

A camouflage conundrum: unexpected differences in winter coat color between sympatric species

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Abstract. Across the globe, more than 21 species undergo seasonal changes in coloration, molting white in winter to become camouflaged against snow. Given the adaptive value of seasonal camouflage against local snow duration, one might predict that sympatric coat color changing species would have similar winter coat color. This hypothesis, however, contrasts with anecdotal evidence and modeling results that predict sympatric winter white and winter brown species in some areas with transient snow cover. In one such area, West Virginia, we document coat color phenology between three sympatric species: snowshoe hares (*Lepus americanus*), long-tailed weasels (*Mustela frenata*), and least weasels (*Mustela nivalis*). Using a combination of field methods, we document and quantify each species' winter coat color, illustrating an interspecific polymorphic response in winter coloration among sympatric winter white snowshoe hares and winter brown weasels. We then hypothesize what forces drive the interspecific differences between snowshoe hare and weasel winter coloration, highlighting areas of focus for future seasonal coat color research.

Key words: camouflage; coat color change; *Lepus americanus*; *Mustela frenata*; *Mustela nivalis*; phenology; West Virginia.

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INTRODUCTION

Strong selection for camouflage is a major driver of animal coloration (Caro 2005). Across taxa, animals have evolved different camouflage strategies in response to the selective pressure of predation (Stevens and Merilaita 2009). In particular, many species camouflage themselves by changing their color to resemble the surroundings. Color change can occur very quickly for some species while taking much longer for others. For example, some cephalopods can change color in seconds, whereas some mustelids take weeks to change

color. These mustelids are part of a group of at least 21 species of birds and mammals that undergo seasonal changes in coloration, molting white in winter to match snow cover, thus reducing predation risk from visually hunting predators (Zimova et al. 2018). One of the most persistent and widespread signals of climate change in the northern hemisphere, however, is a reduction in the number of days with snow on the ground. As snow duration decreases, animals in white winter coats become more conspicuous against snowless ground, suffering increased mortality (Mills et al. 2013, Zimova et al. 2016, Wilson et al. 2018).

Across the geographic ranges of these seasonal coat color changing species, natural selection has shaped winter coat color to track the average duration and ephemerality of snow, creating intraspecific geographic clines that include regions of all brown winter morphs, all white winter morphs, and polymorphic regions with sympatric winter brown and white individuals (Mills et al. 2018). In snowshoe hares, the winter brown versus winter white morph is controlled by genetic variation at a single gene (Jones et al. 2018), making this an adaptive trait subject to natural selection. Given the adaptive value of seasonal camouflage against local snow duration and the demonstrated direct effect of snow on the color molt (Kumar 2015), one might predict that sympatric color molting species would show similar winter coat colors. This hypothesis, however, contrasts with anecdotal findings (Hall 1951, Brooks 1955) and global spatial modeling results (Mills et al. 2018) that predict regions of sympatric winter white and winter brown species in areas with transient snow cover. In one such purported region, West Virginia, we document winter coat color of three coat color changing species: snowshoe hares (*Lepus*

americanus), long-tailed weasels (*Mustela frenata*), and least weasels (*Mustela nivalis*) to elucidate interspecific color molting patterns of sympatric species.

We used a combination of field methods to document winter coat color in snowshoe hares and weasels in West Virginia in 2014. We live trapped 12 molting snowshoe hares from West Virginia to confirm that they molt white in winter (Fig. 1), validating historical accounts (Brooks 1955). Because weasels are notoriously difficult to capture in the wild, we used a non-invasive sampling framework consisting of remote cameras and bait tubes to detect and monitor weasels. We recorded 31 photographs of long-tailed weasels and five of least weasels between November and February, months when both weasel species should be all or mostly white if they adopt the white winter coat. Unlike the winter white snowshoe hares, both long-tailed weasels and least weasels at our study site were winter brown (Fig. 2). Together these figures depict an interspecific polymorphic response in winter coloration among sympatric winter white hares and winter brown weasels.



Fig. 1. A snowshoe hare in West Virginia midway through its fall brown to winter white coat color molt on 10 November 2014.



Fig. 2. A brown long-tailed weasel in West Virginia (a) on a snowless brown background on 12 November 2014 and (b) on a snowy background on 16 November 2014. Photographs were taken at the same location four days apart.

Because we could not distinguish individual weasels based on photographs, we established two criteria to reduce pseudoreplication arising from sampling the color molt of the same individual multiple times. Our approach was derived from average weasel movement parameters across space and time (home range diameter of 1.5 km; movement rate of five meters/minute; Gehring and Swihart 2004). Using these criteria, photographs represented different individuals when they were separated by (1) more than the expected distance moved over time and (2) more

than an average home range diameter regardless of time. Using these criteria, our 36 photographs represent a minimum of three winter brown long-tailed weasels and one winter brown least weasel. Our findings support historical accounts of winter brown long-tailed weasels (Hall 1951) and winter white snowshoe hares (Brooks 1955) in West Virginia, as well as modeling results (Mills et al. 2018).

If winter coat color has evolved to maintain camouflage against local snow conditions, then why do snowshoe hares molt white and weasels

Hypothesized Factors Driving Winter Coloration

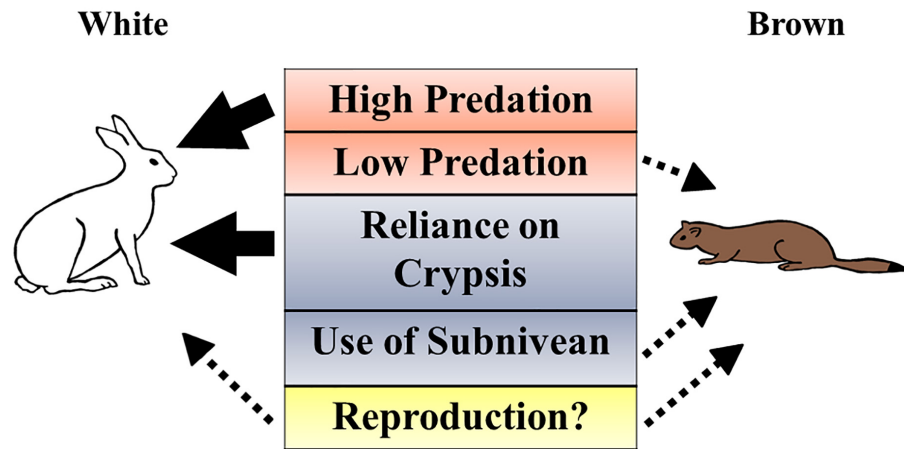


Fig. 3. Potential forces that drive maintenance of year-round brown coloration or selection for winter white coloration. Because snow is present, white would seem to be the preferred winter wardrobe as seen in snowshoe hares. Despite seasonal snow cover, however, weasels maintain brown coloration in winter. Dotted arrows depict weak/unclear relationship.

molt brown in winter in the same population in West Virginia (Fig. 3)? One possibility is that one of the molts is maladaptive now or in the recent past. Alternatively, selective costs and benefits may differ between the two species due to behavioral or life history differences. For example, weasels may remain brown year-round due to lower consequences of staying brown or to higher costs of molting white. Snowshoe hares spend their days resting in forms moving very little and relying on crypsis to avoid detection. Weasels, however, move frequently and inhabit burrows and subnivean space below snow possibly decreasing their risk of predation and ultimately lowering the consequence of staying brown.

Snowshoe hares and weasels also have different reproductive and life history strategies, which could affect winter color tradeoffs. For instance, snowshoe hares and least weasels both undergo direct implantation (i.e., the zygote passes through all stages of development without any detectable pause), whereas in long-tailed weasels implantation is delayed for nine to ten months until the following spring. In addition,

weasels are born altricial and depend on heavy investment by their mothers, whereas snowshoe hares are precocial with little to no maternal care other than nursing. These differences in breeding life history could lead to differences in exposure to predation. Also, because hormones regulating reproduction simultaneously affect seasonal coat color, reproductive differences between species may constrain species color molts (Wright 1942, Rust 1965, Zimova et al. 2018).

Coat color changing species are of special interest in the context of climate change. A reduction in snow duration is one of the strongest predicted outcomes of climate change in the northern hemisphere (Pederson et al. 2011). A rapid reduction in the number of days with snow cover would increase the number of days of camouflage mismatch if snowshoe hare molt phenology does not track decreases in snowpack duration (Mills et al. 2013, Zimova et al. 2014). In addition, mismatched snowshoe hares have reduced survival, which could lead to a decrease in population growth rate in the absence of an adaptive response (Zimova et al. 2016). Furthermore, snowshoe hares have experienced recent

range contractions linked to reduced snow duration and possibly mismatch related mortality (Burt et al. 2016, Diefenbach et al. 2016, Sultaire et al. 2016). Range contractions are especially relevant for hares in West Virginia, the southeastern limit of their range. Snowshoe hares exist at a very low density in West Virginia and had the lowest genetic diversity of any population sampled in a range-wide snowshoe hare genetic analysis (Cheng et al. 2014).

As climate-induced mismatch increases, persistence of hares in this region depends on successful adaptation. Although limited plasticity in seasonal coat color phenology exists for hares (Kumar 2015, Zimova et al. 2018), another possibility would be to evolve to forego the winter white molt entirely, remaining brown year-round like weasels in West Virginia. Winter brown morphs would be expected to be selectively favored over winter white individuals as snow duration decreases (Mills et al. 2018). Thus, regions with different winter coat color among species such as we described here provide an excellent opportunity to study how different species respond to similar climate-induced selective pressure.

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