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To cite this article: W. Mitsuzuka W. MITSUZUKA, M. Kato M. KATO & T. Oshida (2019) Seasonal pelage color change of two sympatric arboreal squirrel species in the subarctic region, The European Zoological Journal, 86:1, 443-451, DOI: [10.1080/24750263.2019.1682694](https://doi.org/10.1080/24750263.2019.1682694)

To link to this article: <https://doi.org/10.1080/24750263.2019.1682694>



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

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(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 *Sciurus vulgaris* Linnaeus, 1758 and the Siberian flying squirrel *Pteromys volans* (Linnaeus, 1758) are arboreal and sympatrically distributed in the subarctic northern Eurasian Continent and Sakhalin and Hokkaido islands. We expect that diurnal *S. vulgaris* may demonstrate more conspicuous difference between summer and winter pelages than nocturnal *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 *S. vulgaris orientis* Thomas, 1906 and *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 *S. vulgaris* than in *P. volans*. As *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, *P. volans* may not need this reddish and yellowish pelage. *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, *Sciurus vulgaris orientis*, *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 & Tumilson 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 *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

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cabins of human populated areas (Camargo et al. 2006). Although little is known of how mammals without white 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 sympatrically 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 & Kiristaja 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 & Kiristaja 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; Zizda 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

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

Subspecies	Pelage	Collection month										Total
		Jan.	Feb.	Mar.	Apr.	Jun.	Jul.	Aug.	Sep.	Oct.	Dec.	
<i>Sciurus vulgaris orientis</i>	Summer	–	–	–	–	5	10	5	10	10	–	40
	Winter	5	12	11	8	–	–	–	–	–	9	45
<i>Pteromys volans orii</i>	Summer	–	–	–	–	2	3	4	2	5	–	16
	Winter	4	1	4	7	–	–	–	–	–	0	16

A dash indicates mean no specimens were collected that month.

mammal specimens is more reddish or yellowish than that of younger specimens [(the red bat *Lasius 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*, we defined summer and winter pelages as June to October and December to April, respectively (Table I). We used the same time periods for *P. volans orii* (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 $\phi 3$ mm measurement area, specular component included (SCI), illuminant D₆₅ 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 and lower backs (mean lightness of back) and right and left sides (mean lightness of sides). Countershading values were calculated by subtracting the mean lightness values of the back and sides from the lightness value of the chest, respectively. Higher values indicate stronger countershading (Kamilar & Bradley 2011).

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

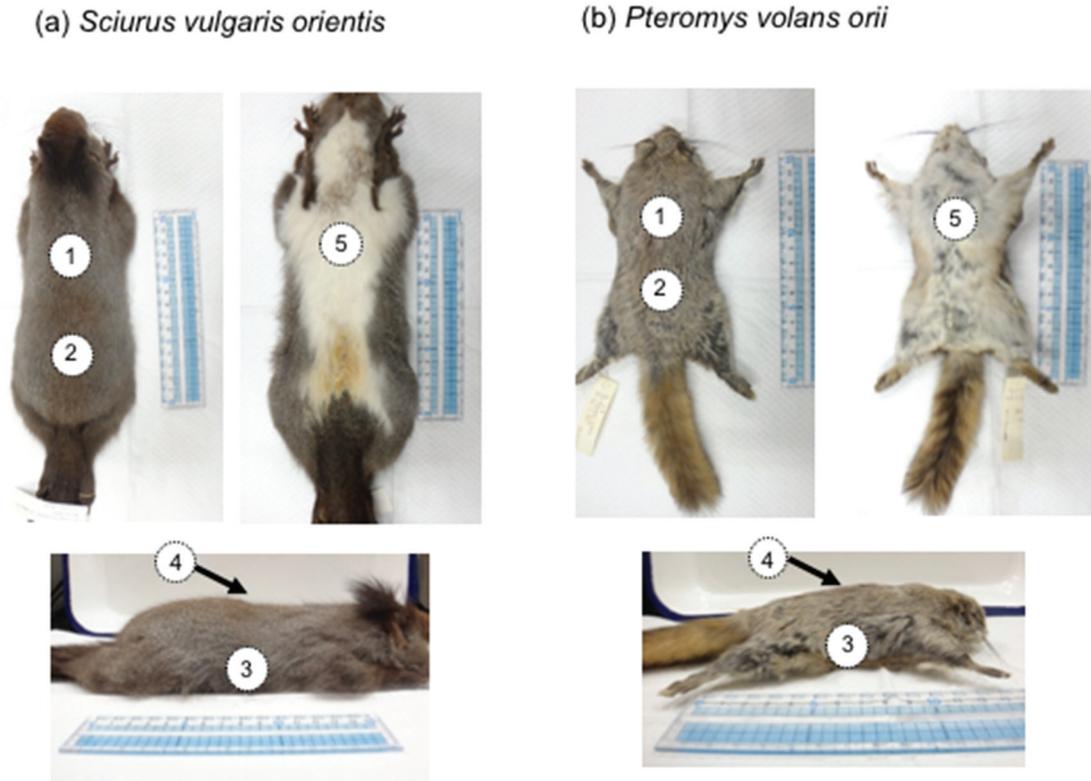


Figure 1. Measuring points on specimens and materials of squirrels in the present study. We measured pelage color at five points: (1) upper back, (2) lower back, (3) right side, (4) left side and (5) chest.

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*

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	Pelage		<i>P</i> value
			Summer	Winter	
<i>Sciurus vulgaris orientis</i>	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
<i>Pteromys volans orii</i>	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).

orii in both seasons showed a significant correlation with collecting year (Table III).

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 III. Results of the Spearman rank correlation analysis between pelage color and collecting year of squirrels. *P* value was determined with Mann–Whitney U-test. Color values of L*, a* and b* represent lightness, redness and yellowness, respectively. r_s = Spearman rank correlation coefficient.

Subspecies	Measurement point	Color value	Pelage				
			Summer		Winter		
			r_s	<i>P</i> value	r_s	<i>P</i> value	
<i>Sciurus vulgaris orientis</i>	Upper back	L*	0.16	0.37	-0.06	0.74	
		a*	-0.03	0.85	-0.16	0.40	
		b*	-0.05	0.78	-0.19	0.31	
	Lower back	L*	-0.05	0.76	-0.01	0.95	
		a*	-0.07	0.67	0.00	0.99	
		b*	-0.07	0.67	-0.14	0.46	
	Right side	L*	-0.06	0.73	-0.07	0.73	
		a*	0.20	0.24	-0.47	< 0.01	
		b*	0.06	0.75	-0.63	< 0.001	
	Left side	L*	0.05	0.75	-0.18	0.34	
		a*	0.12	0.48	-0.26	0.15	
		b*	0.00	1.00	-0.38	< 0.05	
	<i>Pteromys volans orii</i>	Chest †	L*	0.13	0.44	0.61	< 0.001
		Upper back	L*	0.06	0.86	-0.11	0.72
			a*	0.29	0.37	0.00	0.99
b*			0.20	0.53	-0.13	0.67	
Lower back		L*	0.39	0.22	0.00	0.99	
		a*	0.60	<0.05	0.07	0.82	
		b*	0.39	0.21	0.01	0.98	
Right side		L*	-0.32	0.31	-0.31	0.27	
		a*	-0.33	0.30	-0.04	0.88	
		b*	-0.45	0.14	-0.32	0.27	
Left side		L*	-0.15	0.63	-0.26	0.37	
		a*	-0.11	0.73	-0.05	0.86	
		b*	-0.21	0.51	-0.28	0.33	
Chest §		L*	0.80	< 0.01	0.77	< 0.01	

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*) (Törnberg 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

communication)]. Nevertheless, *S. vulgaris orientis* had higher countershading than *P. volans orii*, supportive of our hypothesis. Countershading may be more effective for concealment when counter-shaded animals are exposed to sunlight from above (Caro 2005; Kamilar & Bradley 2011). Previous studies report that counter-shaded mammals are diurnal: lagomorphs in grasslands (Stoner et al. 2003a), bovids and artiodactyls in deserts (Stoner et al. 2003b), and sciuriforms in forests (Ancillotto & Mori 2017). Nocturnal primate species, however, have similar countershading to diurnal species (Kamilar 2009), as moonlight tends to increase the activity of nocturnal primates (Prugh & Golden 2014). This is an unusual pattern for mammals. Moonlight tends to decrease the activity of nocturnal rodents (Prugh & Golden 2014). Countershading in *S. vulgaris orientis* and *P. volans orii* may be associated with differences in circadian rhythm rather than body size. The counter-shaded body of *S. vulgaris orientis* may enhance concealment effectively in daytime. Moreover, countershading of *S. vulgaris orientis* in summer was clearer than in winter. This countershading may be more helpful for concealment during summer, since *S. vulgaris* is more active in summer than in winter (Gurnell 1987; Wauters & Dhondt 1987).

Kiltie (1989) demonstrated that countershading reduced shading in the dorsoventral gradient, when counter-shaded grey squirrel (*Sciurus carolinensis* Gmelin, 1788) specimens were placed horizontally. Kamilar and Bradley (2011) show that the more primate species spent time in a horizontal position, the more they displayed higher countershading, suggesting that countershading is an important anti-predator adaptation for species moving and feeding in a horizontal position. Therefore, the countershading of *S. vulgaris* may work as concealment, when travelling, foraging and seed-hoarding in a horizontal position on branches and ground.

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; Koprowski & 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](#).

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