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Function and underlying mechanisms of seasonal colour moulting in mammals and birds: what keeps them changing in a warming world?

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ABSTRACT

Animals that occupy temperate and polar regions have specialized traits that help them survive in harsh, highly seasonal environments. One particularly important adaptation is seasonal coat colour (SCC) moulting. Over 20 species of birds and mammals distributed across the northern hemisphere undergo complete, biannual colour change from brown in the summer to completely white in the winter. But as climate change decreases duration of snow cover, seasonally winter white species (including the snowshoe hare *Lepus americanus*, Arctic fox *Vulpes lagopus* and willow ptarmigan *Lagopus lagopus*) become highly contrasted against dark snowless backgrounds. The negative consequences of camouflage mismatch and adaptive potential is of high interest for conservation. Here we provide the first comprehensive review across birds and mammals of the adaptive value and mechanisms underpinning SCC moulting. We found that across species, the main function of SCC moults is seasonal camouflage against snow, and photoperiod is the main driver of the moult phenology. Next, although many underlying mechanisms remain unclear, mammalian species share similarities in some aspects of hair growth, neuroendocrine control, and the effects of intrinsic and extrinsic factors on moult phenology. The underlying basis of SCC moults in birds is less understood and differs from mammals in several aspects. Lastly, our synthesis suggests that due to limited plasticity in SCC moulting, evolutionary adaptation will be necessary to mediate future camouflage mismatch and a detailed understanding of the SCC moulting will be needed to manage populations effectively under climate change.

Key words: coat colour moult, seasonal adaptation, camouflage mismatch, climate change, phenotypic mismatch, hare, arctic fox, weasel, Siberian hamster, ptarmigan.

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I. INTRODUCTION

Species occupying temperate and polar latitudes have multiple physiological and life-history adaptations that help them cope with harsh winters and high seasonality (Blix, 2016). Those circannual traits include seasonal migration, hibernation and coat colour moults, and their occurrence and optimal phenology is critical for maintaining fitness (Varpe, 2017). However, as global warming alters temperatures and snow cover across much of the northern hemisphere, seasonal adaptations become compromised (Pauli *et al.*, 2013; Williams, Henry, & Sinclair, 2015; Berteaux *et al.*, 2017). Understanding whether adaptation in these traits can occur is of intense interest (Helm *et al.*, 2013; Williams *et al.*, 2017) and requires comprehensive knowledge of the traits in question.

A key adaptive trait increasingly compromised by climate change is seasonal coat colour (SCC) moulting from dark pigmented fur or plumage in the summer to white in the winter. Although colour change is found across vertebrates (Duarte, Flores, & Stevens, 2017), complete SCC moults to match presence or absence of snow is unique to several bird and mammal species. The biannual phenotypic shifts are controlled with complex physiological mechanisms entrained by photoperiod and optimized to match local conditions. However, as seasonal duration and extent of snow cover declines due to climate change (Vaughan *et al.*, 2013; Kunkel *et al.*, 2016), SCC species become colour mismatched against their surroundings (Mills *et al.*, 2013) (Fig. 1B, C).

To understand how seasonally colour-changing species may respond to declining snow cover, we must first understand the ecological significance and the underlying mechanisms of this highly specialized trait. Although the ecology and physiology of SCC moults have received substantial attention from naturalists and scientists over the last century, insights from these fields have not been compiled across disciplines and species, or connected to

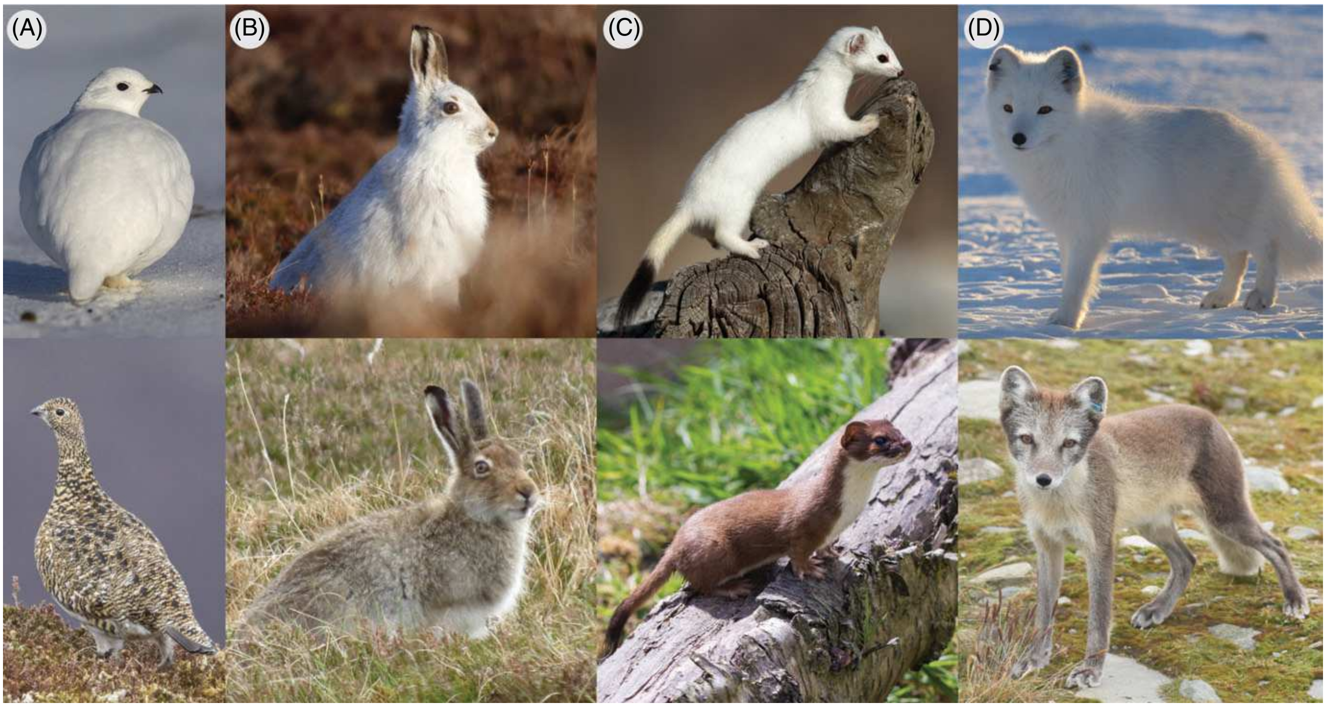

Fig. 1. Seasonal coat colour (SCC) species in their winter (top row) and summer (bottom row) coats. (A) Rock ptarmigan; (B) mountain hare; (C) stoat; (D) Arctic fox. Photos by stock.adobe.com: Pilipenko D, Paul Carpenter, Stephan Morris, Diego Cottino; Mills lab research photo, and Seoyun Choi.

climate change. Herein, we summarize current knowledge on the function and molecular and physiological control of SCC moults in birds and mammals. This cross-disciplinary synthesis and comparison across taxa provides a foundation for study of the effects of climate change on SCC species and their ability to adapt to it in the future.

II. SPECIES AND FUNCTION OF SCC MOULTS

Most mammal and bird species inhabiting temperate and arctic environments undergo periodical moults one to three times a year. The moults replace worn out and old hairs or feathers and result in new, structurally different coats better suited for the upcoming season (Ling, 1972). In the group of species that we focus on here, brown or greyish brown summer coats are annually shed and replaced with new fully or mostly white fur or plumage. Therefore, in SCC species, individuals are capable of producing multiple phenotypic morphs (polyphenism; Mayr, 1963), i.e. winter white and summer brown colour morphs, and therefore SCC species fundamentally differ from others exhibiting non-seasonal discrete colour polymorphisms (Karell *et al.,* 2011; McLean & Stuart-Fox, 2014).

Seasonal colour moulting has likely independently evolved in 21 species from five families of birds and mammals, although the precise understanding of the evolution of the trait within and across groups of species is limited. SCC species include both prey and predators and collectively occupy much of the northern hemisphere (Mills *et al.,* 2018) (Table 1). The mammals include six species of leporids (e.g. snowshoe hare *Lepus americanus*), eight muroids (e.g. Siberian hamster *Phodopus sungorus*), three mustelids (e.g. stoat *Mustela erminea*), and one canid (i.e. Arctic fox *Vulpes lagopus*). Birds include three SCC species, all in the genus *Lagopus* (e.g. rock ptarmigan *L. muta*) (Fig. 1). Within genera, seasonal moult to white often appears scattered throughout the phylogeny, as can be seen from the phylogenies of hares (Melo-Ferreira *et al.,* 2012) or weasels (Koepfli *et al.,* 2008). Species that seasonally acquire additional to already existing white colouration (e.g. snow bunting *Plectrophenax nivalis*) or undergo winter moults to lighter but not completely white coat [e.g. small vesper mouse *Calomys laucha* (Camargo, Colares, & Castrucci, 2006)] are not considered as SCC moulting by our definition.

The function of this phenological trait has long been under debate, with the two primary (not mutually exclusive) adaptive hypotheses centering on camouflage and thermoregulatory properties of the seasonal brown and white coats.

(1) Camouflage

The white coat undoubtedly promotes camouflage against snow, as long proclaimed by many prominent naturalists (e.g. Wallace, 1879; Cott, 1940). Natural selection on cryptic colouration (or camouflage) is prevalent in nature and camouflage is one of the strongest evolutionary forces driving colouration in mammals (Caro, 2005). Strong selection for camouflage and adaptive value of cryptic colouration

Table 1. Species exhibiting seasonal coat colour (SCC) moult, their trophic level, references describing intra-specific winter colour polymorphisms, and their geographical distribution. Taxonomy follows the IUCN Red List

Common name	Latin name	Trophic level	Winter colour polymorphism	Distribution
Leporidae				
Alaskan hare	*Lepus othus*	Prey		W and SW Alaska
Arctic hare	*Lepus arcticus*	Prey		N Canada, Canadian Arctic islands, Greenland
Japanese hare	*Lepus brachyurus*	Prey	Nunome *et al.* (2014)	Japan (except Hokkaido)
Mountain hare	*Lepus timidus*	Prey	Bergengren (1969); Jackes & Watson (1975); Flux & Angermann, 1990); Thulin (2003); Watson (1963)	Palearctic; N Eurasia, isolated mountain ranges and some islands
Snowshoe hare	*Lepus americanus*	Prey	Dalquest (1942); Nagorsen (1983)	Canada, N and mountainous USA
White-tailed jackrabbit	*Lepus townsendii*	Prey	Hansen & Bear (1963)	W and central North America
Muridae				
Collared lemming	*Dicrostonyx groenlandicus*	Prey		N Canada, N Alaska, N and NE Greenland, some Arctic islands
Nelson's collared lemming	*Dicrostonyx nelsoni*	Prey		W and SW Alaska
Ogilvie mountains collared lemming	*Dicrostonyx nunatakensis*	Prey		NC Yukon Territory, Canada
Palearctic collared lemming	*Dicrostonyx torquatus*	Prey		N Russia and some Arctic islands
Richardson's collared lemming	*Dicrostonyx richardsoni*	Prey		NC Canada
Siberian [Djungarian] hamster	*Phodopus sungorus*	Prey		SW Siberia, E Kazakhstan
Ungava collared lemming	*Dicrostonyx hudsonius*	Prey		N Quebec and Labrador, Canada
Wrangel Island collared lemming	*Dicrostonyx vinogradovi*	Prey		Wrangel Island, Russia
Mustelidae				
Least weasel	*Mustela nivalis*	Prey, predator	Easterla (1970); King (1979); Stolt (1979); Abramov & Baryshnikov (2000); Zima & Cenevova (2002)	Europe, N Africa, N Asia, N North America, introduced to New Zealand and other islands
Long-tailed weasel	*Mustela frenata*	Prey, predator	Hamilton (1933); Hall (1951)	North America from S Canada to N South America
Stoat	*Mustela erminea*	Prey, predator	Hamilton (1933); Rothschild (1942); Hall (1951); Gaiduk (1977); Hewson & Watson (1979); Van Soest & Van Bree (1969); King & Moody (1982); Feder (1990)	Europe, Asia, North America, Greenland and S Arctic islands, introduced to New Zealand and other islands
Canidae				
Arctic fox	*Vulpes lagopus*	Prey, predator	Braestrup (1941); Hersteinsson (1989)	Arctic North America and Asia, Arctic Islands, Greenland
Tetraonidae				
Rock ptarmigan	*Lagopus muta*	Prey	Cramp & Simmons (1980); Hewson (1973); Jacobsen, White, & Emison (1983); Salomonsen (1939)	Arctic and mountainous Eurasia, Canada, Alaska, Greenland, Arctic Islands
White-tailed ptarmigan	*Lagopus leucurus*	Prey		Mountains in S Alaska, W Canada, and W USA
Willow ptarmigan	*Lagopus lagopus*	Prey	Cramp & Simmons (1980); Thom (1986)	Eurasia, North America, some S Arctic islands

Fig. 2. Different winter colour morphs. (A) Different winter colour morphs of least weasels, eastern United States, (B) red grouse, UK, (C) blue morph of Arctic fox, Norway, (D) blue morph of mountain hare, Sweden. Access to specimens provided by National Museum of Natural History, Washington DC, and Swedish Museum of Natural History, Stockholm. Photos by Mark Medcalf/stock.adobe.com, Seoyun Choi, and Mills lab research photo.

has been widely demonstrated in birds and mammals; for example, experiments with live predators showed strong selection on protective colouration in mice (Dice, 1947; Kaufman, 1974; Vignieri, Larson, & Hoekstra, 2010), and multiple studies have shown local adaptation to reduce predation risk *via* crypsis (e.g. Kiltie, 1989; Slagsvold, Dale, & Kruszewicz, 1995; Vignieri *et al.,* 2010). In contrast to the myriad studies demonstrating strong selection on permanent coat colour, the selective advantage of SCC moult has been rarely quantified in the wild (Duarte *et al.,* 2017). However, Zimova, Mills, & Nowak (2016) showed a selective advantage of background matching in wild populations of snowshoe hare, as animals mismatched with their background suffer decreased survival. Likewise, rock ptarmigan in the Alps exhibited lower survival during years with delayed autumn snowfall, possibly due to compromised camouflage (Imperio *et al.,* 2013).

A second line of evidence for a camouflage function of SCC moulting is the strong correspondence of moult phenology and local snow cover duration. Inter-population variation in SCC moult has been shown to correlate with local snow duration [e.g. weasels (Hall, 1951; Hewson & Watson, 1979), snowshoe hare (Zimova *et al.,* 2014)] suggesting selection against colour mismatch. Further, different species in the same area appear to have similar moult phenology suggesting convergent evolution; for example, moult timing and duration is similar for sympatric rock ptarmigan and mountain hare (*L. timidus*) in Scotland (Hewson, 1958).

Similarly, SCC species show clinal variation in winter colour in relation to snow cover (Mills *et al.,* 2018). Populations found in areas where snow is brief, erratic or absent exhibit patches with pigmented or partially pigmented hairs or feathers [e.g. least weasel *M. nivalis* in the southern portion of their range (Easterla, 1970) or rock ptarmigan in Amchitka Island, Alaska (Jacobsen *et al.,* 1983)], or winter fur with grey or 'blue' undertones [e.g. mountain hare in Sweden (Thulin, 2003)] (Table 1, Fig. 2). Further, some individuals acquire a completely brown-pigmented winter coat similar in colour to their summer coat, and we refer to such as colour invariant or non-polyphenic in SCC moult; e.g. snowshoe hare along the Pacific coast of North America (Dalquest, 1942; Nagorsen, 1983), mountain hare in Ireland ['Irish hare' *L. timidus hibernicus* (Flux & Angermann, 1990)], or the subspecies of willow ptarmigan found in Scotland [*L. lagopus scotica*, 'red grouse' (Cramp & Simmons, 1980; Thom, 1986)] (Table 1, Fig. 2). Populations comprising both winter white and invariant winter brown colour morphs tend to associate with areas of low or unpredictable seasonal snow cover (Mills *et al.,* 2018); e.g. Arctic fox (Hersteinsson, 1989), Japanese hare [*Lepus brachyurus* (Nunome *et al.,* 2014)], or stoat (Hewson & Watson, 1979).

Lastly, if seasonal change to white is an adaptation to increase crypsis, animals may be expected to show active maintenance of such crypsis. Many colour-changing invertebrates, fish, and reptiles can perceive their colour and modify their behaviour to increase background matching (Ryer *et al.,* 2008; Kjernsmo & Merilaita, 2012), but the evidence is sparse for SCC species. Snowshoe hares in the USA showed no behavioural plasticity in response to camouflage mismatch, including the degree of hiding behind vegetation, flight-initiation distance and microsite selection (Kumar, 2015; Zimova *et al.,* 2014; but see Litvaitis, 1991). In contrast to mammals, birds exhibit a high degree of self-awareness, potentially due to highly refined sexual selection on plumage colouration (Montgomerie, Lyon, & Holder, 2001). Ptarmigan adjust their behaviour to actively maintain camouflage such as resting in areas that match their colouration [rock ptarmigan (MacDonald, 1970; Jacobsen *et al.,* 1983), white-tailed ptarmigan *L. leucurus* (Braun & Rogers, 1971)]. For example, willow ptarmigan in Scandinavia fed in areas that matched their plumage colour even when of inferior nutritious quality (Steen, Erikstad, & Hoidal, 1992) and rock ptarmigan in Canada dirtied themselves when mismatched after snowmelt (Montgomerie *et al.,* 2001).

(2) Thermoregulation

Thermoregulatory properties provide a complementary function to crypsis for the white winter pelage or plumage. This is achieved *via* its overall composition and the individual hair/feather microstructure.

(*a*) *Microstructure*

The major structural difference between the winter and summer coat is that the winter white guard hairs contain more air (as opposed to pigment), which increases their insulative ability. Russell & Tumlison (1996) compared the microstructure between winter and summer guard hairs (i.e. the long coarse hairs forming a layer over the short wooly underfur) of multiple SCC species (stoat, least weasel, Arctic hare *L. arcticus*, snowshoe hare, and Arctic fox) and found considerable interspecific variation in how increased insulation might be achieved. The most common differences between the two different coloured hairs were that the hair shaft of the white guard was wider or consisted of more air-filled cells, both of which allowed for increased air trapped within the shaft. Additionally, all species (except least weasel) exhibit a thinner lower part of the guard hair, which could increase coat density irrespective of their hair colour (i.e. by providing room for more down hairs or by increasing the volume of air trapped in the bottom layer of the fur).

(*b*) *Composition*

In most animals occupying temperate and arctic regions, fur/feather composition changes seasonally and provides greater insulation, regardless of the winter colour (Hart, 1956; Walsberg, 1991). Mammalian winter fur is denser and or longer in most species in those regions (e.g. Al-Khateeb & Johnson, 1971; Nixon *et al.,* 1995), which may overwhelm the thermal effects of concurrent changes in hair microstructure and pigmentation (Dawson, Webster, & Maloney, 2014). For SCC species, white winter fur is also denser and longer [snowshoe hare (Grange, 1932; Lyman, 1943; Hewson, 1958), Arctic fox (Underwood & Reynolds, 1980), collared lemming *Dicrostonyx groenlandicus* (Maier & Feist, 1991; Reynolds, 1993), Siberian hamster (Kuhlmann, Clemen, & Schlatt, 2003)]. Furthermore, winter fur changes with latitude and temperature; e.g. snowshoe hares have longer, denser, and warmer coats in northern as opposed to southern parts of their range (Gigliotti, Diefenbach, & Sheriff, 2017).

The thermoregulatory function of SCC moults is less important in weasels and ptarmigans. Weasels have short fur year-round, perhaps facilitating locomotion, and the length of the dorsal fur (including guard hairs) does not increase in winter in least weasels and stoats (Casey & Casey, 1979). Although structural differences exist between white and brown hairs in these species (Russell & Tumlison, 1996), the two seasonal coats have the same thermal conductance (Casey & Casey, 1979). It is possible that weasels thermoregulate in winter by increasing their metabolism (Szafranska, Zub, & Konarzewski, 2007), and by resting in subnivean nests of lemmings lined with rodent fur [least weasel and stoat (MacLean, Fitzgerald, & Pitelka, 1974)]. In rock ptarmigan, winter white plumage may be longer and denser than summer plumage (Salomonsen, 1939), but no difference in mass was found in rock ptarmigan in Norway (Mortensen, Nordøy, & Blix, 1985). Furthermore, density or plumage depth were similar between white willow ptarmigan and red grouse, implying no differences in thermal resistance and minimal differences in heat gain (Ward *et al.,* 2007).

(*c*) *Optical properties*

Although some authors have argued that white hairs offer a thermal advantage *via* their spectral properties, these hypotheses have been rejected. One idea suggests that white coats are warmer because they lose less heat *via* radiation than dark pigmented coats (Stullken & Hiestand, 1953). Importantly, arctic and winter white animals appear white only in the visible spectrum; however, most of the radiative exchange occurs in the far infra-red (IR) and therefore white and darkly coloured animals experience equally high emission of the absorbed heat (Hammel, 1956; Johnsen, 2012). Additionally, for SCC species occupying open polar regions (e.g. Arctic hare, Arctic fox), radiative loss to the environment is further augmented by the increased exposure to clear sky and extensive snow and ice.

The observation that white arctic and SCC animals appear black under ultra-violet (UV) light (Reynolds & Lavigne, 1981; Leblanc *et al.,* 2016) led to a premise that they would be warmer because the white hairs act as optical fibres that transmit UV heat to the skin below (Grojean, Sousa, & Henry, 1980). This idea has been rejected based on the evidence that low UV reflection of the fur is instead due to high absorption by the hair protein keratin (Bohren & Sardie, 1981; Koon, 1998), and because UV represents only about 1% of the solar spectrum. Therefore, no strong evidence supports thermal benefits of winter white coats due to their spectral properties.

III. HAIR AND FEATHER GROWTH

(1) Regenerative cycling and moulting in mammals

SCC moults arise from complete shedding and regrowth of brown or white hairs as opposed to colour bleaching. The complete moults are accomplished by the regenerative ability of hair follicles, facilitating life-long growth of new hairs (Schneider, Schmidt-Ullrich, & Paus, 2009). The hair growth cycle in all mammals can be described by four main stages: active hair proliferation (anagen), regression (catagen), rest (telogen), and shedding (exogen) (Stenn & Paus, 2001). The exogen and anagen stages often overlap, and the old hair shaft may not shed until the new hair is fully grown, as occurs during some SCC moults.

The moulting process and the level of synchrony between individual hair follicles varies across mammalian taxa, and the controlling mechanisms are still not fully understood. Some species [e.g. guinea pig *Cavia porcellus* (Chase, 1954)] show minimal synchrony in anagen entry between neighbouring hair follicles and steady asynchronous moulting. In mice and most domesticated mammals, however, hair cycling is a highly synchronized, endogenously controlled process. Hair regeneration starts in a certain region where all hair follicles enter anagen synchronously and from there moves posteriorly and dorsally as moulting waves (Chase, 1954; Whiteley & Ghadially, 1954; Plikus & Chuong, 2008).

The physiology and phenology of hair follicle cycling has been rarely described in seasonally moulting species. It has been suggested that seasonal moults also proceed in growth waves, but unlike in mice, waves are restricted to short moulting periods initiated by changing day length; during winter and summer, hair follicles rest in the telogen stage (Nixon *et al.,* 1995; Geyfman *et al.,* 2015). A gene expression study on skin tissues of the snowshoe hare is compatible with this suggestion, as expression waves in the spring moult mostly represent the mechanism of hair shedding and regrowth, although there is a lag between gene expression and visible coat colour (Ferreira *et al.,* 2017). Although no histological studies have described hair regeneration throughout the year in any SCC species, a wave-like regeneration process controlled by externally stimulated hormonal levels is supported by multiple studies of captive stoats (e.g. Rust, 1962). Further, the winter white fur period is long and fur most likely rests in telogen in most SCC species; for example, in snowshoe hares (Severaid, 1945; D. J. R. Lafferty & L. S. Mills, unpublished data) and stoats (Feder, 1990) hair growth only begins after the removal of hair follicles (as opposed to mere shaving or cutting).

A different model of hair regeneration was described in hamsters, for whom recurrent moulting waves seem to replace lost and damaged hairs as a continuous and endogenous process independent of photoperiodic changes. Siberian hamsters exhibit waves independent of photoperiod and the skin of the winter and summer coats contains moulting patches and follicles at different stages including anagen (Kuhlmann *et al.,* 2003; Paul *et al.,* 2007). Therefore, it has been argued that hamsters do not undergo seasonal moults, but rather a continuous, endogenously controlled moulting combined with seasonal, photoperiodically controlled changes in hair composition and colour. Thus, moulting and colour change may be independently controlled processes, with only colour change being controlled by changing prolactin levels (Badura & Goldman, 1992; Kuhlmann *et al.,* 2003).

(*a*) *Moulting patterns in SCC mammals*

Differences in the moult pattern exist among taxa, but closely related species show similar patterns across the body, proceeding in the reverse order in the spring compared with the autumn. For example, the autumn moult in SCC leporids progresses in a distinct pattern, with brown hairs not shed until the white hairs are nearly or fully grown [mountain hare (Hewson, 1958; Flux, 1970; Slotta-Bachmayr, 1998), snowshoe hare (Grange, 1932;Lyman, 1943 ; Severaid, 1945), Arctic hare (Best & Henry, 1994), white-tailed jackrabbit *Lepus townsendii* (Lim, 1987)] (Fig. 3A). The moult starts on some parts of the head and feet, continues onto the shoulders and thighs, and subsequently spreads dorsally and along the sides. The area along the posterior dorsal midline and some portions of the face turn white last. In the spring, old hairs are shed as the new brown hairs begin their growth [snowshoe hare (Lyman, 1943; Severaid, 1945), mountain hare (Hewson, 1958), Arctic hare (Nelson, 1909)], causing a reverse and less defined pattern. Shedding may potentially be accelerated by grooming [mountain hare (Flux, 1970), Arctic hare (Best & Henry, 1994)]. In addition, a third seasonal moult (sometimes referred to as 'summer' or 'preliminary fall moult') has been described only in leporids (Lyman, 1943; Hewson, 1958); it occurs prior to the white moult and results in another brown coat.

In mustelids, the autumn moult is faster and the pattern more diffused than in the spring moult (Rothschild, 1942). It starts on the belly, chest and throat and progresses upward and toward the back [stoat (Hamilton, 1933; Bissonnette & Bailey, 1944; Rust, 1962; Van Soest & Van Bree, 1969; Feder, 1990), least weasel (King, 1979; Smith, 1980), long-tailed weasel *Mustela frenata* (Glover, 1942; Sheffield & Thomas, 1997)] (Fig. 3C). The area between the ears and shoulders becomes white last, or sometimes stays brown throughout the winter (Fig. 2A). In the spring, brown hairs first appear along the posterior dorsal midline and continue ventrally to the belly, breast and throat, in a definite moult line. The last to become brown are some parts of the head and the belly. As in hares, shedding in the spring may potentially be accelerated by grooming [long-tailed weasel (Glover, 1942)].

In Arctic foxes, the autumn moult has a diffused and non-sequential pattern and the exact progress of this moult is unclear (Chesemore, 1970; Moberg, 2017). Studies provide conflicting evidence on whether the white hairs appear and spread uniformly across the whole body (Pocock, 1912), or instead grow first on the belly or the head (Lavrov, 1932; Chesemore, 1970; Underwood & Reynolds, 1980). The last

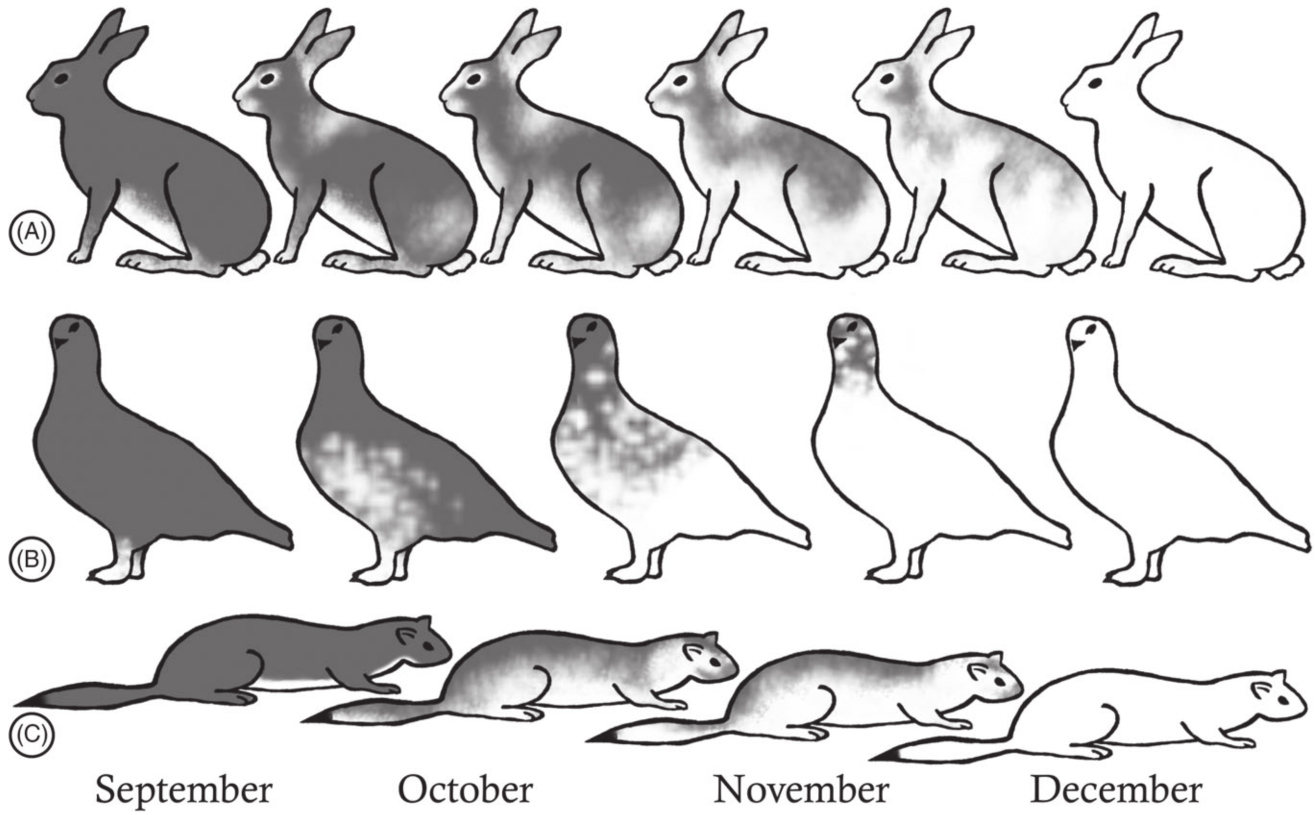

Fig. 3. Typical autumn moult progression in (A) mountain hare, (B) willow ptarmigan, and (C) stoat.

regions to turn fully white are the centre of the back and tail. Spring moult usually starts on the legs and some parts of the face (Pocock, 1912; Underwood & Reynolds, 1980). Then shedding usually occurs rapidly along the mid-dorsal line on the back, and in large patches on the flanks and legs, with the tail being the last to change. The moult in the winter blue colour morph in the spring and autumn occurs in the same sequence and manner as in the white morph (Pocock, 1912; Moberg, 2017).

In murids, moult patterns appear different between lemmings and hamsters. In collared lemmings, autumn moult begins ventrally and spreads from the flanks dorso-anteriorly (Degerbøl & Møhl-Hansen, 1943; Hansen, 1959). The hair growth progresses with the gradual appearance of white patches within the dark summer fur, or the fur along the mid-dorsal line gradually becomes lighter until it reaches full white. The last area to gain winter pelage is usually the head. The head and shoulders are the first to start moulting in the spring and the new growth progresses posteriorly and ventrally. In Siberian hamsters, the autumn moult starts on the face and on two spots on the posterior part of the back (Figala, Hoffmann, & Goldau, 1973; Kuhlmann *et al.*, 2003). These spots then spread over the dorsal part of the body towards the neck and then in a posterior direction towards the tail, while the belly and flanks become increasingly whiter. A remnant of the dorsal line usually remains dark throughout the winter. In the spring, animals become increasingly more greyish-brown all over the body.

(2) Regenerative cycling and moulting in birds

Despite the significance of moults for birds, avian moulting remains relatively poorly studied (Payne, Farner, & King, 1972; Rohwer, Thompson, & Young, 1992). In general, however, feather regeneration is analogous to hair regeneration in mammals, and feather follicles facilitate lifelong feather growth. The feather growth cycle has the same stages of growth (anagen, catagen, telogen and exogen) and equally resumes each time it is shed or plucked (Lin et al., 2013*b*; Chen *et al.*, 2015). Moulting itself occurs in a regular and highly synchronized pattern; it always begins at certain points on the body and progresses from these in a wavelike pattern (Payne *et al.*, 1972).

Most adult bird species undergo one (i.e. pre-basic moult, also called post-nuptial) or two moults (i.e. pre-basic and pre-alternate moult, also called pre-nuptial) (Humphrey & Parkes, 1959; Pittaway, 2000). The pre-basic moult is the more complete moult that occurs following the breeding season or laying cycle and results in 'basic' pelage. The pre-alternate moult results in 'alternate' or 'breeding' plumage, which is brighter and more colourful in many species, while almost identical in others.

(*a*) *Moulting patterns in SCC birds*

Ptarmigans are unusual among birds in that they have three moults: pre-basic, pre-alternate and pre-supplemental.

The terminology, however, differs among authors; first, studies disagree on identifying moult homologies between ptarmigans and other grouse species (Cramp & Simmons, 1980; Watson & Moss, 2008). Second, white feathers are occasionally retained in spring and summer at high latitudes (Watson & Moss, 2008). Lastly, inter-sexual differences in feather growth and moult phenology suggest that moults may have evolved separately in each sex (Pyle, 2007). Despite these nuances, we refer to the moults as 'spring', 'summer' and 'autumn' as all species clearly undergo three major annual moults. The only exception is the willow ptarmigan subspecies, red grouse, that omits the autumn brown to white moult (Cramp & Simmons, 1980).

In rock ptarmigan, the autumn moult starts on the underparts and spreads upwards to finish on the back and head, with white feathers appearing among old pigmented ones (Salomonsen, 1939; Watson, 1973). Some populations (e.g. Scotland, Amchitka Island) show dark-pigmented or partially coloured feathers (Watson, 1973; Cramp & Simmons, 1980; Jacobsen *et al.,* 1983) during winter. In the spring, new feather growth does not proceed in a sharp distinguishable line, but generally starts on the crown and moves down to the breast and back, finishing on the underparts (Watson, 1973). In arctic populations, the spring moult occurs much later in males than in females; male breeding plumage is white which is likely a consequence of sexual selection for bright and conspicuous plumage during breeding season (Montgomerie *et al.,* 2001). Interestingly, during the summer brown to brown moult, some white feathers are already acquired in certain areas (e.g. wings, legs, belly) (Salomonsen, 1939; Hewson, 1973; Watson, 1973).

In willow ptarmigan, autumn moults are similar to rock ptarmigan with mosaic-like growth of white feathers among pigmented feathers (Cramp & Simmons, 1980) (Fig. 3B). In the spring, however, willow ptarmigan males develop conspicuous, partially pigmented breeding plumage. In this partial moult [not recognized by some as a pre-alternate moult (Höhn & Braun, 1980)], pigmented feathers develop in males on the head, upper neck, upper anterior breast and lastly on the back, while the ventral and wing feathers remain white (Cramp & Simmons, 1980). At the end of the breeding period, males begin to moult into a pigmented summer plumage. Females start to grow pigmented feathers later in the spring, and feather replacement is not as sequential, although it still starts on the head and upper breast, and finishes with the back and tail. After brooding, a summer moult occurs when brown summer pelage is grown in both sexes, although great variation exists among individuals.

White-tailed ptarmigan moults are similar to those of willow ptarmigan, with males having partially pigmented plumage during the breeding season (Braun, Martin, & Robb, 1993). But unlike other ptarmigan species, males retain a white lower breast and abdomen throughout the year and both sexes have white primaries and white tail feathers year-round.

IV. MOLECULAR CONTROL OF SCC MOULTS

(1) Pigmentation

Although the genetic and physiological bases of colour pigment synthesis and deposition have been widely studied in vertebrates (Dupin & Le Douarin, 2002; Slominski *et al.,* 2004), the development and regulation of seasonal colour moults is poorly understood. Colouration in mammals and birds is mainly caused by endogenously produced melanin pigments, the products of complex biochemical events starting from the amino acid tyrosine and its metabolite dopa (Prota, 1995; Slominski *et al.,* 2004; McGraw, 2006). Tyrosinase, the main enzyme regulating melanin synthesis (i.e. melanogenesis) is encoded by the TYR locus and is highly conserved among species (Del Marmol & Beermann, 1996).

Melanogenesis occurs exclusively during the anagen stage of hair/feather growth and is restricted to pigment-producing cells (i.e. melanocytes) in hair/feather follicles (Stenn & Paus, 2001). Melanins are transferred *via* melanosomes into keratinized cells (i.e. keratinocytes) of the developing hair or feathers (Slominski *et al.,* 2004; Chen *et al.,* 2015).

The two main types of melanins are eumelanin (black or brown pigments) and phaeomelanin (yellow to red pigments) and their ratio along individual hairs and feathers and spatial distribution across the body determines an animal's overall coat colour (Slominski *et al.,* 2004; Lin et al., 2013*a*). The production of a specific melanin type in each cell is regulated primarily by melanocortin-1 receptor (MC1R) in melanocytes and its two ligands: α-melanocyte stimulating hormone (α-MSH), secreted from the pituitary, and the agouti signalling protein (ASIP) (Slominski *et al.,* 2004; Chen *et al.,* 2015). When activated by α-MSH, melanocytes produce dark eumelanin. Binding of the other ligand ASIP, inhibits MC1R activity and causes a switch to light phaeomelanin production (Vrieling *et al.,* 1994; Barsh, 1996). The relative contributions of ASIP and other endocrine signals (see Sections V.2 and V.3) on the production of white colouration in SCC species is not yet fully understood. However, in many species the winter white appearance is achieved by the absence of pigment in the guard hairs or feathers (Hadwen, 1929; Dyck, 1979; Russell & Tumlison, 1996; Paul *et al.,* 2007).

(2) Genetics of coat colour

The genetic underpinnings of non-seasonal variation in melanin-based colouration have been extensively described in a number of well-studied model systems. Over 150 genes that affect animal colour and patterning have been identified but only a few appear to serve as major contributors to colour variation across a wide array of animal taxa (Protas & Patel, 2008; San-Jose & Roulin, 2017). *Mc1r* and its antagonist *Agouti* are the most widely studied pigmentation genes in vertebrates (Hubbard *et al.,* 2010; Manceau *et al.,* 2010). *Mc1r* is highly conserved and many studies have shown a link between variation in *Mc1r* and pigmentation across vertebrates (Roulin, 2004; Hoekstra, 2006). The majority of these studies have identified one or more amino acid changes associated with a discrete colour polymorphism (e.g. Hoekstra *et al.*, 2006; Uy *et al.*, 2009; McRobie *et al.*, 2014). The large number of instances in which colouration differences are explained by protein-coding mutations in *Mc1r* is likely due to its minimal pleiotropic effects, large mutational target size, and high mutation rate (Hubbard *et al.*, 2010).

Several *Agouti* mutations have also been associated with colour variation (e.g. Hiragaki *et al.*, 2008; Carneiro *et al.*, 2014). Unlike the *Mc1r* mutations, which usually involve protein-coding changes that are inferred to be directly causative, coat colour variation linked to *Agouti* is usually associated with genetic variants that impact gene expression; for example, increased expression of *Agouti* results in light-coloured deer mice *Peromyscus maniculatus* (Linnen *et al.*, 2009; Manceau *et al.*, 2011). Fewer causative mutations have been identified at *Agouti*, likely due to a more complex exon and regulatory structure relative to *Mc1r*, and the general inherent difficulties of identifying causative regulatory variants. Additionally, several other pigmentation genes have been shown to play important roles in determining colour variation in animals, including genes encoding tyrosinase and tyrosinase-related proteins [e.g. *Tyrp1* (Delmore *et al.*, 2016), *Tyr* (Ekblom *et al.*, 2012)] and other components of the melanocortin pathway (Anderson *et al.*, 2009). Collectively, intra-specific colour variation may have different genetic bases (i.e. different genes or mutations), yet remarkable genetic convergence with *Mc1r* and *Agouti* underlies adaptive coat colour evolution across a broad range of species. Recent high-throughput sequencing technologies will allow extending such studies to a broader number of species and colouration traits (San-Jose & Roulin, 2017).

(3) Genetics of SCC moults

The genetic basis of seasonal colouration is poorly known. Yet it is expected that genes and pathways are similar to non-seasonal colour variation due to the highly conserved nature of pigmentation in vertebrates. The strong genetic control of SCC moult has long been evident from translocation experiments and common garden studies. For example, winter white and winter brown snowshoe hares from a polymorphic population in Washington, USA continued changing to their winter colours when exposed to identical temperature and light condition in a ‘common garden’ environment (L.S. Mills & D.J.R. Lafferty, unpublished data), and mountain hares from Austria maintain their regular seasonal changing cycle over several years when translocated to Portugal (P.C. Alves, unpublished data). Similar observations were described in other mammal transplants [long-tailed weasel (Hall, 1951), stoat (Feder, 1990; but see: King & Powell, 2007; Rothschild & Lane, 1957), white-tailed jackrabbit (Hansen & Bear, 1963)].

The mechanisms underlying the evolution of SCC remain unknown, but some studies have focused on the genetics of colour variation in SCC species. Notably, extensive research into the basis of colour polymorphism in wild white and blue Arctic foxes has been driven by their economic importance. The white morph is completely white in winter, but in summer it is brownish grey dorsally and light grey ventrally (Fig. 1D). By contrast, the blue morph lacks the light brown during winter and is uniformly chocolate brown during the summer (Fig. 2C) (Chesemore, 1970). The blue colour morph is inherited as a simple Mendelian trait that is dominant to white and caused by two cysteine substitutions in the *Mc1r* gene (Våge *et al.*, 2005). Importantly, however, the mutations resulting in colour polymorphism affect both summer and winter pelage and therefore are not seasonally expressed *per se*. Also, major dominant genes may determine the winter grey/blue morph in Swedish mountain hares [called ‘heath-hares’ (Fig. 2D) (Bergengren, 1969)] and the winter brown *M. nivalis vulgaris* morph in least weasels (Stolt, 1979), but particular gene mutations were not investigated. Nunome *et al.* (2014) found no differentiation between Japanese hare populations of winter white and winter brown morphs in three candidate genes (*Agouti*, *TYR*, *Mc1r*). Similarly, no association has been found between colour polymorphism and *Mc1r* and three other candidate genes (*Tyr*, *Tyrp1*, and *Dct*) in willow ptarmigan (Skoglund & Hoglund, 2010).

Very few studies have investigated the regulatory underpinnings of SCC moults (as opposed to colour polymorphism) and of their phenology. In snowshoe hares, Ferreira *et al.* (2017) pinpointed three known pigmentation genes, *Agouti*, *Myo7a* and *Spns2*, that were differentially expressed during spring moult and thus may play important functional roles in regulating the seasonal production of brown pelage. This suggests that known pigmentation pathways with transient regulation may underlie SCC. Another study using hybrids of Siberian and Campbell’s dwarf hamsters (*P. campbelli*, a sister species that is brown year-round) suggested recessive heritability of SCC moulting and a potentially simple genetic basis (Clare-Salzler, 2017).

V. PHYSIOLOGICAL REGULATION OF SCC MOULTS

(1) Photoperiodism

The phenology of SCC moults is coordinated by the same mechanisms that control the annual timing of other life events such as reproduction, hibernation, and migration. In vertebrates, these mechanisms are based on an internal circannual rhythm synchronized with external stimuli (*Zeitgeber*), most commonly day length (photoperiod) (Gwinner, 2003; Hofman, 2004). Organisms in polar and temperate regions depend on their ability to assess and use day length (photoperiodism) to time seasonal events optimally (Bradshaw & Holzapfel, 2007).

Mammals and birds have central clocks or pacemakers that are entrained to the 24 h light cycle and provide a ‘reference clock’ for the reading of calendric information. Melatonin is the chief humoral signal that translates photoperiodic information and induces a wide variety of effects on the animals’ physiology. Mammals have one central circadian clock located in the brain in the suprachiasmatic nucleus (SCN) that synchronizes clock genes expression in other tissues (Balsalobre, 2002). By contrast, birds have a system of at least three independent yet interacting circadian clocks in the SCN, the retina of the eyes and the pineal gland (Kumar *et al.,* 2010).

Despite advances in understanding the circadian clock in mammals and birds, the molecular basis of circadian time measurement and how it is used to measure photoperiod and regulate circannual timing is still not fully understood (Schwartz & Andrews, 2013). The circadian timing is generated endogenously by a cell autonomous mechanism involving a small number of core clock genes, with transcription factor genes *Clock* and *Bmal1*, and *Period* and *Cryptochrome* genes playing crucial roles (Reppert & Weaver, 2002; Ono, Honma, & Honma, 2015). Their expression in the master pacemakers as well as in most cells throughout the body (Balsalobre, 2002; Reppert & Weaver, 2002) including the skin, plays a role in the regulation of hair cycling (Lin *et al.,* 2009; Geyfman *et al.,* 2015). Recently, Ferreira *et al.* (2017) detected expression waves of circadian rhythm genes in snowshoe hare skin during the moulting process.

(*a*) *Circannual rhythms in mammals*

The degree to which animals rely on internal clock *versus* photoperiodic stimuli varies among species and two primary long-term timekeeping mechanisms or circannual rhythms are recognized (Paul, Zucker, & Schwartz, 2008). Type I rhythm is common among many short-lived temperate and boreal mammals and works like an hourglass timer measuring the lapse of time since a photoperiodic cue (Goldman, 2001). In many long-lived species, the internal circannual cycle predominates (Type II rhythm), with continued expression of circannual cyclicity in the absence of annual change in day length or other external stimuli over mutliple years.

Siberian hamsters are one of the best-studied animal models for seasonality. Type I rhythm clearly governs their seasonal changes including moults and reproduction (Wade, Bartness, & Alexander, 1986). A short photoperiod during the autumn increases melatonin concentration and subsequent prolactin suppression, triggering an endogenous interval timer. The same pathway also drives the loss of a response to day length (i.e. photorefractoriness) in the spring and reversal of the initial physiological response without additional external stimuli (Lincoln, Andersson, & Loudon, 2003). Multiple studies with captive hamsters demonstrated that the brown to white autumn moults are triggered by decreasing day lengths (Kuhlmann *et al.,* 2003; Paul *et al.,* 2007). Subsequently, white to brown spring moult occurs independently of external stimuli; when exposed to a prolonged period of short days, hamsters show a characteristic refractory response as they revert to the summer phenotype (i.e. brown pelage, reproductive status, decreased body mass) within 38 weeks (Duncan & Goldman, 1984; Paul *et al.,* 2007). On the contrary, they remain indefinitely in the summer pelage until exposure to short day lengths, resetting their circannual clock.

Although the role of endogenous mechanisms on any seasonal moults has not been intensively studied in other species, the relative importance of external stimuli seems to be higher than in Siberian hamsters. For example, in snowshoe hares, autumn moults can be arrested by an artificially long photoperiod, and the refractory response occuring in the spring is not as striking as in hamsters; after prolonged exposure to short days, hares still underwent spring moult, but it was delayed or incomplete (Lyman, 1943). However, both autumn and spring moults can be initiated by changes in photoperiod at any time of the year in hares (Lyman, 1943) and collared lemmings (Maier & Feist, 1991; Gower, Nagy, & Stetson, 1993; Nagy, Gower, & Stetson, 1993). In long-tailed weasels and stoats both spring and autumn moults were induced and reversed using photoperiod manipulation (Bissonnette & Bailey, 1944; Rust, 1962, 1965). Importantly, however, endogenous control is still evident, because reversions can be made only after a latent period of about three months after the change in photoperiod (Bissonnette & Bailey, 1944).

(2) **Neuroendocrine and endocrine regulation in mammals**

The photoperiod cue controlling the major humoral signal (melatonin) responsible for the phenology of many annual events, including moults, is received solely by the eyes in mammals [snowshoe hare (Lyman, 1943), mountain hare (Novikov & Blagodatskia, 1948)]. Specialized photosensitive ganglion cells in the eye retina forward the signal *via* a neural pathway to the SCN located directly above the optic chiasm in the hypothalamus. From the SCN the signal is conveyed to the pineal gland, which produces the hormone melatonin (Moore, 1995) (Fig. 4). Melatonin is produced exclusively at night at a rate inversely proportional to day length. The circadian and circannual variation in melatonin signal duration is then used as a critical input signal for the pituitary gland and its pars tuberalis (PT) that regulate seasonal prolactin secretion (Lincoln *et al.,* 2006). Prolactin is mainly associated with reproduction and lactation, but also influences hair growth (Foitzik, Langan, & Paus, 2009; Paus *et al.,* 2014).

(*a*) *Melatonin and prolactin*

Melatonin acts *via* inhibition of prolactin production and this hormonal interaction serves as the main humoral signal controlling the phenology of many seasonal events including reproduction, migration and moult (Lincoln *et al.,* 2006; Paul *et al.,* 2008) (Table 2, Fig. 4). In SCC species, prolactin plays an important role in regulating moults, but the exact mechanisms remain unclear. Increased prolactin concentrations are associated with initiation of reproduction and spring moult [collared lemming (Gower *et al.,* 1993), stoat (Rust, 1965), snowshoe hare (Lyman, 1943)]. Administration of prolactin can induce or artificially maintain pigmentation of the fur in Siberian hamsters despite changing day lengths (Duncan & Goldman, 1984, 1985). On the contrary,

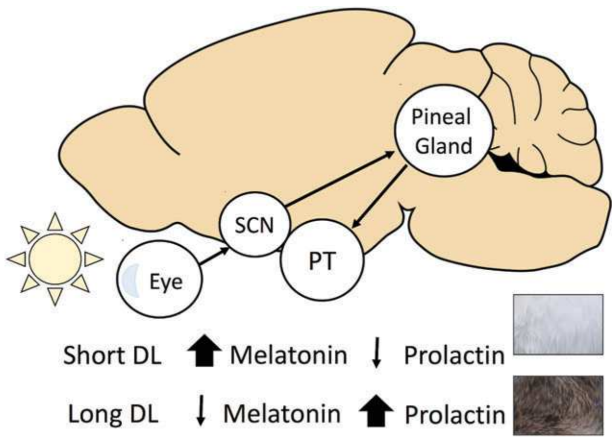

Fig. 4. Main hormonal pathway regulating seasonal coat colour (SCC) moults in mammals. The photoperiodic signal enters the brain *via* the eye and is forwarded to the suprachiasmatic nucleus (SCN) and endocrine glands. Short day length (DL) yields high production of pineal melatonin leading to low secretion of prolactin by the pars tuberalis (PT) of the pituitary gland, resulting in white winter fur. The opposite is true for the production of brown summer fur.

artificially suppressed prolactin secretion induces moult to the white winter pelage [Siberian hamster (Niklowitz & Hoffmann, 1988; Badura & Goldman, 1992), collared lemming (Gower *et al.,* 1993), stoat (Rust & Meyer, 1969; Feder, 1990), Arctic fox (Nieminen *et al.,* 2004)], delays spring moult [Arctic fox (Smith *et al.,* 1987)] or results in the growth and maintenance of white coat regardless of photoperiod [stoat (Rust, 1965)].

Despite the overwhelming evidence that melatonin affects moult phenology indirectly *via* changing prolactin levels, the hormone may also directly affect hair pigmentation. Melatonin inhibits enzymes in the tyrosine to melanin production pathway or directly affects melanin by local production in the skin, leading to white colouration (Logan & Weatherhead, 1978; Slominski *et al.,* 2002). However, the direct effects of melatonin on hair melanization are not understood.

(*b*) *Other hormones*

SCC moults are chiefly regulated by the interactions between melatonin and prolactin, but other circulating hormones play a role (Table 2). α-MSH, released by the pituitary, signals MC1R leading to the production of dark eumelanin, while ASIP is an antagonist that leads to the production of lighter phaeomelanin (see Section IV.1). Whether and how the production of ASIP is regulated throughout the year in SCC species remains unknown. Additional endocrines involved with melanization and hair regeneration include other hormones of the hypothalamic–pituitary–gonadal (HPG) axis (most notably gonadal steroids), thyroid hormones, and glucocorticoids as described below.

(*i*) *Gonadal steroids.* Gonadal steroids, chiefly testosterone and oestradiol have long been known to affect reproduction as well as hair growth (Wright, 1942; Johnson, 1958*a*), but are only secondary drivers of SCC moults. They affect hair growth cycle and pigmentation largely *via* stimulation of circulating prolactin levels. In experiments comparing groups with different levels of gonadal steroids, animals with lower levels moulted more rapidly and more completely in the autumn [collared lemming (Gower *et al.,* 1993, 1994), Siberian hamster (Duncan & Goldman, 1984)], and exhibited heavier or earlier spring moults [snowshoe hare (Lyman, 1943), least weasel (King, 1979)].

(*ii*) *Thyroid hormones and glucocorticoids.* Hormones of the thyroid gland or adrenal cortex are known to be involved in hair regeneration (Maurel, Coutant, & Boissin, 1987; Paul *et al.,* 2007), but controlled experiments failed to find effects on SCC moults [snowshoe hare (Lyman, 1943), stoat (Rust, 1965), Siberian hamster (Barrett *et al.,* 2007; Scherbarth & Steinlechner, 2010)]. Hormones of the adrenal cortex, mainly glucocorticoids, inhibit moulting by suppressing the anagen hair growth stage, whereas adrenalectomy accelerates the growing process (Johnson, 1958*b*; Rose & Sterner, 1992). However, no effect of cortisol on the induction of moult or pigmentation was found in hypophysectomized weasels (Rust, 1965).

(3) Neuroendocrine and endocrine regulation in birds

In birds as in mammals, seasonal moults are stimulated by photoperiod (Höst, 1942; Dawson *et al.,* 2001), but the photoperiodic control in birds is less clear, partially because they have at least three independent pacemakers (Gwinner, 2003; Kumar, Singh, & Rani, 2004). In fact, light cues are not only sent and perceived by the melatonin-producing pineal gland (Cassone *et al.,* 2009), but also through photoreceptors located in the mediobasal hypothalamus and in the eyes (Ikegami & Yoshimura, 2012). Because of these two extra pacemakers/receptors, birds do not rely as critically on the pineal gland (and melatonin) for the photoperiodic response. Moult and reproduction are timed such that moult starts immediately after breeding; if breeding activity continues beyond the photoperiodic timing of moult, the start of moult is delayed, but then occurs at a faster rate (Dawson, 1998).

Although avian mechanisms of seasonal regulation are not fully understood, it is clear that moults are largely controlled by hormones released from the pituitary and thyroid glands (Payne *et al.,* 1972; Chen *et al.,* 2015) (Table 2). Administration of pituitary hormones, including α-MSH, follicle stimulating hormone (FSH), and luteinizing hormone (LH), can induce unseasonal feather pigmentation in winter in willow and white-tailed ptarmigan (Höhn & Braun, 1980). Additionally, different studies showed that captive willow ptarmigan, kept at low winter temperatures, can be induced to moult prematurely into pigmented breeding or summer plumage (and gonadal activity) by being artificially exposed to a long-day photoperiod (Höst, 1942; Novikov & Blagodatskia, 1948; Stokkan, 1979*b*).

Table 2. Effect of hormones on spring and autumn moult phenology in seasonal coat colour (SCC) species

Hormone	Species	Effect on spring moult	Effect on autumn moult	References
Cortisol	Stoat	No effect	–	Rust (1965)
Prolactin	Arctic fox	Strong association	Suppression	Nieminen *et al.* (2004); Smith *et al.* (1987)
	Collared lemming	Strong association	Suppression	Gower *et al.* (1993)
	Stoat	Strong association	Suppression	Rust (1965); Rust & Meyer (1969); Feder (1990)
	Siberian hamster	Pigmentation stimulation, maintenance	Suppression	Badura & Goldman (1992); Duncan & Goldman (1984, 1985); Niklowitz *et al.* (1988)
	Snowshoe hare	Strong association	–	Lyman (1943)
	White-tailed ptarmigan	Strong association	–	Höhn & Braun (1980)
	Willow ptarmigan	Strong association	–	Höhn & Braun (1980)
Sex steroids	Collared lemming	–	Suppression (testosterone)	Gower et al. (1993); Gower, Nagy, & Stetson (1994)
	Least weasel	Suppression (oestrogen)	–	King (1979)
	Rock ptarmigan	Suppression (testosterone)	–	Salomonsen (1950); MacDonald (1970)
	Siberian hamster		Suppression (testosterone)	Duncan & Goldman (1984)
	Snowshoe hare	Lighter moult (testosterone)	No effect	Lyman (1943)
	Willow ptarmigan	Stimulation (testosterone)	No effect	Stokkan (1979*a*); Braun & Höhn (1977)
Thyroid	Stoat	No effect	No effect	Rust (1962)
	Snowshoe hare	No effect	No effect	Lyman (1943)
	White-tailed ptarmigan	No effect or stimulation	Stimulation	Höhn & Braun (1980); Braun & Höhn (1977)
	Willow ptarmigan	No effect or stimulation, pigmentation	–	Novikov & Blagodatskia (1948); Höhn & Braun (1980)

(*a*) *Prolactin*

Hormones of the HPG axis are strongly involved with moult regulation. In general, moult initiation is associated with high prolactin levels and moults can be experimentally induced by prolactin administration (Kuenzel, 2003; Dawson, 2006). Further, prolactin is likely involved in pigmentation as well; Höhn & Braun (1980) demonstrated that several hormones of the pituitary, mainly prolactin and LH, were involved in feather pigmentation in white-tailed ptarmigan.

(*b*) *Gonadal steroids*

In most birds, moulting starts after the end of reproduction and the inhibitory effects of gonadal steroids on moult contribute to this separation in time (Payne *et al.*, 1972). Experimental studies have shown that implants of testosterone can delay, prevent or interrupt moults (Nolan *et al.*, 1992; Dawson, 1994). Such a mechanism would delay the start of moult until the time of gonadal regression; for example, in male rock ptarmigan which moults to brown summer plumage after breeding, testicular hormones likely suppress initiation of the moult (Salomonsen, 1950; MacDonald, 1970). The influence of gonadal steroids on moult and pigmentation is unclear in willow ptarmigan, but likely differs due to the overlap of moulting and breeding activity (Höst, 1942); some studies reported spring moult advancement in response to increased testosterone (Stokkan, 1979*a*,b; Hannon & Wingfield, 1990), but others found no effect on moulting between castrated and intact birds (Braun & Höhn, 1977; Höhn & Braun, 1980).

(*c*) *Thyroid hormones and glucocorticoids*

Thyroid hormones and hormones of the adrenal cortex (i.e. glucocorticoids) appear to be important regulators of avian moult phenology, more so than in mammals. Similarly to gonadal steroids, glucocorticoids are elevated during the breeding season in birds and decrease during moulting (Romero, 2002). By contrast, thyroid hormones can stimulate moults (Kuenzel, 2003) and removal of the thyroid gland prevents them (Yoshimura, 2013); however, this may not reflect a direct effect of thyroid hormones since they influence prolactin and corticosterone secretion (Goldsmith & Nicholls, 1984). For SCC birds, similar effects of thyroid hormones have been described; increased thyroid concentration was associated with all three moults in white-tailed ptarmigan (Höhn & Braun, 1977). However, whether thyroid affects feather regeneration alone or also pigmentation is unclear; while Höhn & Braun (1980) found no effect of thyroid hormones on pigmentation in willow and white-tailed ptarmigan, Novikov & Blagodatskia (1948) reported that excessive administration of thyroid powder induced feather pigmentation in willow ptarmigan.

Table 3. Effect of extrinsic and intrinsic factors on spring and fall moult phenology in seasonal coat colour (SCC) species

Factor	Species	Effect on spring moult	Effect on fall moult	References
Temperature	Arctic fox	No effect	No effect	Hersteinsson (1989)
	Collared lemming	–	Cold accelerated	Degerbøl & Møhl-Hansen (1943)
	Mountain hare	Cold slowed down	Cold and snow accelerated, or no effect	Flux (1970); Jackes & Watson (1975); Watson (1963); Clinging (1982)
	Rock ptarmigan	Cold and snow slowed down	Cold accelerated, and whiter winter plumage	Hewson (1973); Watson (1973); Salomonsen (1939)
	Stoat	Cold slowed down	–	Rust (1962)
	Siberian hamster	–	Cold accelerated	Larkin, Freeman, & Zucker (2001)
	Snowshoe hare	Cold and snow slowed down	No effect	Zimova *et al.* (2014); Kumar (2015)
Sex	Arctic hare	Females earlier	Males earlier	Manning (1943); Banfield (1974)
	Collared lemming	Females earlier	–	Degerbøl & Møhl-Hansen (1943)
	Least weasel	No effect	–	King (1979)
	Mountain hare	Females earlier	Males earlier	Flux (1970); Bergengren (1969); Hewson & Watson (1979)
	Rock ptarmigan	Males earlier, females earlier, or no effect	Females earlier, males whiter, or no effect	Hewson (1973); Watson (1973); Jacobsen *et al.* (1983); Montgomerie *et al.* (2001); Salomonsen (1939)
	Stoat	Females earlier	Females earlier	Hewson & Watson (1979); Van Soest & Van Bree (1969)
	Siberian hamster	No effect	Males earlier	Butler & Zucker (2009)
	Snowshoe hare	Females earlier	Females earlier or no effect	Zimova *et al.* (2014); Mills *et al.* (2013); Aldous (1937); Severaid (1945)
	White-tailed ptarmigan	Males earlier	Males earlier	Braun *et al.* (1993)
	Willow ptarmigan	–	Males earlier	Stokkan (1979*b*)
Age	Arctic fox	–	Juveniles later	Chesemore (1970); Blomstedt (1998)
	Collared lemming	–	Juveniles earlier	Degerbøl & Møhl-Hansen (1943)
	Least weasel	–	No effect, or late-born juveniles later	King (1979)
	Mountain hare	–	Juveniles later and darker winter fur	Flux (1970); Watson (1963) Bergengren (1969); Hewson & Watson (1979)
	Rock ptarmigan	–	Juveniles later	Hewson (1973)
	Siberian hamster	No effect	No effect	Butler & Zucker (2009)
	Snowshoe hare	–	Juveniles later	Severaid (1945); Grange (1932)
	White-tailed ptarmigan	–	Juveniles later	Braun *et al.* (1993)
Condition	Mountain hare	Less aggressive and sick later, or no effect	Sick or injured later	Flux (1970); Hewson (1958)

VI. OTHER FACTORS INFLUENCING SCC MOULTS

(1) Temperature and snow cover

Exogenous cues, particularly temperature and snow cover, have modifying effects on the rate and sometimes completeness of SCC moults (Table 3). As previously described, photoperiod regulates the onset of moults; without shifts in photoperiod, temperature alone cannot induce moulting in captive animals [snowshoe hare (Lyman, 1943), weasels (Bissonnette & Bailey, 1944; Rust, 1962; Feder, 1990)]. Similarly, wild populations show nearly identical date of moult onset each year [mountain hare (Watson, 1963; Jackes & Watson, 1975), snowshoe hare (Zimova *et al.*, 2014; but see Kumar, 2015)], confirming the overwhelming effect of photoperiod. While temperature and probably snow appear to modify the rate of moults, the physiological connection between those exogenous cues and most seasonal traits including SCC moults has not been established (Caro *et al.*, 2013).

Once the white moult has been initiated in the autumn, cold temperatures can accelerate growth of the white coat in both mammals [mountain hare (Watson, 1963; Jackes & Watson, 1975), stoat (Rothschild, 1942), Siberian hamster (Larkin *et al.*, 2001), collared lemming (Degerbøl & Møhl-Hansen, 1943)], and birds [rock ptarmigan (Salomonsen, 1939; Watson, 1973)]. The modifying effect of temperature is strong in weasels; captive stoats kept under cold temperatures completed the brown to white moult in three days while animals exposed to warm temperatures took 10–20 days (Rothschild, 1942). Furthermore, in ptarmigan, temperature can also affect the completeness of the autumn moult; individual captive rock ptarmigan grew more dark-pigmented winter feathers when exposed to warm winter temperature (Hewson, 1973) or when translocated to a warmer locality (Salomonsen, 1939).

In the spring, warm temperatures can accelerate the white to brown moults [snowshoe hare (Zimova *et al.,* 2014; Kumar, 2015), stoat (Rothschild, 1942)]. Rust (1962) found that stoats exposed to warm temperatures in the spring changed their entire dorsum in less than two days and moulting was more diffuse, with an undefined line of new brown fur, than in animals exposed to cold temperatures.

The effects of snow are uncertain due to challenges in separating its effects from temperature. However, multiple field studies indicate some influence of snow cover on moult rate. Based on both population means and individuals observed over multiple years, animals exhibited a slower rate of moult during colder and snowier springs [mountain hare (Watson, 1963; Flux, 1970; Clinging, 1982), snowshoe hare (Zimova *et al.,* 2014; Kumar, 2015), rock ptarmigan (Watson, 1973)]. In another study, Jackes & Watson (1975) found that the brown to white moult was related initially to air temperature, particularly days with a minimum of 0°C or less, and later in the season to snow cover. However, no phenotypic plasticity in response to cooler temperature or more snow cover was observed in the autumn moult in mountain (Flux, 1970) and snowshoe hares (Zimova *et al.,* 2014). In Arctic foxes, the evidence for plasticity is mixed; minimal plasticity in response to temperature or snow has been described in both moults (Hersteinsson, 1989) (but see Moberg, 2017).

(2) Intrinsic factors

All SCC species exhibit large intra-population variation in moult phenology. Some of this variation can be explained by gender, age and to a lesser degree condition and social rank (Table 3), all of which are correlated with underlying hormonal levels.

(*a*) *Sex*

Gender-specific differences in phenology have been described for multiple species in both moults. Inter-sexual differences in moult phenology in the spring are likely related to varying levels of gonadal hormones, which spike at different times in each sex during reproduction. In most mammal species, females initiated the spring moults earlier than males [mountain hare (Bergengren, 1969; Flux, 1970; Hewson, 1973), snowshoe hare (Aldous, 1937; Severaid, 1945; Zimova *et al.,* 2014), collared lemming (Degerbøl & Møhl-Hansen, 1943), Arctic hare (Banfield, 1974), stoat (Van Soest & Van Bree, 1969), Arctic fox (Moberg, 2017)], but no sex differences were observed in least weasels (King, 1979) and Siberian hamsters (Butler & Zucker, 2009). In ptarmigan, the breeding plumage and consequently effect of sex on phenology differs among species. Male willow and white-tailed ptarmigan initiate the pigmented moult earlier than females (Stokkan, 1979*b*; Braun *et al.,* 1993; Watson & Moss, 2008). Female rock ptarmigan, however, exhibited more complete summer plumage with less winter white retained on the underparts and no white feathers on the back (Watson & Moss, 2008). Male rock ptarmigan in Scotland begin the moult first but finish at about the same time as females (Hewson, 1973; Watson, 1973), but in subarctic and arctic regions remain white much longer than females (Salomonsen, 1939; Jacobsen *et al.,* 1983; Montgomerie *et al.,* 2001).

Differential moult phenology between the sexes has been described in the autumn as well, although physiological mechanisms including links to changes in gonadal steroid levels are less clear. Hewson & Watson (1979) suggested that the smaller sex, presumably more susceptible to cold (e.g. females in stoat and ptarmigan; males in hares) initiates the autumn moult earlier. Accordingly, male mountain hares (Bergengren, 1969; Flux, 1970), Arctic hares (Manning, 1943) and Siberian hamsters (Butler & Zucker, 2009) initiated the moult earlier than females. By contrast, female snowshoe hares (Aldous, 1937; Severaid, 1945) and stoats (Hewson & Watson, 1979) initiated the autumn moult before males. Furthermore, in stoats, a higher proportion of the brown or piebald winter phenotype are females (Hamilton, 1933; Flintoff, 1935; Hall, 1951; Hewson & Watson, 1979; King & Moody, 1982). Also, female mountain hares appeared more patchy than males during spring and autumn moults (Flux, 1970). In rock ptarmigan, Salomonsen (1939) showed that both sexes completed the moult at the same time across their range, but some exceptions were recorded in milder climates; e.g. in Scotland and Amchitka Island, females completed moulting first but males achieved whiter plumage (Hewson, 1973; Watson, 1973; Jacobsen *et al.,* 1983). White-tailed ptarmigan males initiated moult before females (Braun *et al.,* 1993).

(*b*) *Age*

Age may also affect moult phenology and the completeness of the moult, especially in the autumn. In some species younger animals tend to exhibit delayed phenology [mountain hare (Watson, 1963), snowshoe hare (Grange, 1932; Severaid, 1945), Arctic fox (Chesemore, 1970), ptarmigan spp. (Hewson, 1973), willow ptarmigan (Stokkan & Steen, 1980), white-tailed ptarmigan (Braun *et al.,* 1993)] or acquire a greyish hue in winter [mountain hare (Watson, 1963; Flux, 1970)]. Further, later birth date correlates with later moult in the following autumn; juvenile mountain hares born in early summer moulted to white earlier than juveniles born later (Bergengren, 1969).

By contrast, juvenile collared lemmings initiated autumn moults before adults (Degerbøl & Møhl-Hansen, 1943) and in captive-bred blue foxes older cubs initiated the autumn moult earlier than younger cubs, but finished at the same time (Blomstedt, 1998). The effect of age is unclear in Siberian hamsters, with some evidence for juveniles skipping autumn moults and some for no effect of age (Butler & Zucker, 2009). In mustelids, juveniles vary much more widely in moult pattern than older individuals but phenology is not considerably different (Hamilton, 1933; King, 1979).

(*c*) *Body mass and condition*

Condition is a function of factors such as nutrition, disease, and stress, and so might logically belong in the exogenous factors section above. However, the effects of condition are similar to the effects of age and may explain some of its effects (Flux, 1970). In general, lighter, injured or sick animals as well as females that reproduced late show delayed autumn moults compared to healthier individuals in mountain hares (Hewson, 1958; Bergengren, 1969). In the spring, no effect of body condition (e.g. body mass, fat ratio) on moult phenology was found in mountain hares except for very sick individuals that show delayed moult (Flux, 1970). Notably, more-aggressive mountain hare males moulted earlier than less-aggressive, lighter males (Verkaik & Hewson, 1985), perhaps due to differences in testosterone level. Lastly, evidence from non-SCC species connects diet to melanin production (McGraw, 2003), but more research is required.

VII. ADAPTIVE POTENTIAL TO CAMOUFLAGE MISMATCH

Research investigating the ecology and underlying basis of SCC moults has declined since the 1980s and many aspects of SCC moulting remain unresolved. Recently, the direct connection between winter white coats and anthropogenic climate change has led to renewed interest in SCC species (Imperio *et al.,* 2013; Mills *et al.,* 2013; Sultaire *et al.,* 2016; Zimova *et al.,* 2014; Zimova *et al.,* 2016; Pedersen, Odden, & Pedersen, 2017; Mills *et al.,* 2018). Both snow cover duration and extent are projected to decrease dramatically across most of the northern hemisphere, especially during spring and autumn (Ning & Bradley, 2015; Danco *et al.,* 2016; Musselman *et al.,* 2017), driving increased camouflage mismatch and population declines in the absence of an adaptive response (Zimova *et al.,* 2016). Below, we synthesize the current understanding of adaptive potential to camouflage mismatch *via* phenotypic plasticity and evolution.

(1) Phenotypic plasticity

Despite a strong influence of photoperiod on moult phenology, SCC species show some ability to adjust moult phenology in response to temperature and snow conditions and reduce camouflage mismatch [e.g. snowshoe hare (Zimova *et al.,* 2014)]. Furthermore, ptarmigan may also adjust the presence and amount of dark pigmented feathers in their winter plumage [e.g. rock ptarmigan (Hewson, 1973)]. Overall, however, little is known about the extent or mechanisms through which abiotic factors or behaviours may mediate moult phenology or winter coat colour. Further, we do not understand to what degree plasticity is limited by correlations with other life-history traits that share the same basic physiological pathway [e.g. reproduction (Paul *et al.,* 2008)], and how those correlations affect potential adaptation *via* plasticity. Carefully designed physiological studies in the future may resolve the neuroendocrine and endocrine mechanisms that regulate SCC moults and are critical for predicting future adaptive responses.

(2) Evolutionary shifts

Strong selection connected against camouflage mismatch [recently quantified in snowshoe hares (Zimova *et al.,* 2016)] combined with variation in SCC moulting suggests adaptive capacity *via* evolutionary shifts in SCC moult phenology or in the resulting winter colour (Mills *et al.,* 2018). First, past adaptive evolution *via* moult phenology is evident across SCC species; for example, snowshoe hare (Grange, 1932; Zimova *et al.,* 2014), mountain hare (Couturier, 1955; Watson, 1963), Arctic fox (Lavrov, 1932), weasels (Hamilton, 1933; Feder, 1990; King & Powell, 2007), and ptarmigan (Salomonsen, 1939; Cramp & Simmons, 1980) exhibit range-wide inter-population variation in moult phenology correlated with altitude, winter onset and winter duration as opposed to latitude. Further, intra-population variation is equally common; during spring or autumn moults a full range of moult stages (ranging from brown to white) can be observed on the same day within a population [e.g. snowshoe hare (Zimova *et al.,* 2016), mountain hare (Bergengren, 1969; Clinging, 1982), Arctic fox (Underwood & Reynolds, 1980), rock ptarmigan (Salomonsen, 1939; Watson, 1973)]. The molecular basis of variation in moult phenology remains unknown, but the extensive genetic machinery is amenable to genomic and transcriptomic approaches across taxa.

Microevolution in winter colour phenotype (instead of or in combination with microevolution in moult phenology) is also possible in response to climate change. Local variation in winter coat colour is tightly linked with local climate and especially snow duration across all SCC species (Mills *et al.,* 2018). Furthermore, some populations are polymorphic in their winter colour phenotype (Mills *et al.,* 2018) (Table 1) and rapid evolutionary shifts may have potentially occurred, for example in mountain hares in the Faroe Islands (Degerbol, 1940). The strong underlying molecular basis of winter colour phenotype is evident from latitudinal translocations, common garden experiments [e.g. stoat (Feder, 1990)] and a several genetic studies [e.g. Arctic fox (Våge *et al.,* 2005)]. Because adaptation will be critical to allow persistence under climate change due to limited plasticity, we need to understand the genetic basis in all SCC species, including correlations with phenology of other circannual traits.

VIII. CONCLUSIONS

(1) Although SCC moults have a dual function of increased crypsis and thermoregulation, camouflage against snow in the winter appears to be more significant. First, strong natural selection for cryptic colouration has been demonstrated across taxa, including some SCC species. Second, all SCC species show clinal distributions of winter coat colour phenotypes across snow gradients, including the loss of winter white in moderate climates. Third, some species (i.e. ptarmigan) exhibit behavioural plasticity to maintain camouflage when mismatched against their background. Lastly, white winter coats of some SCC species are not

warmer (i.e. weasels, ptarmigan), confirming the primary benefits of increased camouflage.

(2) SCC hair/feather regeneration is similar across species, with some differences in the details of moulting and moulting patterns. The underlying hair growth and moult processes are complex and relatively unknown. Some SCC mammals (e.g. weasels, hares) conform to the standard view of seasonal moulting: short periods of photoperiod-stimulated hair proliferation and shedding, alternating with longer periods of hair follicle inactivity. Others (i.e. Siberian hamsters) undergo endogenously regulated continuous moulting with periodical changes in hair structure and pigmentation. In ptarmigan, SCC moulting varies among species and the moult patterns and processes are less understood than in mammals.

(3) The molecular basis of SCC moults remains mostly unknown. To date, research has focused on the genetic basis of invariant winter brown morphs, and simple genetic differences have been described for the different winter colour morphs in SCC mammals (e.g. Arctic fox, mountain hare). Major candidate colouration genes (i.e. *Mc1r* and *Agouti*) are likely involved in SCC moults in both mammals and birds, but other genes such as those regulating hair regeneration and melanization, and seasonal rhythms (e.g. 'clock' genes) likely play important roles too.

(4) The endocrine basis of SCC moults is not fully understood in any taxa. Generally, moults are stimulated by photoperiod, triggering a network of neural and hormonal pathways that initiate moulting. The hormonal signals remain important throughout the moult duration; for example, moulting can be arrested or reversed by photoperiod manipulation alone. Mammals have one central clock entrained to photoperiod and the physiological basis of moults is largely driven by the interaction of melatonin and prolactin. In birds, multiple pacemakers direct prolactin, thyroid and gonadal hormones. In both groups, the same hormonal pathways regulating moults and pigmentation also drive other seasonal events such as reproduction. Therefore, any shifts in moult phenology may have strong epistatic effects on the other circannual traits and impact fitness.

(5) Several external and internal factors can modify moult phenology in all SCC species. Temperature and potentially snow cover can accelerate or decelerate moult phenology, although the evidence for snow effects is less clear. The physiological mechanisms by which those two environmental factors modify moults are unknown, considerably obstructing our understanding of their role on moult phenology. Similarly, several intrinsic factors contribute to inter-individual variation in phenology, probably interacting with gonadal steroids. These intrinsic factors include sex, age and to lesser degree mass and condition.

(6) Current climate change leads to increased colour mismatch between SCC and background colour. Adaptation could occur either in the polyphenic SCC trait (*via* shifts in moult phenology) or *via* complete loss of winter whitening. Adaptation *via* phenotypic plasticity could occur, but to date its capacity appears limited, especially in mammals. Adaptive shifts *via* microevolution in moult phenology or winter colour morph are possible due to high variation in the SCC trait and strong selection for background matching. A detailed understanding of the ecological, physiological, and molecular bases of SCC moult will be needed to manage populations effectively under climate change.

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