Polar Biology (2023) 46:277–290
https://doi.org/10.1007/s00300-023-03118-8

ORIGINAL PAPER

Seasonal changes in plumage density, plumage mass, and feather morphology in the world's northernmost land bird, the Svalbard Rock Ptarmigan (*Lagopus muta hyperborea*)

Andreas Nord[1,2] · **Vidar Holje**[1] · **Benjamin Judik**[3] · **Lars P. Folkow**[2] · **Péter L. Pap**[3]

Received: 21 September 2022 / Revised: 7 February 2023 / Accepted: 22 February 2023 / Published online: 24 March 2023

Abstract

The Svalbard Rock Ptarmigan, *Lagopus muta hyperborea,* is the only year-round resident terrestrial bird in the high Arctic. Many of the physiological and morphological adaptations permitting its winter endurance in this harsh environment are well understood. However, it remains unknown how the conspicuous moult from a greyish brown summer to a white winter plumage, and any underlying changes in plumage structure and feather morphology, contribute to seasonal acclimatisation. We used standard morphometric techniques to describe the seasonal change in plumage and feather characteristics in six body regions. Then, we investigated whether winter plumage traits differed between first-winter and adult (second winter, or older) birds, because a difference in coat insulation has been suggested as an explanation for why first-winter Svalbard Ptarmigan loose more heat than adults. Plumage feather density (i.e., feathers × cm^{-2}) and mass density (i.e., mg feathers × cm^{-2}) were higher in winter, particularly on the head and feet where individual feathers were also heavier, longer, and downier. Seasonal changes in other regions (back, tarsi) indicated acclimatisation primarily to resist physical wear and wind. First-winter and adult birds had similar feather densities. However, mass density in first-winter birds was significantly lower than in adults in all but one body region (back) because individual feathers weighed less. This can explain previous observations of higher heat loss rates in first-winter birds. Our study suggests that plumage acclimatisation contributes to optimising the winter phenotype of Svalbard Rock Ptarmigan, both through higher insulative capacity and by improved resistance to harsh weather. The extent of these adaptations may be determined by the time or energy available for feather growth, exemplified here by inferior insulation in first-winter birds.

Keywords Arctic · Feather · Moult · Plumage · Polar · Thermoregulation

Introduction

Animals that reside permanently in high-latitude environments must deal with pronounced seasonal variations in air temperature, photoperiod, and precipitation. This can be challenging in winter, when low air temperatures increase thermoregulatory energy costs at the same time as short days and inclement weather make it more difficult to find food. Hence, high-latitude residents exhibit seasonal adaptation of physiology, morphology, and behaviour (Blix 2016), such that winter-acclimatised animals are typically more efficient both in producing heat and in minimizing heat loss compared to summer-acclimatised individuals (Mortensen and Blix 1986; Blix 1989; Haftorn 1992; Signer et al. 2011; Swanson and Vézina 2015; Nord and Folkow 2018).

Heat loss rate can be altered immediately by increasing or decreasing (skin) temperature in the body periphery, by way of adjustments in blood flow rate and/or circulatory pattern (e.g. Irving and Krog 1955; Midtgård 1981; Johansen and Bech 1983). This allows animals to respond quickly to changes in their energy budget or thermal environment (Ekimova 2005; Tattersall et al. 2009; Winder et al. 2020). However, the most decisive factor for heat balance in terrestrial

---

✉ Andreas Nord
andreas.nord@biol.lu.se

[1] Department of Biology, Lund University, Lund, Sweden

[2] Department of Arctic and Marine Biology, University of Tromsø – The Arctic University of Norway, Tromsø, Norway

[3] Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeș-Bolyai University, Cluj-Napoca, Romania

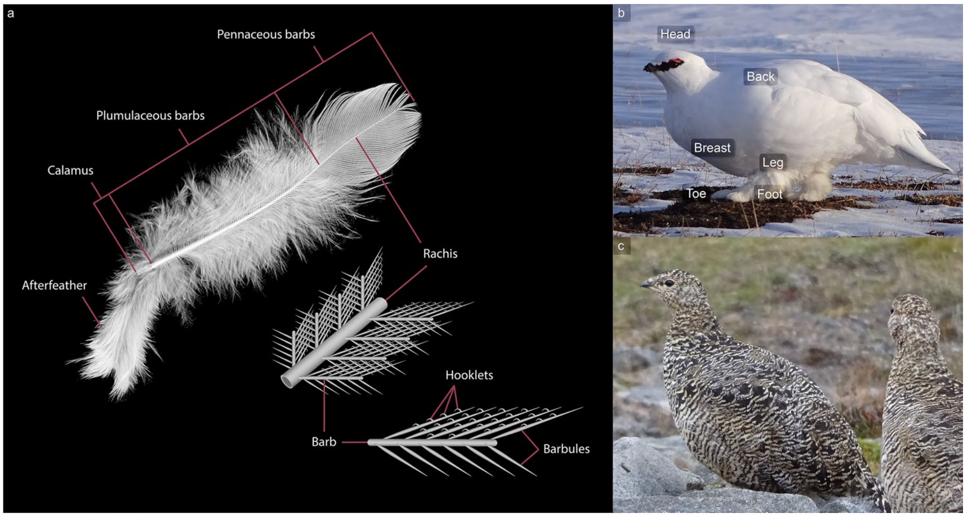

Fig. 1 Overview of feather structure and seasonal changes in plumage appearance in Svalbard Rock Ptarmigan, *Lagopus muta hyperborea*. **a** A representative photograph of a back feather from the winter plumage of a Svalbard Ptarmigan (individual 89–137) showing morphological traits referred to in the running text. The illustrations show the microstructure of the barbs and barbules, also referenced in the text. **b** A Svalbard Ptarmigan male in winter plumage in late spring, overlooking the Arctowski mountain on Spitsbergen, Svalbard. Body regions measured for seasonal changes in plumage morphology are indicated in the figure. **c** Svalbard Ptarmigan females in summer plumage in Endalen, Spitsbergen, Svalbard. The feather in panel **a** was photographed by Benjamin Judik and the illustrations made by Vidar Holje. Andreas Nord photographed the birds in panels **b** and **c**

animals is the pelage (Scholander et al. 1950). In birds, this is provided by body feathers that cover most of the integument. The distal ('pennaceous') end of these feathers makes up the external layer of the plumage that protects the inner plumage layers from the environment (including convective heat loss by wind, precipitation, and low temperature) and serves in social signalling (Prum and Brush 2002). The inner plumage layer contributes most of the insulation and is composed of the proximal downy, or 'plumulaceous', parts of the body feathers (Fig. 1a) as well as specialised down feathers and semiplumes (Pap et al. 2020). Many species also have an auxiliary down-like feather attached to the base of the contour feathers ('afterfeather'; Prum and Brush 2002) that is believed to also function mostly in insulation (Williams et al. 2015). The plumage keeps birds warm by trapping air (and thereby body heat) in a matrix of interlocking barbs and barbules of the contour feathers (Fig. 1a). This probably explains why, across the bird phylogeny, species that occupy colder environments have more feathers per unit area, and individual feather elements that are downier and loftier (i.e., have fewer barbs along the shaft), than do species that reside in warmer environments (Pap et al. 2017; Osváth et al. 2018). The same applies within species, where cold-hardier populations typically have downier contour feathers (Koskenpato et al. 2016; Barve et al. 2021).

It is unsurprising that birds residing in colder areas are particularly cold-tolerant. Even so, relatively few studies describe the role of the plumage in seasonal acclimatisation to winter conditions. However, thermal conductivity of the plumage was nearly 30% higher in summer than in winter in Rufous-collared Sparrows (*Zonotrichia capensis*), a Central and South American sparrow (Novoa et al. 1994). Moreover, in Dark-eyed Juncos (*Junco hyemalis*), a temperate North American sparrow that breeds far into the Arctic, the dry mass of contour feathers was 31% higher in winter than in summer, which coincided with a seasonal increase in thermogenic capacity and cold tolerance (Swanson 1991). On the other hand, while the winter plumage in some cardueline finches from central North America was significantly heavier than the summer plumage (Dawson and Carey 1976; Middleton 1985), the seasonal improvement in cold tolerance was not associated with the development of a thicker coat (Dawson and Carey 1976). While previous work provides mixed evidence for a role of the plumage in winter acclimatisation, it should be noted that these studies have been performed using small (<50 g) species with inherently high heat loss rates. These phenotypic traits require small birds to rely predominantly on a seasonal improvement in thermogenic capacity to stay warm in the winter (Swanson and Vézina 2015). By contrast, larger species can exploit improved insulation to a greater extent because of their larger thermal mass (Blix 2016). Yet, to our knowledge there are no studies of seasonal changes in the micro- and macroscopic morphology of feathers and plumages in large birds.

To elucidate the role of body insulation in the winter energy balance of a large bird species, we studied the seasonal changes in plumage and feather traits in the Svalbard Rock Ptarmigan (*Lagopus muta hyperborea* Sundevall, 1845; henceforth 'Svalbard Ptarmigan'), the world's most northerly distributed land bird. In winter, this bird experiences low temperature and continuous darkness for four months, during which time foraging opportunities are scarce and unpredictable. To survive in this environment, the Svalbard Ptarmigan exhibits a range of morphological and physiological seasonal adaptations, including conspicuous autumnal fattening starting in late summer (Stokkan et al. 1986a) and downregulation of metabolically expensive processes such as immune function and locomotion in winter (Lindgård et al. 1995; Nord et al. 2020). There is also a post-nuptial moult from a greyish-brown summer coat into a white winter coat, so that the birds are excellently well camouflaged both on bare ground in the summer and on snow in the winter (Fig. 1b, c). It is not known whether this conspicuous seasonal moult entails structural changes to plumage or feathers that act in concert with physio-morphological responses to improve winter energy balance. Hence, we studied plumage thickness and density, as well as the macro- and microstructure of feathers, in key body regions for heat exchange, in summer- and winter-acclimated Svalbard Ptarmigan. If winter acclimatisation occurs also on the level of the plumage, we hypothesised that winter birds would have a denser plumage with heavier feathers. We also hypothesised that the individual feathers would be more conducive for heat retention, that is, with a larger proportion of down and fewer feather elements along the shaft (i.e., fewer barbs). We have shown that there is a difference in the extent of the seasonal metabolic downregulation between first-winter and second-winter, or older, (henceforth 'adult') Svalbard Ptarmigan, whereby the former maintain higher metabolic and heat loss rates than the latter throughout winter (Nord and Folkow 2018). Since moulting into a more insulating plumage requires both nutritional resources, energy, and time (Lindström et al. 1993; Nilsson and Svensson 1996; Pap et al. 2008; Broggi et al. 2011), juvenile birds might face a resource-based trade-off between investing in physical maturation and investing in feather or plumage growth (Butler et al. 2008). In line with this, we previously proposed that the thermal and metabolic differences between first-winter and adult Svalbard Ptarmigan could be explained by age-related differences in growth of the winter coat (Nord and Folkow 2018). Here, we tested this hypothesis by comparing winter plumage traits between first-winter and adult birds, under the prediction that the former would have a thinner, less dense plumage than the latter. This study provides new information on causes and constraints on seasonal adaptation of body insulation and lays new pieces to the puzzle that explains the basis for winter existence in the world's northernmost terrestrial bird.

Materials and methods

Data on plumage characteristics were collected opportunistically from 37 Svalbard Ptarmigan that had died of natural causes or been euthanised for tissue collection for other studies, between 2009 and 2017. The birds were either bred at UiT—the Arctic University of Norway (34 of 37 birds) or were caught as young chicks (< 3 weeks old) near Longyearbyen, Svalbard (78° N) between 1.5 to 3 years before being sampled (3 of 37 birds). Regardless of origin, all birds completed their somatic growth and moult in captivity in Tromsø, either in indoor facilities in thermoneutrality (0 to + 5 °C; Mortensen & Blix 1986; Nord and Folkow 2018; 31 of 37 birds) with simulated Svalbard photoperiod or outdoors subject to natural Tromsø photoperiod (69° N) and temperature (6 of 37 birds). Previous research has shown that the basic physiological and morphological adaptations associated with winter acclimatisation, such as fat deposition, food intake, and energy expenditure, do not differ in birds of wild and captive origin (e.g. Stokkan et al. 1986a, b; Lindgård and Stokkan 1989). Nine birds were in summer plumage (3 males and 6 females) and 28 in winter plumage (11 females, 16 males, 1 of unknown sex).

All birds were stored in – 20 °C prior to sampling, which occurred in 2016 and 2018. Plumage density characteristics were measured in six body regions with previously demonstrated significances for heat exchange (Mercer and Simon 1987; Nord and Folkow 2018, 2019), viz. in the crown area of the skull ("head"), between the scapulae ("back"), in the pectoralis area laterally to the sternal keel ("breast"), laterally on the outward-facing part of the tibiotarsus ("tarsus"), dorsally on the metatarsus ("foot"), and laterally on the outward-facing aspect of the innermost the forward-pointing digit ("toe") (Fig. 1b). Data were collected following protocols from our previous work (Osváth et al. 2018; Pap et al. 2020). Briefly, all feathers were plucked individually from the region of interest in completely thawed birds (to make sure no soft tissue adhered to the calamus), after which the bare skin area was photographed against a scale reference (1 × 1-mm grid paper). The feathers were then counted and put into a drying oven at 37 °C for 48 h before being weighed to the nearest 0.1 mg. Pilot measurements confirmed that drying beyond 48 h did not cause any further reduction in sample mass. The area of the plucked region was measured using ImageJ (Schneider et al. 2012) to derive: (1) plumage feather density (feathers × cm^{-2}); (2) mean feather mass (total sample mass / feather sample count; in mg), and (3) plumage mass density (mg feathers × cm^{-2}). Sample size varied between plumages, ages, and body parts depending on which tissues had been harvested for other projects before measurements were taken (Tables 1, 2).

Table 1 Model estimates ± standard errors (s.e.m.), raw data means ± s.e.m., sample sizes (n) and test statistics for models investigating seasonal changes in plumage density and mass characteristics in captive Svalbard Rock Ptarmigan, *Lagopus muta hyperborea*

Model	Estimate ± s.e.m.	Mean ± s.e.m	$n_{\text{summer}}\|n_{\text{winter}}$	LRT	d.f	p	$\sigma_{\text{Bird}}\|\sigma_{\text{Residual}}$
Plumage feather density (feathers × cm^{-2})							
Plumage × body part				58.5	5	**< 0.0001**	
Head*			9|25				
Summer	3.30 ± 0.12	28.33 ± 3.03					
Winter	3.65 ± 0.07	39.09 ± 1.75					
Back			9|28				
Summer	2.16 ± 0.12	9.01 ± 0.88					
Winter	1.99 ± 0.07	7.54 ± 0.40					
Breast*			9|16				
Summer	1.34 ± 0.12	4.53 ± 0.86					
Winter	1.63 ± 0.07	5.62 ± 0.47					
Tarsus			9|28				
Summer	1.96 ± 0.12	7.49 ± 0.89					
Winter	1.72 ± 0.07	5.80 ± 0.33					
Foot			9|28				
Summer	4.04 ± 0.12	59.93 ± 7.40					
Winter	4.02 ± 0.07	59.16 ± 3.96					
Toe*			9|28				
Summer	4.07 ± 0.12	74.04 ± 18.88					
Winter	5.00 ± 0.07	153.21 ± 6.73					
Plumage							
Body Part							
Bird ID (random)				10.4	1	**0.0013**	0.14|0.31
Feather mass (mg)							
Plumage × body part				88.8	5	**< 0.0001**	
*Head			9|25				
Summer	− 7.57 ± 0.10	0.53 ± 0.05					
Winter	− 6.84 ± 0.06	1.09 ± 0.05					
Back			9|28				
Summer	− 4.70 ± 0.10	9.15 ± 0.40					
Winter	− 4.63 ± 0.06	10.06 ± 0.49					
Breast*			9|16				
Summer	− 5.00 ± 0.10	7.13 ± 0.78					
Winter	− 5.46 ± 0.07	4.85 ± 0.55					
Tarsus			9|28				
Summer	− 5.73 ± 0.10	3.37 ± 0.11					
Winter	− 5.78 ± 0.06	3.14 ± 0.11					
Foot			9|28				
Summer	− 7.03 ± 0.10	0.91 ± 0.08					
Winter	− 7.18 ± 0.06	0.82 ± 0.08					
Toe*			9|28				
Summer	− 7.82 ± 0.10	0.45 ± 0.07					
Winter	− 6.97 ± 0.06	0.98 ± 0.05					
Plumage							
Body part							
Bird ID (random)				9.4	1	**0.0021**	0.12|0.28
Plumage mass density (mg × cm^{-2})							
Plumage × body part				113.6	5	**< 0.0001**	
Head*			9|25				

Table 1 (continued)

Model	Estimate ± s.e.m.	Mean ± s.e.m	$n_{\mathrm{summer}}\|n_{\mathrm{winter}}$	LRT	d.f	p	$\sigma_{\mathrm{Bird}}\|\sigma_{\mathrm{Residual}}$
Summer	− 4.26 ± 0.16	15.10 ± 2.15					
Winter	− 3.18 ± 0.10	42.53 ± 2.70					
Back			9|28				
Summer	− 2.54 ± 0.16	81.63 ± 8.32					
Winter	− 2.64 ± 0.09	76.27 ± 6.17					
Breast			9|16				
Summer	− 3.65 ± 0.16	34.16 ± 0.29					
Winter	− 3.86 ± 0.12	29.28 ± 5.43					
Tarsus			9|28				
Summer	− 3.78 ± 0.16	26.79 ± 5.25					
Winter	− 4.06 ± 0.09	18.04 ± 1.13					
Foot			9|28				
Summer	− 3.00 ± 0.16	55.56 ± 9.62					
Winter	− 3.17 ± 0.09	49.91 ± 3.93					
Toe*			9|28				
Summer	− 3.75 ± 0.16	34.59 ± 10.41					
Winter	− 1.96 ± 0.09	152.16 ± 10.93					
Plumage							
Body Part							
Bird ID (random)				26.2	1	**< 0.0001**	0.26|0.41

All dependent variables were log-transformed before statistical testing and estimates are presented on the log scale. Mean values were calculated from the raw data. No estimates are provided for main effects in models where the interaction is significant

LRT likelihood ratio test statistic; *d.f.* degrees of freedom. σ_{Bird} standard deviation of the random intercept, $\sigma_{\mathrm{Residual}}$ residual standard deviation

For interactions, pairwise comparisons were performed between plumages within body regions, and significant between-plumage differences are denoted by asterisks. Significant p-values are highlighted in bold font

To measure feather macro- and microstructure, we collected up to three feathers from the head, back, breast and leg of 14 live birds in summer coat (2 females, 12 males), and again from the same birds once they had completed moult into their winter plumage. In addition, we collected winter feathers from three male birds that could not be sampled in summer. All birds had been kept indoors in thermoneutrality under simulated Svalbard photoperiod for a minimum of 1 year before sampling. Of the 14 birds sampled in both seasons, 5 were of wild origin and 9 had been hatched at UiT. Of the three additional birds that were sampled in winter only, 2 were of wild origin and 1 had been bred at UiT. The wild-origin birds were caught at Svalbard as young chicks and had completed their post-juvenile and first prebreeding moult in captivity. We photographed one representative feather per bird, body region, and season against a 1 × 1-mm grid. Our previous work has shown that repeatability of feather traits between feathers within the same individual is high (i.e., 0.6–0.9 for all traits considered; Pap et al. 2017). We used the photographs to determine (using ImageJ): (1) total feather length (i.e., fan + calamus; in mm); (2) the length of the plumulaceous (downy) part of the feather relative to total feather length; and (3) pennaceous and plumulaceous barb and barbule densities (i.e., barbs or barbules × mm^{-1}). These morphological structures are illustrated in Fig. 1a. We were not able to measure the density of plumulaceous barbules on the head feathers because this structure was too small to meter accurately with our microscope. Leg feathers were downy in entity in both summer and winter, and so there are no data for pennaceous barbs and barbules for this feather type.

Statistical analyses

All statistical analyses were performed using R version 4.0.3 (R Core Team 2021). Because females were both underrepresented in the data sets and unevenly replicated across age and plumage categories, we pooled the sexes in all analyses. Previous work on Svalbard Ptarmigan shows that there is no sexual dimorphism in body or organ size (Mortensen et al. 1983), and no meaningful sex differences in diet composition (Unander et al. 1985) at any time of the year. Thus, there is reason to expect similar selection for plumage and feather structure in males and females.

We used linear mixed effects models (lmer function in lme4) (Bates et al. 2015) to test for summer-to-winter

Table 2 Model estimates ± standard errors (s.e.m.), raw data means ± s.e.m., sample sizes (*n*) and test statistics for models comparing the differences in winter plumage characteristics between first-winter and adult Svalbard Ptarmigan

Model	Estimate ± s.e.m	Mean ± s.e.m	$n_{\text{first-winter}} \mid n_{\text{adult}}$	LRT	*d.f*	*p*	$\sigma_{\text{Bird}} \mid \sigma_{\text{Residual}}$
Plumage feather density (feathers × cm^{-2})							
Age × body part				5.3	4	0.2577	
Age				2.7	1	0.1008	
Body part				439.6	4	**< 0.0001**	
Head^{a}	3.66 ± 0.05	39.09 ± 1.75	14|11				
Back^{b}	1.99 ± 0.05	7.54 ± 0.40	14|14				
Tarsus^{c}	1.72 ± 0.05	5.80 ± 0.33	14|14				
Foot^{d}	4.02 ± 0.05	59.16 ± 3.96	14|14				
Toe^{e}	5.00 ± 0.05	153.21 ± 6.73	14|14				
Bird ID (random)				8.8	1	**0.0030**	0.13|0.24
Feather mass (mg)							
Plumage × body part				6.3	4	0.1749	
Age				23.9	1	**< 0.0001**	
First-winter^{a}	−6.40 ± 0.03	3.02 ± 0.40	14|14				
Adult^{b}	−6.16 ± 0.03	3.80 ± 0.43					
Body part				391.2	4	**< 0.0001**	
Head^{a}	−6.83 ± 0.05	1.01 ± 0.05	14|11				
Back^{b}	−4.63 ± 0.05	10.06 ± 0.49	14|14				
Tarsus^{c}	−5.78 ± 0.05	3.14 ± 0.11	14|14				
Foot^{d}	−7.18 ± 0.05	0.82 ± 0.08	14|14				
Toe^{ae}	−6.97 ± 0.05	0.98 ± 0.05	14|14				
Bird ID (random)				0.0	1	1.00	0.00|0.24
Plumage mass density (mg × cm^{-2})							
Age × body part				13.7	4	**0.0082**	
Head*							
First-winter	−3.31 ± 0.09	37.45 ± 2.54	14|11				
Adult	−3.04 ± 0.10	48.99 ± 4.66					
Back							
First-winter	−2.71 ± 0.09	70.43 ± 7.15	14|14				
Adult	−2.58 ± 0.09	82.11 ± 10.08					
Tarsus*							
First-winter	−4.21 ± 0.09	15.23 ± 0.99	14|14				
Adult	−3.91 ± 0.09	20.85 ± 1.77					
Foot*							
First-winter	−3.50 ± 0.09	32.68 ± 3.82	14|14				
Adult	−2.83 ± 0.09	61.15 ± 4.29					
Toe*							
First-winter	−2.14 ± 0.09	125.87 ± 12.08	14|14				
Adult	−1.79 ± 0.09	178.44 ± 15.61					
Age							
Body part							
Bird ID (random)				11.0	1	**< 0.0001**	0.17|0.29

All dependent variables were log-transformed before statistical testing and estimates are presented on the log scale. Mean values were calculated from the raw data. No estimates are provided for main effects in models where the interaction is significant

LRT likelihood ratio test statistic, *d.f.* degrees of freedom, σ_{Bird} standard deviation of the random intercept, σ_{Residual} residual standard deviation

For interactions, pairwise comparisons were performed between age categories within body regions, and significant differences between the ages are denoted by asterisks. For main effects, significant differences between factor levels are denoted by different superscript, lowercase, letters. Significant *p*-values are highlighted in bold font

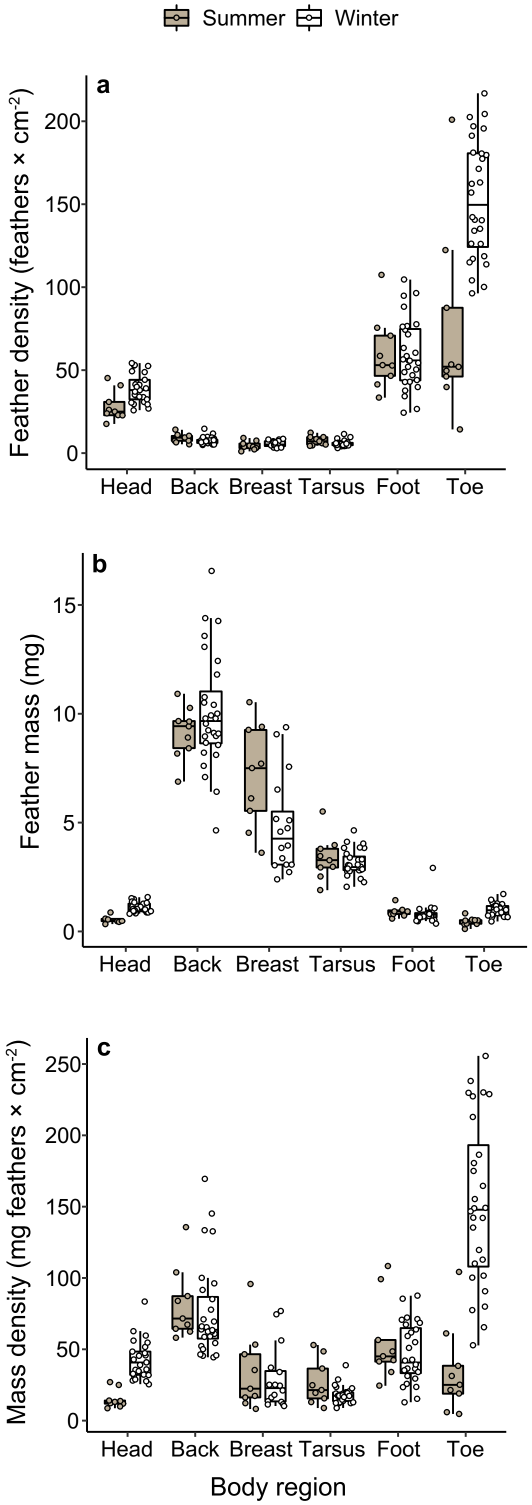

Fig. 2 Seasonal changes in plumage properties in the Svalbard Ptarmigan. The figure shows seasonal changes in feather density (**a**), mean feather mass (**b**), and plumage mass density (**c**) in six body regions. References to body parts are provided in the main text and in Fig. 1. Different birds were measured in the different seasons and sample sizes are provided in Table 1. Boxes show medians, first and third quartiles, and whiskers extend to the last observations with 1.5 × the interquartile range. Points show raw data

differences in plumage feather density, mean feather mass, and plumage mass density, and whether any such seasonal changes differed between body regions. We fitted separate models for each plumage or feather trait, all with season (summer or winter), body part, and season × body part, as fixed effects, and bird ID as a random effect. The inclusions of the interaction term allowed us to test whether any seasonal plumage change was uniform across the body, or whether it was particularly pronounced in body parts important for, for example, heat exchange and locomotion (such as the head and feet, respectively).

To test for age differences (first-winter or adult) in plumage traits, we used lmer models with the structure above, but using age in lieu of season as the explanatory variable. These models were fitted using the winter subset only since we did not have access to any first summer birds (i.e., growing chicks). However, measurement on such birds would likely not have been meaningful, because Svalbard Ptarmigan never attain a discrete post-juvenile summer plumage in their first year (A. Nord, pers. Obs.). Nor would measurement on birds in their first summer plumage (i.e., when in their second calendar year) have been suitable to test the hypothesis on constraints on optimal moult in young birds, because all age-related differences in heat production and heat loss rates have disappeared by this time in Svalbard Ptarmigan (Nord and Folkow 2018). Finally, we were unable to compare plumage traits on the breast between the age categories, because the pectoral muscles in all but two first-winter birds were excised for use in another study prior to feather sampling.

All feather structure data (apart from the proportion of plumulaceous barbs) were analysed using lmer models with the same fixed and random structure as for the seasonal-difference-in-plumage tests. The proportion of plumulaceous barbs was analysed using a generalised linear mixed effects model (glmer in lme4) with a binomial error structure and the fixed and random terms above.

Significances were assessed using likelihood ratio tests in all cases. Non-significant (i.e., $p > 0.05$) interactions were removed from the models but main effects were always retained. When interactions were significant, we performed pairwise comparisons between plumage types or age categories within body parts, using the emmean function in the emmeans package (Lenth 2019). All dependent variables (except for the proportion of plumulaceous barbs) were log-transformed before analyses to meet parametric assumptions (as inferred from diagnostic plots).

Results

Seasonal differences in plumage traits

Plumage feather density and mean feather mass differed significantly between summer and winter on the head, breast, and toes, whereas mass density differed seasonally on the head and toes (Table 1). The largest seasonal changes occurred on the toes, where the model predicted a 2.5-fold increase in feather density, a 2.3-fold increase in mean feather mass, and a 6.0-fold increase in mass density, between summer and winter (Fig. 2). As a result, the proportion of bare skin in contact with the ground (i.e., on the underside of the feet) decreased from 44 to 0% (data not shown). The head plumage also showed pronounced seasonal changes. Specifically, head feather density increased 1.4-fold (Fig. 2a) and mean feather mass 2.1-fold (Fig. 2b) between summer and winter, causing a 2.9-fold increase in head plumage mass density (Fig. 2c). In winter, the breast plumage was 1.3-fold denser than in summer (Fig. 2a), but individual feathers weighed 0.7-fold less (Fig. 2b). As a result, breast plumage mass density did not differ between summer and winter (Fig. 2c).

Age differences in plumage traits

There were no differences in feather density between first-winter and adult Svalbard Ptarmigan in any body region (Fig. 3a, Table 2). However, adult winter feathers were, on average, 1.3-fold heavier than in first-winter birds (Fig. 3b). Accordingly, plumage mass density was significantly higher in adults in all regions but the back (Table 2). Specifically, on the head and tarsi, adult mass density was 1.3-fold higher compared to first-winter birds. On the feet and toes, it was 2.0-fold and 1.4-fold higher in adults than in first-winter birds (Fig. 3c, Table 2).

Seasonal differences in feather structure

Seasonal changes in feather length were recorded on the head, back and tarsus, and in the proportion of plumulaceous barbs (i.e., 'downiness') on the head and back (Table 3). Specifically, in winter, head feathers were 1.5-fold longer and 2.8-fold downier than in summer, whereas back feathers were 0.9-fold shorter but 1.3-fold downier (Fig. 4a, b). Tarsus feathers were also 0.9-fold shorter in winter compared to summer (Fig. 4a). Barb density changed between summer and winter in the head and tarsus feathers (Table 3). Accordingly, individual head feathers were loftier in winter, showing a 0.4-fold decrease in pennaceous barb density and a 0.9-fold decrease in plumulaceous barb density compared to summer (Fig. 4c, d). By contrast, tarsus feathers (which were always plumulaceous in entity) showed a 1.2-fold *increase* in barb density in winter (Fig. 4d). There were no body part-specific changes to pennaceous barbule density (Table 3). However, when averaging over body parts, pennaceous barbule density was 0.9-fold lower in winter than in summer (Fig. 4e). Across seasons, pennaceous barbule density was higher on the back compared to the head which, in turn, had higher pennaceous barbule density than the breast (Fig. 4e). Plumulaceous barbule density did not differ between summer and winter and was the highest on the back, followed by the breast and tarsus (Table 3, Fig. 4f).

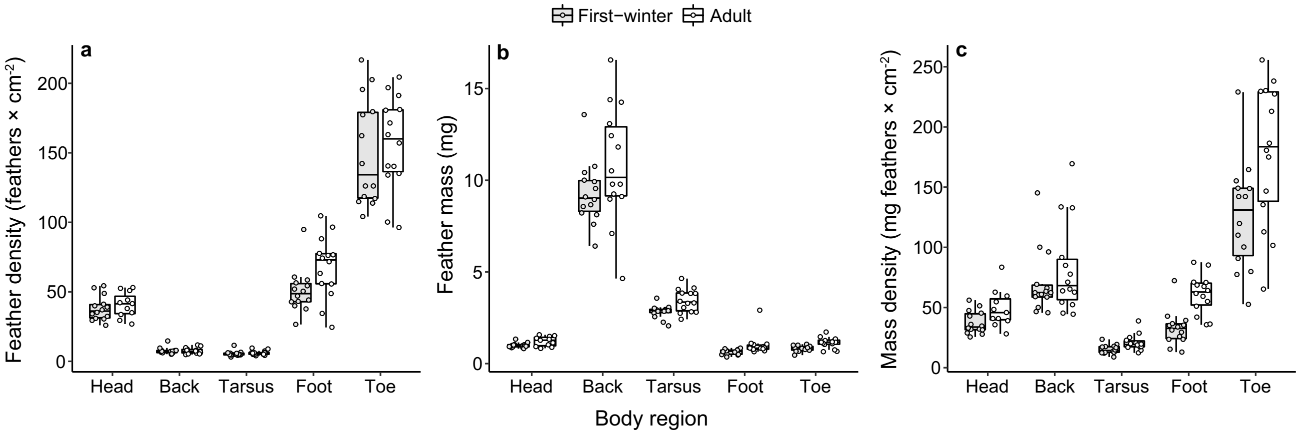

Fig. 3 Age-related differences in winter plumage properties in Svalbard Ptarmigan. The panels show feather density (**a**), mean feather mass (**b**), and plumage mass density (**c**) in first-winter (grey boxes and points) and adult (white boxes and points) birds that had completed their post-juvenile and post-nuptial moults, respectively, in captivity. References to body regions are provided in the main text and in Fig. 1. Sample sizes are provided in Table 2. Boxes show medians, first and third quartiles, and whiskers extend to the last observations with 1.5 × the interquartile range. Points show raw data

Table 3 Model estimates ± standard errors (s.e.m.), raw data means ± s.e.m., sample sizes (*n*) and details on statistical tests for models comparing seasonal changes of the macro- and microstructure of contour feathers in Svalbard Ptarmigan

Model	Estimate ± s.e.m	Mean ± s.e.m	$n_{\text{summer}}\|n_{\text{winter}}$	LRT	*d.f*	*p*	$\sigma_{\text{Bird}}\|\sigma_{\text{Residual}}$
Feather length (mm)			14|17				
Plumage × body part				74.3	3	**< 0.0001**	
Head*							
Summer	2.96 ± 0.03	19.53 ± 0.80					
Winter	3.35 ± 0.03	28.55 ± 0.56					
Back*							
Summer	4.15 ± 0.03	63.86 ± 2.30					
Winter	4.04 ± 0.03	57.25 ± 1.18					
Breast							
Summer	3.65 ± 0.03	38.57 ± 0.81					
Winter	3.71 ± 0.03	41.04 ± 0.88					
Tarsus*							
Summer	3.89 ± 0.03	49.47 ± 1.65					
Winter	3.81 ± 0.03	45.44 ± 1.50					
Plumage							
Body part							
Bird ID (random)				1.4	1	0.2380	0.03|0.11
Proportion plumulaceous barbs			14|17				
Plumage × body part				19.5	2	**< 0.0001**	
Head*							
Summer	− 1.46 ± 0.15	0.192 ± 0.006					
Winter	− 0.42 ± 0.09	0.397 ± 0.007					
Back*							
Summer	− 0.42 ± 0.07	0.395 ± 0.018					
Winter	− 0.12 ± 0.06	0.468 ± 0.015					
Breast							
Summer	− 0.20 ± 0.09	0.449 ± 0.015					
Winter	− 0.08 ± 0.08	0.479 ± 0.016					
Plumage							
Body part							
Bird ID (random)				0.0	1	0.8963	0.00|-
Pennaceous barb density (barbs × mm^{-1})			14|17				
Plumage × body part				55.7	2	**< 0.0001**	
Head*							
Summer	0.82 ± 0.05	2.27 ± 0.07					
Winter	0.02 ± 0.05	1.03 ± 0.04					
Back							
Summer	0.66 ± 0.05	1.95 ± 0.05					
Winter	0.60 ± 0.05	1.83 ± 0.04					
Breast							
Summer	0.37 ± 0.05	1.47 ± 0.06					
Winter	0.27 ± 0.05	1.38 ± 0.10					
Plumage							
Body part							
Bird ID (random)				1.0	1	0.3234	0.05|0.19
Plumulaceous barb density (barbs × mm^{-1})			14|17				
Plumage × body part				20.1	3	**0.0002**	
Head*							
Summer	1.29 ± 0.03	3.65 ± 0.13					
Winter	1.16 ± 0.03	3.25 ± 0.13					
Back							
Summer	1.05 ± 0.03	2.86 ± 0.06					

Table 3 (continued)

Model	Estimate ±s.e.m	Mean ±s.e.m	$n_{\text{summer}}\vert n_{\text{winter}}$	LRT	*d.f*	*p*	$\sigma_{\text{Bird}}\vert\sigma_{\text{Residual}}$
Winter	1.03 ± 0.03	2.81 ± 0.06					
Breast							
Summer	1.08 ± 0.03	2.94 ± 0.05					
Winter	1.09 ± 0.03	2.97 ± 0.06					
Tarsus*							
Summer	0.18 ± 0.03	1.21 ± 0.04					
Winter	0.32 ± 0.03	1.38 ± 0.05					
Plumage							
Body Part							
Bird ID (random)				0.9	1	0.3365	0.03|0.11
Pennaceous barbule density (barbules × mm^{-1})			14|17				
Plumage × body part				5.3	2	0.0724	
Plumage				16.6	1	**< 0.0001**	
Summer^{a}	2.98 ± 0.02	14.95 ± 1.24					
Winter^{b}	2.85 ± 0.02	13.15 ± 0.97					
Body part				30.0	2	**< 0.0001**	
Head^{a}	2.92 ± 0.03	18.77 ± 0.69					
Back^{b}	3.02 ± 0.03	20.48 ± 0.49					
Breast^{c}	2.80 ± 0.03	16.58 ± 0.41					
Bird ID (random)				1.5	1	0.2134	0.04|0.14
Plumulaceous barbule density (barbules × mm^{-1})			14|17				
Plumage × body part				1.2	2	0.5357	
Plumage				3.5	1	0.0624	
Body part				91.5	2	**< 0.0001**	
Back^{a}	3.10 ± 0.03	22.55 ± 0.65					
Breast^{b}	2.90 ± 0.03	18.61 ± 0.60					
Tarsus^{c}	2.63 ± 0.03	13.93 ± 0.22					
Bird ID (random)				0.0	1	1.00	0.0|0.15

All dependent variables were log-transformed before statistical testing and estimates are presented on the log scale. Mean values were calculated from the raw data. Estimates for main effects are not provided when the interaction is significant

LRT likelihood ratio test statistic, *d.f.* degrees of freedom, σ_{Bird} standard deviation of the random intercept, σ_{Residual} residual standard deviation

For interactions, pairwise comparisons were performed between plumages within body parts, and significant between-plumage differences are denoted by asterisks. For main effects, significant differences between factor levels are denoted by different superscript letters. Significant *p*-values are highlighted in bold font

Discussion

Our study shows that the post-nuptial moult into a white winter plumage in Svalbard Ptarmigan not only serves to maintain year-round camouflage, but that it is also associated with morphological adaptation to counter low temperature, increased snow depth, and inclement weather during the cold season. On average, the winter plumage had more feathers and individual feather elements were heavier, loftier (i.e., barb density was lower), and had more insulating down than in summer. These traits will improve insulation by increasing air space within the coat and correspond well to plumage and feather adaptation to low temperature reported in interspecific studies (Pap et al. 2017, 2020; Osváth et al. 2018).

Seasonal adaptation of plumage and feathers varies between body regions

Seasonal acclimatisation varied in both type and magnitude between body regions, which probably reflects the multiple simultaneous roles of the plumage as a physical barrier between the body and the environment (Prum and Brush 2002). We found large seasonal changes on the head, where the winter plumage was denser, and individual feather elements were heavier, longer, downier, and loftier than in summer. It is not surprising that morphological adaptation of head plumage and feathers was stronger than in other body regions. Specifically, the proximal location and high surface-area-to-volume ratio of the Ptarmigan head, in combination with continuous high circulation to the brain, make

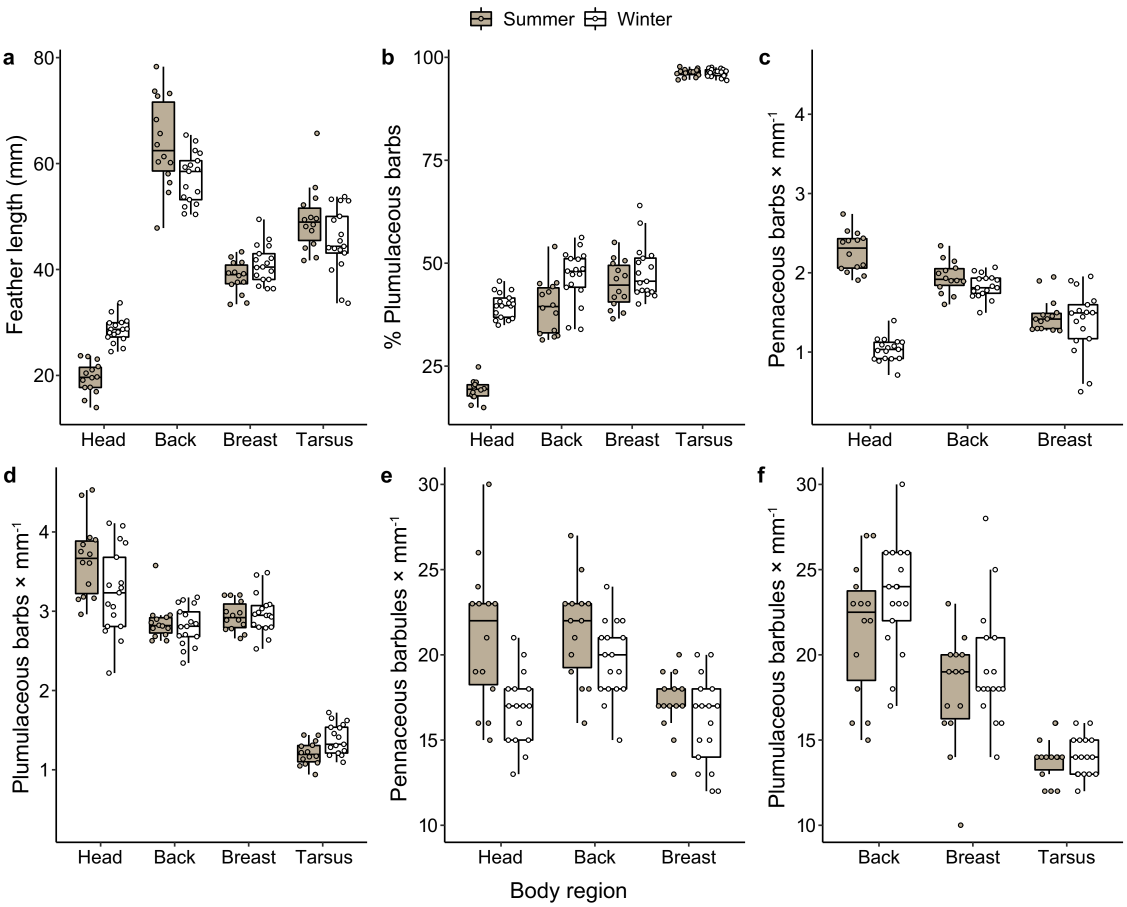

Fig. 4 Seasonal changes in the macro- and microstructure of Svalbard Ptarmigan feathers in four body regions. The panels show total feather length (**a**), the proportion of plumulaceous barbs on the feather (**b**), pennaceous and plumulaceous barb density (**c**, **d**), and pennaceous and plumulaceous barbule density (**e**, **f**), in summer (tan boxes and points) and winter (white boxes and points). References to body regions and feather traits are provided in the main text and in Fig. 1. Fourteen of 17 birds were sampled in both summer and winter, and three birds were sampled in winter only. Tarsus feather barbs were always plumulaceous in entity. Data on plumulaceous barbule density are lacking for head feathers since this structure was too small to be accurately counted. Boxes show medians, first and third quartiles, and whiskers extend to the last observations with 1.5 × the interquartile range. Points show raw data

it a heat-sink (Nord and Folkow 2018, 2019) to the point where a significant proportion of winter heat production must be allocated just to keeping the head warm (Nord and Folkow 2018). Because peripheral cooling (local heterothermy) in the head region could impair cognitive ability (Rashotte et al. 1998; Carr and Lima 2013) and consequently increase predation risk (Carr and Lima 2013; Brodin et al. 2017), investment in head insulation seems a prudent fitness consideration.

While *area-specific* heat loss from the head is the highest across the Ptarmigan integument (Nord and Folkow 2018), *total* heat loss is probably the highest from the body trunk because of its considerably larger surface area (cf. McCafferty et al. 2013). In view of this, it is surprising that there were few seasonal changes to plumage- and feather traits across the back and breast. For example, breast plumage density increased between summer and winter (Fig. 2a), but because individual feathers were lighter (Fig. 2b), there was no seasonal improvement in plumage mass density (Fig. 2c). Thus, there were probably no marked seasonal changes in plumage insulation in this body part. It is possible that a denser (i.e., more feathers per unit area) coat is more resistant to wear, which could be an important consideration since Ptarmigan sport their winter plumage for 9 months of the year (Steen and Unander 1985; Stokkan et al. 1986b). Alternatively, or additionally, it is possible that the plumage covering the pectoral muscles (the most thermogenic tissue in birds; Hohtola 2004) represents a trade-off between the need to minimise heat loss at rest, while still allowing sufficient heat dissipation during strenuous activity, for which a sparsely feathered ventral surface is important (Nord and Nilsson 2019). Back feathers were 0.9-fold shorter, but 1.3-fold downier, in winter than in summer. These feathers were by far the longest and heaviest year-round, so it is possible that a seasonal increase in either length or density on the back might not be compatible with other plumage functions, such as keeping drag minimal during flight. Yet, the back plumage is key to sheltering thoracic/abdominal organs since, even at rest and in inclement weather, Svalbard Ptarmigan will often have the entire dorsal surface exposed (AN, pers. obs.). It is therefore possible that the added insulation from more down on winter feathers (Fig. 4b) countered any negative effect on insulation from a seasonal reduction in back feather length. Moreover, shorter feathers might be less susceptible to disruption by strong winds, helping to keep the feather layer intact during spells of inclement weather in winter. This protective role of the back plumage could also explain why plumulaceous barbule density was the highest in back feathers (Fig. 4f), facilitating adhesion between feather elements in the insulative layer (Prum and Brush 2002).

The snowshoe effect

Feathering on the ventral and lateral aspects of the foot ("toes") increased markedly between summer and winter (Fig. 2), such that the proportion of ventral skin in contact with the ground surface decreased from 44% in summer to 0% in winter. This change could provide energetic benefits by reducing conductive heat loss through the feet (Gates 1980, Monteith and Unsworth 2013) and, not the least, help to reduce the risk of foot freeze injuries in winter. However, conductance through foot tissue will probably be low even without seasonal plumage adaptation since counter-current vascular arrangements together with control of motor state in the blood vessels (Midtgård 1981) presumably allow Ptarmigan to regulate foot pad temperature near ambient (Mercer and Simon 1987). Efficient physiological (cardiovascular) control of leg and feet heat loss could also explain why there were no seasonal differences in plumage traits on the legs and dorsal aspects of the foot. In fact, leg feathers were shorter and had increased barb density in winter than in summer (Fig. 4a, d). This probably resulted in lower leg insulation in winter. However, the same traits should also have increased resistance to physical wear, suggesting that seasonal changes in leg feather structure might be tailored to maintain plumage integrity more than to improving insulative value.

The seasonal development of plumage may contribute to the energy budget independently of insulation. In the context of the seasonal growth of digit plumage, it is plausible that energetic benefits were gained from the "snowshoe effect", that is, a reduction in load when walking on soft snow (Höhn 1977). Reducing load on the feet is important, because staying on top of ground substrate in winter will reduce the cost of transport (Mármol-Guijarro et al. 2021). When coupled to a seasonal improvement in the energetic efficiency of locomotion in Svalbard Ptarmigan (Lees et al. 2010), the snowshoe effect might, therefore, be more influential for the energy budget than reducing heat loss from the foot pad. This notion should be quantified in future studies.

First-winter birds sport a less insulating plumage than adults

Feather density was relatively similar between the winter plumages of first-winter and adult birds (Fig. 3a), but plumage mass density was significantly higher in nearly all body regions in adults (Fig. 3c). This is in keeping with the notion of temporal and energetic constraints on moult in juvenile birds (Butler et al. 2008) that might carry over to plumage insulation (Nilsson and Svensson 1996; Broggi et al. 2011). Our study, therefore, supports the hypothesis that time- or energy allocation-based constraints on investment in plumage growth, together with lower fat deposits, can explain the elevated heat loss rates in first-winter compared to adult Svalbard Ptarmigan (Nord and Folkow 2018). Here, this trade-off between completing somatic growth and investing in a high-quality plumage was evident not by the number of feathers but instead by their lower mass (Fig. 3b). Our birds were captive with unlimited food resources to invest in both somatic development and feather growth. Yet, even though both wild and captive Svalbard Ptarmigan chicks double their body mass every week from hatching, they still weigh only about two-thirds of adults when moult commences (Steen and Unander 1985); a difference that is maintained through the first winter (Nord and Folkow 2018). Hence, it can be speculated that the main constraint on feather development was time, in line with what has previously been suggested for songbirds (Vágási et al. 2010, 2012; Broggi et al. 2011). On the other hand, being raised under sheltered captive conditions may have caused acclimation-related effects on first-winter plumage mass and quality. Future studies should critically test these aspects by studying wild birds and by measuring the thermal conductivity of plumaged skin samples (e.g. Ward et al. 2007) or, preferably, whole plumaged skins (e.g. Bakken et al. 1981, 1983) in first-winter and adult birds over a range of relevant environmental conditions.

Conclusions

Our study suggests that seasonal changes in plumage and feather traits optimise the winter phenotype in Svalbard Ptarmigan beyond maintained camouflage. These seasonal adaptations differ between body regions and feather types in line with the multiple functional roles of the plumage, entailing providing insulation, aiding locomotion, and shielding from wind and precipitation. However, the extent of these adaptations is balanced by the time and/or energy available for feather growth, much like what is found in other bird species. It would be relevant for future studies to address, longitudinally, the causes of within- and between-individual variation in plumage and feather traits. This could shed light on currently unexplored questions in thermal biology, including the contributions of genetic and environmental variation, and phenotypic plasticity, to coat properties. Ultimately, this would contribute towards elucidating the ontogeny of, and natural selection on, plumage insulation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-023-03118-8.

Acknowledgements Comments from the Handling Editor and two anonymous reviewers improved a previous version of the article. Hans Lian, Hans Arne Solvang, and Renate Thorvaldsen excellently helped care for the experimental birds. Daniel Appenroth and Gabriela Wagner kindly provided additional material for the plumage characteristics study.

Author contributions AN and PLP conceived the idea and designed the protocol with input from LPF. AN collected the data and measured feather and plumage traits together with BJ and VH. AN, PLP and LPF interpreted the results. AN analysed the data, produced the graphical material (with VH) and wrote the first draft, which was edited by all authors. All authors approved submission and agreed to be accountable for all contents.

Funding Open access funding provided by Lund University. AN was supported by the Swedish Research Council (Grant Nos. 637-2013-7442, 2020-04686), Kungliga Fysiografiska Sällskapet (Grant No. 2017-39034), and the Carl Trygger Foundation for Scientific Research (Grant No. 14-347). PLP was financed by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (HAS).

Data availability Data are deposited in figshare: https://doi.org/10.6084/m9.figshare.22016723.

Declarations

Conflict of interest The authors declare they have no financial or commercial conflicts of interest.

Ethical approval Ethical permission for the upkeep of birds that were used in the feather trait study was granted by the Norwegian Food Safety Authority (approval no. 6639).

References

Bakken GS, Buttemer WA, Dawson WR, Gates DM (1981) Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. Ecology 62:311–318

Bakken GS, Erskine DJ, Santee WR (1983) Construction and operation of heated taxidermic mounts used to measure standard operative temperature. Ecology 64:1658–1662

Barve S, Ramesh V, Dotterer TM, Dove CJ (2021) Elevation and body size drive convergent variation in thermo-insulative feather structure of Himalayan birds. Ecography 44:680–689

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Soft 67:1–48

Blix AS (1989) Arctic resignation: winter dormancy without hypothermia. In: Malan A, Canguilhem B (eds) Living in the cold—2nd International Symposium. John Libbey, London, pp 117–119

Blix AS (2016) Adaptations to polar life in mammals and birds. J Exp Biol 219:1093–1105

Brodin A, Nilsson J-Å, Nord A (2017) Adaptive temperature regulation in the little bird in winter: predictions from a stochastic dynamic programming model. Oecologia 185:43–54

Broggi J, Gamero A, Hohtola E, Orell M, Nilsson J-Å (2011) Inter-population variation in contour feather structure is environmentally determined in great tits. PLoS ONE 6:e24942

Butler LK, Rohwer S, Speidel MG (2008) Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. J Avian Biol 39:629–639

Carr JM, Lima SL (2013) Nocturnal hypothermia impairs flight ability in birds: a cost of being cool. Proc R Soc Lond B 280:20131846

Dawson WR, Carey C (1976) Seasonal acclimatisation to temperature in cardueline finches—I. Insulative and metabolic adjustments. J Comp Physiol 112:317–333

Ekimova IV (2005) Thermoregulation in the pigeon *Columbia livia* during the stress produced by food deprivation. J Evol Biochem Phys 41:78–86

Gates DM (1980) Biophysical ecology. Dover Publications Inc, Mineola, New York

Haftorn S (1992) The diurnal body-weight cycle in titmice *Parus* spp. Orn Scand 23:435–443

Hohtola E (2004) Shivering thermogenesis in birds and mammals. In: Barnes BM, Carey HV (eds) Life in the cold—mechanisms, adaptation and application. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 241–252

Höhn EO (1977) The “snowshoe effect” of the feathering in Ptarmigan feet. Condor 79:380–382

Irving L, Krog J (1955) Temperature of skin in the Arctic as a regulator of heat. J Appl Physiol 7:355–364

Johansen K, Bech C (1983) Heat conservation during cold exposure in birds (vasomotor and respiratory implications). Polar Res 1:259–268

Koskenpato K, Ahola K, Karstinen T, Karell P (2016) Is the denser contour feather structure in pale grey than in pheomelanic brown tawny owls *Strix aluco* an adaptation to cold environments? J Avian Biol 47:1–6

Lees J, Nudds R, Stokkan K-A, Folkow L, Codd J (2010) Reduced metabolic cost of locomotion in Svalbard rock Ptarmigan (*Lagopus muta hyperborea*) during winter. PLoS ONE 5:1–8

Lenth RV (2019) emmeans: estimated marginal means, aka least-squares means. R package version 1.3.3. https://www.CRAN.R-project.org/package=emmeans

Lindgård K, Stokkan K-A (1989) Daylength control of food intake and body weight in Svalbard Ptarmigan *Lagopus mutus hyperboreus*. Orn Scand 20:176–180

Lindgård K, Stokkan KA, Näslund S (1995) Annual changes in body mass in captive Svalbard Ptarmigan: role of changes in locomotor activity and food intake. J Comp Physiol B 165:445–449

Lindström Å, Visser GH, Daan S (1993) The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiol Zool 66:490–510

Mármol-Guijarro A, Nudds R, Folkow L, Sellers W, Falkingham P, Codd J (2021) The Influence of snow properties on speed and gait choice in the Svalbard rock Ptarmigan (*Lagopus muta hyperborea*). Integr Org Biol 3:obab021

McCafferty DJ, Gilbert C, Thierry A-M, Currie J, Le Maho Y, Ancel A (2013) Emperor penguin body surfaces cool below air temperature. Biol Lett 9:20121192

Mercer JB, Simon E (1987) Appropriate and inappropriate hypothalamic cold thermosensitivity in willow Ptarmigan. Acta Physiol Scand 131:73–80

Middleton AL (1985) Seasonal changes in plumage structure and body composition of the American Goldfinch *Carduelis tristis*. Can Field Nat 100:545–549

Midtgård U (1981) The *Rete tibiotarsale* and arteriovenous association in the hind limb of birds: a compartive morphological study on counter-current heat exchange systems. Acta Zool 62:67–87

Monteith JL, Unsworth MH (2013) Principles of environmental physics—plants, animals, and the atmosphere, 4th edn. Edward Arnold, London

Mortensen A, Blix AS (1986) Seasonal changes in resting metabolic rate and mass-specific conductance in Svalbard Ptarmigan, Norwegian rock Ptarmigan and Norwegian willow Ptarmigan. Orn Scand 17:8–13

Mortensen A, Unander S, Kolstad M, Blix AS (1983) Seasonal changes in body composition and crop content of Spitzbergen Ptarmigan *Lagopus mutus hyperboreus*. Orn Scand 14:144–148

Nilsson J-Å, Svensson E (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proc R Soc Lond B 263:711–714

Nord A, Folkow LP (2018) Seasonal variation in the thermal responses to changing environmental temperature in the world's northernmost land bird. J Exp Biol 221:jeb171124

Nord A, Folkow LP (2019) Ambient temperature effects on stress-induced hyperthermia in Svalbard Ptarmigan. Biol Open 8:bio043497

Nord A, Hegemann A, Folkow LP (2020) Reduced immune responsiveness contributes to winter energy conservation in an Arctic bird. J Exp Biol 223:jeb219287

Nord A, Nilsson J-Å (2019) Heat dissipation rate constrains reproductive investment in a wild bird. Funct Ecol 33:250–259

Novoa FF, Bozinovic F, Rosenmann M (1994) Seasonal changes of thermal conductance in *Zonotrichia capensis* (Emberizidae), from central Chile: the role of plumage. Comp Biochem Physiol A 107:297–300

Osváth G, Daubner T, Dyke G, Fuisz TI, Nord A, Pénzes J, Vargancsik D, Vágási CI, Vincze O, Pap PL (2018) How feathered are birds? Environment predicts both the mass and density of body feathers. Funct Ecol 32:701–712

Pap PL, Vágási CI, Czirják GÁ, Barta Z (2008) Diet quality affects postnuptial molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral immune function? Can J Zool 86:834–842

Pap PL, Osváth G, Daubner T, Nord A, Vincze O (2020) Down feather morphology reflects adaptation to habitat and thermal conditions across the avian phylogeny. Evolution 74:2365–2376

Pap PL, Vincze O, Wekerle B, Daubner T, Vágási CI, Nudds RL, Dyke GJ, Osváth G (2017) A phylogenetic comparative analysis reveals correlations between body feather structure and habitat. Funct Ecol 31:1241–1251

Prum RO, Brush AH (2002) The evolutionary origin and diversification of feathers. Q Rev Biol 77:261–295

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rashotte ME, Pastukhov IF, Poliakov EL, Henderson RP (1998) Vigilance states and body temperature during the circadian cycle in fed and fasted pigeons (*Columba livia*). Am J Physiol 44:R1690–R1702

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675

Scholander PF, Walters V, Hock R, Irving L (1950) Body insulation of some Arctic and tropical mammals and birds. Biol Bull 99:225–236

Signer C, Ruf T, Arnold W (2011) Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. Funct Ecol 25:537–547

Steen JB, Unander S (1985) Breeding biology of the Svalbard rock Ptarmigan *Lagopus mutus hyperboreus*. Orn Scand 16:191–197

Stokkan KA, Mortensen A, Blix AS (1986a) Food intake, feeding rhythm, and body mass regulation in Svalbard rock Ptarmigan. Am J Physiol 251:R264–R267

Stokkan KA, Sharp PJ, Unander S (1986b) The annual breeding cycle of the high-arctic Svalbard Ptarmigan (*Lagopus mutus hyperboreus*). Gen Comp Endocrinol 61:446–451

Swanson DL (1991) Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. Condor 93:538–545

Swanson DL, Vézina F (2015) Environmental, ecological and mechanistic drivers of avian seasonal metabolic flexibility in response to cold winters. J Ornithol 156:377–388

Tattersall GJ, Andrade DV, Abe AS (2009) Heat exchange from the Toucan bill reveals a controllable vascular thermal radiator. Science 325:468–470

Unander S, Mortensen A, Elvebakk A (1985) Seasonal changes in crop content of the Svalbard Ptarmigan *Lagopus muta hyperboreus*. Polar Res 3:239–245

Vágási CI, Pap PL, Barta Z (2010) Haste makes waste: accelerated molt adversely affects the expression of melanin-based and depigmented plumage ornaments in House Sparrows. PLoS ONE 5:e14215

Vágási CI, Pap PL, Vincze O, Benkő Z, Marton A, Barta Z (2012) Haste makes waste but condition matters: molt rate-feather quality trade-off in a sedentary songbird. PLoS ONE 7:e40651

Ward JM, McCafferty D, Ruxton GD, Houston DC (2007) Thermal consequences of turning white in winter: a comparative study of red grouse *Lagopus lagopus scoticus* and Scandinavian willow grouse *L. l. lagopus*. Wildl Biol 13:120–129

Williams CL, Hagelin JC, Kooyman GL (2015) Hidden keys to survival: the type, density, pattern and functional role of emperor penguin body feathers. Proc R Soc Lond B 282:20152033

Winder LA, White SA, Nord A, Helm B, McCafferty DJ (2020) Body surface temperature responses to food restriction in wild and captive great tits. J Exp Biol 223:jeb220046