volant, arboreal and aquatic animals, background matching enhances crypsis for view from above by matching their dark dorsal surface with dark ground or deep water and for view from below by matching their light ventral surface with bright sky or water surface (Rowland 2009; Kamilar & Bradley 2011; Kelley et al. 2017). Previous experimental studies report that countershading of artificial prey reduces the frequency of avian predation (Speed et al. 2004; Rowland et al. 2007, 2008), although it is not clear whether and how this concealment functions in natural environments (Caro 2005; Penacchio et al. 2018).

In the present study, we examined seasonal pelage color change and countershading of *S. vulgaris orientis* and *P. volans orii*. We here hypothesize that diurnal *S. vulgaris orientis* show more conspicuous seasonal color change and higher countershading than nocturnal *P. volans orii*, because of protective coloration of *S. vulgaris orientis*. We discuss the ecological significance of their pelage color in their arboreal niche of the subarctic region.

### Materials and methods

#### Materials

We examined skin and stuffed specimens and frozen materials of *S. vulgaris orientis* (*n = 85*) and *P. volans orii* (*n = 32*) (Table I). Skin and stuffed specimens are deposited in the Botanic Garden & Museum, Hokkaido University, and the Obihiro Centennial Museum. Frozen materials, which are dead bodies killed by car accidents, are deposited in the Laboratory of Wildlife Biology, Obihiro University of Agriculture and Veterinary Medicine (Appendix 1). Collection date, sex, body mass and collection locality data are given in Appendix 1. Based on body mass, we categorized both subspecies into adults and subadults. The body mass of adult *S. vulgaris orientis* is > 325 g (Magris & Gurnell 2002). The body mass of adult *P. volans orii* is > 80 g (Yanagawa 2009). To reduce artificial error in measuring color, juvenile individuals were excluded. Pelage color of older small
mammal specimens is more reddish or yellowish than that of younger specimens [(the red bat *Lasiurus borealis* (Müller, 1776): Davis and Castleberry (2010); golden mouse *Ochrotomys nuttalli* (Harlan, 1832) and eastern chipmunk *Tamias striatus* (Linnaeus, 1758): Davis et al. (2013); Budin’s grass mouse *Akodon budini* (Thomas, 1918): Sandoval et al. 2018)]. To diminish the effect of storage time as much as possible, we used specimens of various ages (Appendix 1). Specimens of *S. vulgaris orientis* and *P. volans orii* were obtained from 1910 to 2011 and from 1914 to 2014, respectively. Therefore, for a comparison between two species, we regarded these specimens as useful.

We classified specimens and materials into two pelage groups (summer and winter pelages) based on their collection date. The spring molt of *S. vulgaris* occurs in April and May and lasts for approximately 6 weeks (Gurnell 1987). Autumn molt starts in October (Gurnell 1987). We excluded *S. vulgaris orientis* collected in May and November, because these periods would include individuals with intermediate pelage color. We did not find such complicated pelage color at the beginning of molt and used the individuals in April and October in this examination. For *S. vulgaris orientis* and *P. volans orii* we defined summer and winter pelages as June to October and December to April, respectively (Table I). Some mammals show different pelage colors by sex and age (e.g. northern white-cheeked gibbon *Nomascus leucogenys* Ogilby, 1840; Mootnick 2006). We, however, did not separate by sex and age (adult or sub-adult), since these differences have not been reported for either *S. vulgaris orientis* or *P. volans orii*.

### Measurements of pelage color

The pelage color was quantified with a spectrophotometer (CM-700d, Konica Minolta Sensing Inc., Osaka, Japan) with a φ3 mm measurement area, specular component included (SCI), illuminant D$_{65}$ and observer angle 10°. The pelage color was expressed in the International Commission on Illumination (CIE) color space L*a*b*: lightness (L*), redness (a*) and yellowness (b*) (McGuire 1992). The L* value ranges from darkest black at 0 to brightest white at 100. The a* and b* values represent chroma and hue, respectively. Positive and negative a* values indicate hues of red-purple and bluish-green, respectively. Positive and negative b* values indicate yellow and blue, respectively.

We measured pelage color at five points: upper back, lower back, right dorsal surface, left dorsal surface and chest on ventral surface (Ognev 1966; Gurnell 1987) (Figure 1). We only used the lightness value to analyze chests. Chests of *S. vulgaris orientis* and two *P. volans orii* individuals could not be measured, because of their poor condition. The color was measured 3 times, and the three measurements were averaged. When measuring specimens, parts where hairs had fallen out or were stained were avoided. Frozen materials were measured after thawing naturally and removing water by wiping on paper.

We quantified extent of countershading as the lightness difference between the dorsal and ventral surfaces (Kamilar & Bradley 2011). We averaged upper back, lower back, right dorsal surface, left dorsal surface and chest on ventral surface (Gurnell 1986; Gurnell 1987) (Figure 1). We only used the lightness value to analyze chests. Chests of *S. vulgaris orientis* and two *P. volans orii* individuals could not be measured, because of their poor condition. The color was measured 3 times, and the three measurements were averaged. When measuring specimens, parts where hairs had fallen out or were stained were avoided. Frozen materials were measured after thawing naturally and removing water by wiping on paper.

We used the lightness value to analyze chests. Chests of *S. vulgaris orientis* and two *P. volans orii* individuals could not be measured, because of their poor condition. The color was measured 3 times, and the three measurements were averaged. When measuring specimens, parts where hairs had fallen out or were stained were avoided. Frozen materials were measured after thawing naturally and removing water by wiping on paper.

### Statistical analyses

Pelage color values (L*, a* and b*) and countershading values (back and side) were compared between summer pelage and winter pelage of each subspecies. Countershading values were also compared between the two subspecies for each season to examine the relationship between subspecies and extent of countershading. All comparisons were made with the Mann–Whitney U-test.

Previous studies report that mammal specimens in museum collections showed temporal changes in

### Table I. Number of specimens and squirrel subspecies examined in the present study.

| Subspecies             | Pelage | Collection month |
|------------------------|--------|------------------|
| *Sciurus vulgaris orientis* | Summer | Jan. 5 Feb. 4 Mar. 1 Apr. 3 Jun. 5 Jul. 4 Aug. 3 Sep. 3 Oct. 4 Dec. 3 Total 16 |
|                        | Winter | Jan. 5 Feb. 2 Mar. 5 Apr. 3 Jun. 5 Jul. 4 Aug. 3 Sep. 3 Oct. 4 Dec. 3 Total 16 |
| *Pteromys volans orii*  | Summer | Jan. 2 Feb. 4 Mar. 4 Apr. 3 Jun. 5 Jul. 4 Aug. 3 Sep. 3 Oct. 4 Dec. 3 Total 16 |
|                        | Winter | Jan. 2 Feb. 4 Mar. 4 Apr. 3 Jun. 5 Jul. 4 Aug. 3 Sep. 3 Oct. 4 Dec. 3 Total 16 |

A dash indicates mean no specimens were collected that month.
pelage color (Davis & Castleberry 2010; Davis et al. 2013; Sandoval et al. 2018). Thus, to consider the effect of aging on specimens, we calculated the Spearman rank correlation coefficient ($r_s$) between collecting year and each pelage color value. All statistical analyses were performed with the R program v. 3.4.1 (R Development Core Team 2017).

**Results**

Dorsal lightness of winter pelage was lighter than that of summer pelage in both subspecies ($P < 0.01$), but ventral lightness did not statistically vary between seasons ($S. vulgaris orientis$: $P = 0.10$ and $P. volans orii$: $P = 0.29$; Table II).

Upper back summer pelage of $S. vulgaris orientis$ was more red than winter pelage ($P < 0.05$), but $P. volans orii$ showed no significant difference between seasons ($P = 0.49$) (Table II). Lower back winter pelage of $S. vulgaris orientis$ was more red and yellow than summer pelage ($P < 0.001$), but $P. volans orii$ showed no significant difference between seasons ($a^*$, $P = 0.42$; $b^*$, $P = 0.35$) (Table II). Right and left sides of summer pelage were more red than winter pelage in $S. vulgaris orientis$ ($P < 0.001$; Table II). In $P. volans orii$, only the left side of summer pelage was more red ($P < 0.05$; Table II).

In $S. vulgaris orientis$, countershading values of back [mean (standard deviation, $SD$) = 45.71 (8.72)] and sides [43.09 (8.31)] in summer pelage ($n = 39$) were higher than those [35.40 (9.26) and 29.84 (9.12), respectively] in winter pelage ($n = 45$) ($P < 0.001$). There was no significant difference between seasons in $P. volans orii$ ($P > 0.20$): in summer pelage ($n = 15$), the countershading values of back and sides were 31.89 (9.78) and 31.24 (11.30), respectively; in winter pelage ($n = 15$), they were 27.70 (7.50) and 25.88 (10.48), respectively. $Sciurus vulgaris orientis$ had higher countershading values than $P. volans orii$ on back and sides of summer pelage ($P < 0.001$) and back of winter pelage ($P < 0.01$). There was no significant difference in sides of winter pelage between the two species ($P > 0.10$).

For most measurement points on both subspecies, the Spearman rank correlation coefficient between the collection year and each color value was not statistically significant (Table III). The right side ($a^*$ and $b^*$), left side ($b^*$) and chest ($L^*$) of $S. vulgaris orientis$ winter pelage, lower back ($a^*$) of $P. volans orii$ summer pelage and chest ($L^*$) of $P. volans orii$ summer pelage were measured for comparison.
Discussion

Seasonal pelage color change

Winter pelages of *S. vulgaris orientis* and *P. volans orii* were similarly lighter than their summer pelages (Table II). In Hokkaido, snow cover usually exists from early December to early April, so, lighter pelage color may be a beneficial character. At least 18 mammal species have a white winter pelage (Zimova et al. 2018): six leporids (Severaid 1945; Mills et al. 2013), eight muroids (Hoffmann 1973), three mustelids (Bissonnette & Bailey 1944; Rust & Meyer 1969; Sheffield & Thomas 1997), and one canid (Arctic fox *Vulpes lagopus* (Linnaeus, 1758): Underwood & Reynolds 1980). Their white pelage promotes camouflage against snow by background matching (Zimova et al. 2018). Because of their terrestrial habits, white pelage may be especially effective on snow-covered ground (Nowak 1991).

Although *S. vulgaris* sometimes travels and forages on the ground, it spends most of its time in trees (Wauters & Dhondt 1987). *Pteromys volans* also inhabits the trees and is well adapted to its arboreal niche (Hanski et al. 2000). Therefore, its greyish-white pelage may blend into winter arboreal environments characterized by mingled colors of bark and snow cover on the branches.

Seasonal change in redness and yellowness was clear in *S. vulgaris orientis*, but not in *P. volans orii* (Table II), suggesting that our hypothesis that *S. vulgaris orientis* shows more conspicuous seasonal color change than *P. volans orii* is supported. These results may be caused by the difference in circadian rhythm and the color vision of predators. *Sciurus vulgaris* is active mainly in the daytime (Wauters & Dhondt 1987; Steen & Barmoen 2017), but *P. volans* is active at night (Hokkanen et al. 1977; Törmälä et al. 1980; Yamaguchi & Yanagawa 1995). In south-western and central Finland, *S. vulgaris* is more frequently found in the diet of the diurnal goshawk *Accipiter gentilis* (Linnaeus, 1758) than that of nocturnal eagle owl *Bubo bubo* (Linnaeus, 1758) and the Ural owl *Strix uralensis* Pallas, 1771, although

---

**Table II. Differences of pelage color values [mean (standard deviation)] between seasons.** *P* values determined with Mann–Whitney U-test. Color values L*, a* and b* represent lightness, redness and yellowness, respectively.

| Subspecies               | Measuring point | Color value | Summer       | Winter       | P value |
|-------------------------|-----------------|-------------|--------------|--------------|---------|
| *Sciurus vulgaris orientis* | Upper back     | L*          | 32.63 (4.75) | 40.56 (5.23) | < 0.001 |
|                         |                 | a*          | 5.72 (1.71)  | 4.87 (1.45)  | < 0.05  |
|                         |                 | b*          | 11.06 (2.32) | 11.82 (2.39) | 0.09    |
|                         | Lower back      | L*          | 30.71 (5.39) | 37.98 (4.01) | < 0.001 |
|                         |                 | a*          | 5.27 (1.61)  | 6.29 (1.41)  | < 0.001 |
|                         |                 | b*          | 9.81 (2.87)  | 13.41 (2.29) | < 0.001 |
|                         | Right side      | L*          | 34.56 (6.85) | 44.94 (5.32) | < 0.001 |
|                         |                 | a*          | 4.63 (1.82)  | 2.73 (1.06)  | < 0.001 |
|                         |                 | b*          | 9.87 (2.74)  | 8.75 (1.90)  | 0.13    |
|                         | Left side       | L*          | 34.18 (7.01) | 44.72 (4.93) | < 0.001 |
|                         |                 | a*          | 4.59 (1.76)  | 2.87 (1.12)  | < 0.001 |
|                         |                 | b*          | 9.79 (2.61)  | 8.96 (1.94)  | 0.24    |
|                         | Chest†          | L*          | 77.23 (8.06) | 74.67 (8.85) | 0.1     |
| *Pteromys volans orii*   | Upper back      | L*          | 34.11 (7.10) | 45.06 (5.24) | < 0.001 |
|                         |                 | a*          | 2.75 (0.69)  | 2.73 (1.30)  | 0.49    |
|                         |                 | b*          | 7.50 (2.66)  | 8.82 (3.45)  | 0.24    |
|                         | Lower back      | L*          | 38.30 (8.64) | 48.11 (6.29) | < 0.01  |
|                         |                 | a*          | 3.43 (0.77)  | 3.34 (1.40)  | 0.42    |
|                         |                 | b*          | 9.84 (3.01)  | 10.73 (3.53) | 0.35    |
|                         | Right side      | L*          | 36.06 (8.40) | 46.96 (6.72) | < 0.001 |
|                         |                 | a*          | 2.38 (0.66)  | 2.26 (0.90)  | 0.41    |
|                         |                 | b*          | 7.25 (2.64)  | 8.31 (2.68)  | 0.27    |
|                         | Left side       | L*          | 37.56 (6.28) | 49.73 (8.61) | < 0.001 |
|                         |                 | a*          | 2.95 (0.80)  | 2.02 (0.87)  | < 0.05  |
|                         |                 | b*          | 8.95 (2.80)  | 7.79 (3.29)  | 0.32    |
|                         | Chest§          | L*          | 68.36 (11.88)| 74.16 (6.44) | 0.29    |

*S. vulgaris orientis*: summer pelage *n*= 40, winter pelage *n*= 45 (†: summer pelage *n*= 39, winter pelage *n*= 45); *P. volans orii*: summer pelage *n*= 16, winter pelage *n*= 16 (§: summer pelage *n*= 15, winter pelage *n*= 15).
it is rarely consumed by these avian predators (Selonen et al. 2010). In north Europe, *S. vulgaris* is a common prey of the goshawk, although the goshawk’s main prey is woodland grouse (*Tetraonidae*) (Tornberg et al. 2006). Therefore, *S. vulgaris* may be vulnerable to attack by diurnal avian predators. The color vision of most vertebrates, given in daylight by cone photoreceptors, is dramatically affected by ambient light levels. Performance of diurnal birds is weakened in low light (Kelber & Lind 2010). Compared to nocturnal birds, diurnal birds have more colored oil droplets – spherical optical organelles within the sclera portion of the inner cone photoreceptor segment (Toomey & Corbo 2017). These droplets enhance color discrimination (Vorobyev 2003). Predators of *S. vulgaris* also include mammals, such as the pine marten *Martes martes* (Linnaeus, 1758), stoat *Mustela erminea* Linnaeus, 1758, wild cat *Felis silvestris* Schreber, 1777 and red fox *Vulpes vulpes* (Lurz et al. 2005). Except for some primates and marsupials, most terrestrial mammals have dichromat cones, whereas birds have tetrachromat cones (Hunt et al. 2009). Therefore, the reddish and yellowish pelage patterns of *S. vulgaris* may be important for crypsis from diurnal avian predators. *Pteromys volans* would not need this colored pelage because of its nocturnal habits.

**Countershading**

Although it is difficult to evidentially explain the function of countershading, relationships between body size and countershading have previously been estimated. Small-sized primates have more highly counter-shaded bodies than large-sized primates do (Kamilar 2009). Highly counter-shaded cetacean species are smaller than non-highly counter-shaded cetaceans (Caro et al. 2011). The higher countershading may result from the higher predation risk of smaller mammal species (e.g. Caro et al. 2011). Our results, however, do not correspond to these studies. *Sciurus vulgaris orientis* (body mass: 350–456 g, Lee 1999) is much larger than *P. volans orii* (body mass: 81.3–156.1 g, N. Mori (personal
Temporal changes in pelage color

Pelage color of older small mammal specimens is more reddish or yellowish than that of younger specimens (Davis & Castleberry 2010; Davis et al. 2013; Sandoval et al. 2018). Taking the effect into consideration, our specimens and materials were collected from 1906 to 2017, showing various storage times (Appendix 1). We found that older S. vulgaris orientis specimens were more reddish and yellowish at some measurement points (Table III). Our results may have been caused by the breakdown of eumelanin pigment which makes dark color, leaving a relatively greater proportion of pheomelanin pigment which makes reddish-brown color (Doucet & Hill 2009; Davis et al. 2013). In addition, the chest of older specimens got darker (Table III), probably due to stains from dust. Although future studies should consider specimen storage time, we were still able to show an overall tendency of seasonal pelage color change and countershading in both squirrel species.

Conclusion

The greyish-white winter pelage of S. vulgaris and P. volans may be beneficial to concealment from predators in their arboreal habitat during winter. Their seasonal pelage color change and countershading were probably affected by differences in circadian rhythm; diurnal S. vulgaris orientis shows more conspicuous seasonal color change and higher countershading than nocturnal P. volans orii, because of protective coloration in the daytime. In Sciuromorpha, concealment may be the primary selective force for pelage color, as suggested by Ancillotto and Mori (2017).

Sciurus vulgaris and Pteromys volans are the two widest ranging arboreal squirrels (Gurnell 1987; Kopolowski & Nandini 2008). There are several geographic forms (subspecies) in their region (Ognev 1966; Lurz et al. 2005; Zizda 2018). To generalize seasonal pelage color change in Palearctic arboreal squirrels, further studies should examine these subspecies. To clarify the ecological function of pelage color changes, Nearctic arboreal squirrels that also live in the snow zone should be studied.

Acknowledgements

We thank T. Akasaka and Y. Asari (Obihiro University of Agriculture and Veterinary Medicine) for their helpful comments concerning this study. We are grateful to Y. Ikeda (Obihiro Centennial Museum) for supplying materials and H. Suzuki (Hokkaido University) for lending a spectrophotometer. We thank C. L. Brigman (Tunghai University) for her critical comments on our manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Supplementary material

Supplemental data for this article can be accessed here.
inferred from cytochrome b gene sequences. Zoological Science 17:405–409. DOI: 10.2108/jsz.17.405.

Penacchio O, Lovell PG, Harris JM. 2018. Is countershading camouflage robust to lighting change due to weather? Royal Society Open Science 5:170801. DOI: 10.1098/rsos.170801.

Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. Journal of Animal Ecology 83:504–514. DOI: 10.1111/1365-2656.12148.

R Development Core Team. 2017. R: Language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available: https://www.R-project.org/. Accessed Dec 2018 10.

Rowland HM. 2009. From Abbott Thayer to the present day: What have we learned about the function of countershading? Philosophical Transactions of the Royal Society of London B Biological Sciences 364:519–527. DOI: 10.1098/rstb.2008.0261.

Rowland HM, Cuthill IC, Harvey IF, Speed MP, Ruxton GD. 2008. Can’t tell the uphill from the trees: Countershading enhances survival in a woodland. Proceedings of the Royal Society B Biological Sciences 275:2539–2545. DOI: 10.1098/rspb.2008.0812.

Rowland HM, Speed MP, Ruxton GD, Edmunds M, Stevens M, Harvey IF. 2007. Countershading enhances cryptic protection: An experiment with wild birds and artificial prey. Animal Behaviour 74:1249–1258. DOI: 10.1016/j.anbehav.2007.01.030.

Russell JE, Tumlison R. 1996. Comparison of microstructure of white winter fur and brown summer fur of some arctic mammals. Acta Zoologica 77:279–282. DOI: 10.1111/j.1463-6395.1996.tb01272.x.

Rust CC, Meyer RK. 1969. Hair color, molt, and testis size in male, short-tailed weasels treated with melatonin. Science 165:921–922. DOI: 10.1126/science.165.3896.921.

Sandoval SML, Sandoval JD, Colombo EM, Barquez RM. 2018. The pattern of color change in small mammal museum specimens: Is it independent of storage histories given museum-specific conditions? BMC Research Notes 11:424. DOI: 10.1186/s13104-018-3544-x.

Selenon V, Sulkava P, Sulkava R, Sulkava S, Korpimäki E. 2010. Decline of flying and red squirrels in boreal forests revealed by long-term diet analyses of avian predators. Animal Conservation 13:579–585. DOI: 10.1111/j.1469-1759.2010.00379.x.

Severaid JH. 1945. Pelage changes in the snowshoe hare (Lepus americanus strinthus Bangle). Journal of Mammalogy 26:41–63. DOI: 10.2307/1375031.

Sheffield SR, Thomas HH. 1997. Mustela frenata. Mammal Species 570:1–9. DOI: 10.2307/3504434.

Speed MP, Kelly DJ, Davidson AM, Ruxton GD. 2004. Countershading enhances crypsis with some bird species but not others. Behavioral Ecology 16:327–334. DOI: 10.1093/beheco/arh166.

Steen R, Barmoen M. 2017. Diel activity of foraging Eurasian red squirrels (Sciurus vulgaris) in the winter revealed by camera traps. Hystrix 28:1–5. DOI: 10.4040/hystrix-28.1-11997.

Stoner CJ, Bininda-Emonds OR, Caro T. 2003a. The adaptive significance of coloration in lagomorphs. Biological Journal of the Linnean Society 79:309–328. DOI: 10.1046/j.1095-8312.2003.00190.x.

Stoner CJ, Caro TM, Graham CM. 2003b. Ecological and behavioral correlates of coloration in artiodactyls: Systematic analyses of conventional hypotheses. Behavioral Ecology 14:823–840. DOI: 10.1093/beheco/arg072.

Thayer AH. 1896. The law which underlies protective coloration. The Auk 13:124–129. DOI: 10.2307/4068693.

Thorington Jr RW, Koprowski JL, Steel MA, Whatton JF. 2012. Squirrels of the world. Baltimore: Johns Hopkins University Press.

Timm U, Kirlistraji P. 2002. The Siberian flying squirrel (Pteromys volans L.) in Estonia. Acta Zoologica Lituanica 12:433–436. DOI: 10.1080/13921657.2002.10512535.

Toomey MB, Corbo JC. 2017. Evolution, development, and function of vertebrate cone oil droplets. Frontiers in Neural Circuits 11:97. DOI: 10.3389/fncir.2017.00097.

Törmälä T, Vuorinen H, Hokkanen H. 1980. Timing of circadian activity in the Flying squirrel in central Finland. Acta Theriologica 25:461–474. DOI: 10.4098/0001-7051.

Tombberg, Korpimäki E, Byholm P. 2006. Ecology of the northern goshawk in Fennoscandia. Studies in Avian Biology 31:141–157.

Underwood LS, Reynolds P. 1980. Photoperiod and fur lengths in the Arctic fox (Allopex lagopus L.). International Journal of Biometeorology 24:39–48. DOI: 10.1007/BF02245540.

Vorobyev M. 2003. Coloured oil droplets enhance colour discrimination. Proceedings of Royal Society B Biological Sciences 270:1255–1261. DOI: 10.1098/rspb.2003.2381.

Wauters LA, Dhondt AA. 1987. Activity budget and foraging behaviour of the Red squirrel (Sciurus vulgaris, Linnaeus, 1758) in a coniferous habitat. Zeitschrift Für Säugetierkdo 52:341–353.

Yamaguchi Y, Yanagawa H. 1995. Field observations on circadian activities of the flying squirrel, Pteromys volans orii. Mammalian Science 34:139–149. (in Japanese with English abstract).

Yanagawa H 2009. Ranges and movements of Pteromys volans orii occurring in wind break forests. Reports to the Supporter’s Association of Obihiro University of Agriculture and Veterinary Medicine 37:15–17. (in Japanese).

Zimova M, Hackländer K, Good JM, Melo-Ferreira J, Alves PC, Mills LS. 2018. Function and underlying mechanisms of seasonal colour moulting in mammals and birds: What keeps them changing in a warming world? Biological Review 93:1478–1498. DOI: 10.1111/brv.12405.

Zizda JE. 2018. The colour phases of the European red squirrel in Ukraine: Similarities and differences by craniometric characters. Biosystems Diversity 26:183–187. DOI: 10.15421/011828.